Two core systems of numerical representation in infants

Yi Mou, Kristy vanMarle *

University of Missouri, Columbia, USA

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ABSTRACT

Two nonverbal representation systems, the analog magnitude system (AMS) and the object tracking system (OTS), have been proposed to explain how humans and nonhuman animals represent numerosities. There has long been debate about which of the two systems is responsible for representing small numerosities (<4). This review focuses on findings with human infants to inform that debate. We argue that the empirical data cannot all be explained by a single system, and in particular, infants' failures to compare small and large numerosities – the *boundary effect* – undermines the claim that the AMS can account for infants' numerical abilities in their entirety. We propose that although the two systems coexist throughout the lifespan, competition between the systems is primarily a developmental phenomenon. Potential factors that drive the engagement of each system in infancy, such as stimulus features and task demands, are discussed, and directions for future research are suggested.

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Introduction

"What does a fish know about the water in which it swims all its life?" (Einstein, 1950, p. 5). What do we know about the world full of numerical information in which we live all our lives? What is the nature of our numerical concepts and where do they come from? Four lines of research have contributed to our understanding of these important issues. Comparative psychology has shown that basic numerical concepts are not unique to humans but shared across many animal species, and thus an abstract concept of number is not dependent upon language. Comparative studies also point to the

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* Corresponding author. Address: Department of Psychological Sciences, University of Missouri, 210 McAlester Hall, Columbia, MO 65211, USA. Fax: +1 (573) 882 7710.
E-mail address: vanmarlek@missouri.edu (K. vanMarle).

evolutionary roots of human numerical knowledge and how numerical abilities are critical for organisms' survival (Cantlon, 2012; Dehaene, 1997; Gallistel, 1990; Gallistel & Gelman, 2000; Vallortigara, Chiandetti, Rugani, Sovrano, & Regolin, 2010). Developmental psychology has demonstrated that even preverbal human infants possess abstract numerical concepts and show quite sophisticated numerical abilities. Before age one, infants discriminate, order, and perform arithmetic operations over nonverbal numerical representations (Brannon & Roitman, 2003; Carey, 2009; Gallistel & Gelman, 2000; Piazza, 2010), and the basis for these capacities is present even in newborns (Izard, Sann, Spelke, & Streri, 2009). Such research examines the origins of human numerical concepts and investigates how the concepts change with age, experience and education. Cross-cultural research examines the similarities and differences in humans' numerical abilities within different cultures and emphasizes how cultures may shape and influence these concepts (e.g., Dehaene, 1997). Finally, cognitive neuroscience investigating both normal and brain-injured individuals reveals the physiological basis of these numerical concepts and abilities (e.g., Piazza, 2010). Taken together, the findings from these four areas of research suggest that abstract numerical concepts exist across species, across cultures, and throughout development. Indeed, numerical knowledge is considered one of only a handful of core knowledge domains that may be innate and which plays a fundamental role in the cognition of humans (Carey, 2009; Feigenson, Dehaene, & Spelke, 2004; Spelke, 2000, 2004; Spelke & Kinzler, 2007), and many nonhuman species (Rugani, Vallortigara, & Regolin, 2013; Vallortigara et al., 2010).

Debate continues over the format of nonverbal number representations. Nonetheless, converging evidence from the four research approaches suggests that humans and nonhuman animals share a mechanism that represents both discrete and continuous quantities (e.g., duration and spatial quantities) as fuzzy mental magnitudes (e.g., Beran, Decker, Schwartz, & Schultz, 2011; Brannon & Merritt, 2011; Brannon & Roitman, 2003; Carey, 2009; Dehaene, 1997; Feigenson et al., 2004; Gallistel & Gelman, 2000, 2005; Gibbon, 1977; Meck & Church, 1983; Spelke & Kinzler, 2007). Due to the noisy nature of the analog magnitude system (AMS), the discrimination of two quantities is determined by their ratio, in accord with Weber's law. Despite the wealth of evidence for the AMS, researchers have asked whether humans and nonhuman animals might use a distinct mechanism to represent small numbers ($\leqslant 4$).

The idea that small numbers may be represented differently from large numbers is not new (e.g., Jevons, 1871; Taves, 1941; Warren, 1897). More than six decades ago, Kaufman, Lord, Reese, and Volkmann (1949) showed that adults were fast and accurate when estimating small sets of items (up to about 6), but that estimation for larger sets was error prone and slow, with reaction time (RT) increasing linearly with each additional item for large sets, while it remained relatively constant for sets of 1–6 items. Kaufman et al. concluded that the different slopes for reaction time and accuracy across the small and large number ranges indicated that adults were using distinct processes and coined the term "subitizing" to describe the process used for small sets. More recent studies exploring the two-system hypothesis have proposed that a mechanism of visual attention – the object tracking system (OTS) – may account for adults' fast and accurate performance with small sets (Revkin, Piazza, Izard, Cohen, & Dehaene, 2008; Trick, 2008; Trick, Audet, & Dales, 2003; Trick, Enns, & Brodeur, 1996; Trick & Pylyshyn, 1994). In contrast to the AMS, the signature property of the OTS is its limited capacity (cf. Alvarez & Cavanagh, 2004 and Alvarez & Franconeri, 2007). Instead of representing the overall magnitude of a set (i.e., cardinality), it simultaneously indexes each individual object in an array up to its capacity limit of about 3 or 4 items (Feigenson & Carey, 2003, 2005; Feigenson, Carey, & Hauser, 2002; Pylyshyn & Storm, 1988; Scholl, 2001; vanMarle, 2013). For this system, two sets are discriminable (via a one-to-one correspondence operation) as long as they are both within the capacity limit, regardless of their ratio (e.g., 3v4 is no more difficult than 1v2).

There continues to be substantial debate about the two-system view (Feigenson et al., 2004; Gallistel & Gelman, 2000, 2005; Hyde, 2011; Piazza, 2010; Trick & Pylyshyn, 1994). On one side, researchers argue that a single mechanism, the AMS, suffices for processing numbers throughout the number range, and therefore it is not necessary to posit the engagement of another mechanism (e.g., Beran, 2007; Cordes & Brannon, 2009; Cordes, Gelman, Gallistel, & Whalen, 2001; Gallistel & Gelman, 2000, 2005). Another view is that the two systems are distinct and mutually exclusive, with the OTS limited to representing small numbers and the AMS limited to representing large numbers (Feigenson, Carey, & Hauser, 2002; Piazza, 2010; Xu, 2003). Yet a third view, and the stance taken here,

is that the AMS can and often does represent numbers throughout the number range. However, there is also a role for the OTS to represent small sets under some circumstances, especially early in development.

The classic argument between the two extreme views has been complicated by recent findings from studies of human infants, which have provided empirical support for both views (Cordes & Brannon, 2009; Feigenson & Carey, 2003; Feigenson, Carey, & Hauser, 2002; Feigenson et al., 2004; vanMarle, 2013; vanMarle & Wynn, 2009; Xu, 2003). In this paper, we will first briefly summarize the evidence for the two systems in human adults and other species, and then review and discuss recent findings in the infant literature that bear on the debate. Our approach moves beyond the classic either/or debate, exploring how the two systems may coexist and interact in infants. We emphasize that both systems can represent small numerosities, but that deployment of the OTS occurs only in limited contexts. Our novel contribution, however, is the notion that competition between the two systems may be primarily a developmental phenomenon.

The analog magnitude system (AMS)

Humans and other animals represent both discrete numerosities and continuous quantities (e.g., time and spatial quantities) as analog magnitudes. These representations support judgments of both ordinal relations (e.g., which of two quantities is larger) and cardinality (e.g., the number of items in a set), which are both central to the number concept (Brainerd, 1979; Gallistel & Gelman, 2000, 2005). The representations are themselves continuous, analogous to using a line to represent a quantity, with its length being proportional to the represented magnitude (Brannon & Roitman, 2003; Carey, 2009; Gallistel & Gelman, 2000; Meck & Church, 1983). For example, if a line representing the value '1' was 1 cm long, then a line representing the value '4' would be 4 cm long. One prominent model instantiating this type of system is the *accumulator model* (Meck & Church, 1983). In this model, a pulse generator produces pulses at a roughly constant rate, which can be gated into an accumulator when a switch is closed. In timing mode, the switch is closed at the beginning of a timed interval, allowing pulses to be collected, and opened at the end of the interval. The resulting fullness of the accumulator is then proportional to the elapsed duration. In counting mode, the gate closes briefly once for each item counted, such that the accumulator is incremented by roughly the same amount for each item, with the resulting fullness then being proportional to the number of items counted.

A critical feature of analog magnitude representations is that they are "noisy", such that they represent their corresponding objective magnitudes only approximately (Dehaene, 1997; Gallistel & Gelman, 2000; Gibbon, 1977; Meck & Church, 1983). For example, when nonhuman animals (e.g., rats or pigeons) and humans estimate numbers or durations, the represented magnitudes are not exactly equal to the target value, but instead distributed around that target value (e.g., Allan & Gibbon, 1991; Beran, Taglialatela, Flemming, James, & Washburn, 2006; Cordes et al., 2001; Dale, 2000; Gibbon, Fairhurst, & Goldberg, 1997; King, McDonald, & Gallistel, 2001; Platt & Johnson, 1971; Rakitin et al., 1998; Whalen, Gallistel, & Gelman, 1999). Importantly, estimates of larger values are more variable than estimates of smaller values, with the amount of variability being proportional to the objective magnitude, a property known *as scalar variability* (Gallistel & Gelman, 2005; Gallistel, King, & McDonald, 2004; Gibbon, 1977; cf. Dehaene, 1997).

It is this scalar property that accounts for the fact that the discriminability of two quantities depends on their ratio, rather than their absolute arithmetical difference, a reflection of Weber's law (e.g., Beran, 2001, 2010; Beran, Johnson-Pynn, & Ready, 2011; Brannon & Terrace, 1998, 2000, 2002; Cantlon & Brannon, 2006; Moyer & Landauer, 1967; Parkman, 1971; vanMarle, Aw, McCrink, & Santos, 2006). For example, it is easier to discriminate 5 from 10 (1:2 ratio) than 20 from 25 (4:5 ratio), even though the absolute difference is the same in both cases (5 units). The amount of overlap for various magnitudes is a function of the amount of spread in their distributions (Platt & Johnson, 1971; Whalen et al., 1999). Since larger numbers have wider distributions, there is more overlap between the distributions for 20 and 25 than for 5 and 10, making it more difficult to discriminate the former pair than the latter.

Despite the noisy nature of analog magnitudes, they are nonetheless useful. Humans and nonhuman animals use them not only to make simple discriminations and ordinal judgments, but they

are also the representational medium of nonverbal arithmetic (Barth, La Mont, Lipton, & Spelke, 2005; Barth et al., 2006; Beran, 2001, 2004; Cantlon & Brannon, 2007; Flombaum, Junge, & Hauser, 2005; Santos, Barnes, & Mahajan, 2005). For instance, after seeing two sets of dots presented sequentially on a computer monitor, rhesus monkeys (*Macaca mulatta*) and college students were required to make a choice between a number indicating the numerical sum of the two dot sets and another distracter number. Their performance suggested that they estimated the sum of large numbers, with their accuracy varying as a function of the ratio between the correct sum and the distracter number, consistent with the use of the AMS. Performance was strikingly similar for monkeys and humans, suggesting that they completed the task in the same way (Cantlon & Brannon, 2007). And more generally, the high degree of similarity between the performance of human and nonhuman animals across a range of tasks suggests that the AMS is evolutionarily ancient and likely shared across many different species (Gallistel, 1990; Gallistel & Gelman, 2005; Piazza, 2010; Vallortigara et al., 2010).

Another tenet of the AMS is that the representations are *amodal* – they are not tied to the particular sensory modality in which the numerical information is presented (e.g., Beran, 2012; Gallistel & Gelman, 2005; Jordan, MacLean, & Brannon, 2008). Indeed, the accumulator model was developed in part to account for rats' ability to spontaneously transfer learned quantity discriminations across sensory modalities (Meck & Church, 1983). And like their unimodal number abilities, nonhuman animals and human adults and children can nonverbally compare sets across different modalities, and even perform arithmetic across modalities. Importantly, their intermodal numerical performance in these tasks is also ratio-dependent (Barth, Kanwisher, & Spelke, 2003; Barth et al., 2005, 2006; Jordan, Brannon, Logothetis, & Ghazanfar, 2005; Jordan, Suanda, & Brannon, 2008; Jordan, MacLean, et al. 2008; Roberts, 1982). These findings suggest that quantity information from different sensory modalities is converted into the same amodal analog format, making the representations commensurable.

Neurocognitive research has begun to reveal the neural mechanisms underlying the AMS. In cats, neurons in the posterior associative cortex are sensitive to numerosity (Thompson, Mayers, Robertson, & Patterson, 1970). Subsequent studies localized numerosity-sensitive neurons in the intraparietal sulcus (IPS) in humans and nonhuman primates (Nieder & Dehaene, 2009; Nieder & Miller, 2003, 2004; Piazza, 2010), which responds to numerical information regardless of the sensory modality or symbolic format (Dehaene, Piazza, Pinel, & Cohen, 2003; Piazza, Mechelli, Price, & Butterworth, 2006). In addition, fMRI studies have revealed that responses in the IPS are modulated by the ratio between two compared numerosities (Castelli, Glaser, & Butterworth, 2006; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). Notably, although the IPS is foundational for number encoding and representation, it is also engaged during the processing of several non-numerical dimensions, such as time (i.e., duration) and space (Walsh, 2003), and the groups of neurons that respond to numerical and non-numerical dimensions overlap in this region (e.g., Dehaene, 2009; Piazza et al., 2004). More neurocognitive evidence is needed to show if there are sub-regions in the IPS specific to number alone (Cantlon, Platt, & Brannon, 2009).

The object tracking system (OTS)

A defining characteristic of the AMS is that the representations are noisy, even for the smallest numerosities (e.g., 1, 2, and 3). Therefore, one's processing of small numbers should be qualitatively similar to that of large numbers. However, as noted above, the slopes for reaction time and accuracy appear to differ across the small and large number range (Kaufman et al., 1949; Plaisier, Tiest, & Kappers, 2010), which is not consistent with the AMS. Recently, the OTS has been proposed to account for adults' fast and accurate processing of small visual sets. The current OTS model (sometimes referred to as "parallel individuation"; Carey, 2004) is considered part of infants' core knowledge of objects (Cheries, Mitroff, Wynn, & Scholl, 2009; Leslie, Xu, Tremoulet, & Scholl, 1998; Scholl & Leslie, 1999; Spelke & Kinzler, 2007) and is a reformulation of two previous models, the FINST mechanism (Pylyshyn, 1989, 1994, 2001; Pylyshyn & Storm, 1988; Trick & Pylyshyn, 1994) and the object file mechanism (Kahneman & Treisman, 1984; Kahneman, Treisman, & Gibbs, 1992), both of which are mechanisms of visual attention designed to explain humans' ability to individuate and track visual objects and solve the problem of object correspondence.

Table 1
Summary of specific models falling within the more general categories of the AMS and OTS.

System	Model	Studies	Mechanism	Signature properties
AMS	Accumulator	Meck and Church (1983)	Mental impulses triggered by quantity information are gated into an accumulator. The "fullness" of the accumulator is proportional to the objective magnitude. Objective magnitudes are linearly mapped to mental magnitudes	Approximate; ratio-dependent (Weber's law); amodal; represents both discrete and continuous quantities; operates over the whole number range (no upper limit)
	Neural network	Dehaene and Changeux (1993)	Enumerated items are coded assize-independent representations and summed. The summation activates a given numerosity detector which outputs that given magnitude. Objective magnitudes are logarithmically mapped to mental magnitudes	
OTS	FINST	Pylyshyn and Storm (1988) and Trick and Pylyshyn (1994)	Each tracked visual item is preattentively assigned an index (FINST or Finger of INSTantiation), which is continues to "point" to the item when it moves or even briefly hidden	Exact; absolute difference between numerosities determines discriminability; specific to visual modality; capacity limited
	Object file system	Kahneman and Treisman (1984) and Kahneman, Treisman, and Gibbs (1992)	Episodic visual representations indexed by object location and may store feature information about represented objects. Can be put into one-to-one correspondence with sets of real objects	
	Parallel individuation	Le Corre and Carey (2007)	Short-term memory system that can produce working memory models of small sets and compare them to sets stored in long-term memory on the basis of one-to-one correspondence	Exact; absolute difference between numerosities determines discriminability; may not be specific to visual modality; capacity limited

The OTS consists of a set of indexes that "point" to individual objects, allowing objects to be tracked through time and space (Kahneman et al., 1992; Pylyshyn, 1989). Importantly, although object features (e.g., color, size, shape, kind) can be bound to an index, spatiotemporal information (i.e., an object's location) is prioritized over featural information (Mitroff & Alvarez, 2007; cf. Richard, Luck, & Hollingworth, 2008). Thus, a moving object whose features change while briefly occluded will be seen as the same individual when it reappears so long as the spatiotemporal information (i.e., trajectory and speed) matches that of the object prior to occlusion (Flombaum, Scholl, & Santos, 2009; Kahneman et al., 1992; Pylyshyn, 1989; Pylyshyn & Storm, 1988; Scholl, 2001).

The OTS differs from the AMS in several respects (see Table 1). As noted earlier, the signature property of the OTS is its capacity limit. It can only track as many objects as it has indexes, which appears to be about four for adults (Pylyshyn & Storm, 1988; Scholl, 2001; Trick & Pylyshyn, 1994), and about three for infants (Feigenson & Carey, 2003, 2005; Feigenson, Carey, & Hauser, 2002; vanMarle, 2013). This limit predicts a performance profile in which two sets should be equally discriminable within the small number range regardless of ratio. This is in stark contrast to the predicted profile for the AMS, where performance is strictly ratio-dependent, with accuracy decreasing as the ratio approaches 1:1.

Another important aspect of OTS representations is that they are precise. Unlike analog representations, the OTS assigns an index for each distinct individual in a set, producing a set of episodic representations. However, because there are only tokens for individuals, strictly speaking, the OTS is not a

number system (e.g., Gallistel, 2007; Hyde, 2011). For example, two cars may be encoded as [object, object], but there is no cardinal representation indicating that the set is comprised of 'two' individuals. Nonetheless, the OTS does implicitly represent the number of objects in a set. When two distinct objects are presented simultaneously, the OTS assigns two indexes, each pointing to the spatial location of an object. If the two objects are hidden behind a screen, but only one remains when the screen is removed, only one of the indexes can be put in one-to-one correspondence and a mismatch between the represented set [object, object] and the visible set [object] is detected. In this way, the OTS can identify a change in the number of objects via the correspondence operation (Wynn, 1992; Wynn & Chiang, 1998).

In another case, if one object (e.g., a duck) is hidden behind a screen from one side and an object with different features (e.g., a truck) emerges from the other side of the screen, after 12 months of age, infants predict there should be two distinct objects involved in this event (Xu & Carey, 1996). The OTS assigns an index for the object initially hidden, but the novel features of the revealed object prevent it from being placed in one-to-one correspondence and a new index is assigned based on the mismatch. In this case, because spatiotemporal information is ambiguous (the objects are never seen simultaneously) the number of objects expected behind the screen is based on featural, rather than spatiotemporal information. Using experimental contexts similar to these, studies have shown that both nonhuman animals (e.g., nonhuman primates and chicks (*Gallus gallus*)) and human infants use both spatiotemporal and featural information to individuate objects and thus predict how many objects are hidden behind a screen (Carey & Xu, 2001; Cheries et al., 2009; Fontanari, Rugani, Regolin, & Vallortigara, 2011; Mendes, Rakoczy, & Call, 2008; Uller, Carey, Hauser, & Xu, 1997; Xu & Carey, 1996).

In addition to behavioral evidence, neurocognitive research has revealed that the neural substrates active in object tracking tasks (e.g., the posterior parietal and occipital cortices) differ from those active in typical number discrimination tasks that engage the AMS (Piazza, 2010). Recent fMRI studies reveal that, compared to estimating large numbers, estimating small numbers produced weak activation at attention-related regions (e.g., the posterior parietal and frontal cortices; Piazza, Giacomini, Le Bihan, & Dehaene, 2003) and greater activation at regions related to stimulus-driven attention (e.g., the right temporo-parietal junction; Ansari, Lyons, van Eimeren, & Xu, 2007), suggesting that processing small numbers is to some extent pre-attentive and stimulus-driven. A recent EEG study also demonstrated that an early negative wave (150 ms) in the parietal cortex was related to the change in the absolute values of small numbers, whereas a later positive wave (250 ms) was modulated by the ratio of large numbers (Hyde & Spelke, 2009), suggesting a different time course for the processing of small and large numbers. This body of neuropsychological evidence therefore suggests separate neural substrates for the two different mechanisms.

One or two systems for number?

The one-system view suggests that the AMS can and does represent both small and large numerosities, making the OTS unnecessary. In fact, some researchers who advance the one-system view have suggested that the primary evidence for subitizing, the different slopes in RT in the numerosity estimation task, is misleading. Specifically, although slight, there is an increase in RT as numerosity increases within the small number range, suggesting that items are not processed strictly in parallel (Balakrishnan & Ashby, 1992; Gallistel & Gelman, 2005). In addition, when human adults are required to nonverbally estimate the numbers of dots in an array, and counting is prevented, their RT increases with each item and variability among the estimates of each number is present even in the small number range (Cordes, Gallistel, Gelman, & Latham, 2007; Cordes et al., 2001; Whalen et al., 1999). This is consistent with the AMS model since variability is expected throughout the number range. The reason for the apparent discontinuity between the small and large numbers in adults may be due to the fact that the variability, though present, is negligible in the small number range (Gallistel & Gelman, 2005; Nieder & Miller, 2003). According to Whalen and West (2001) (as cited by Gallistel & Gelman, 2005), variability for numbers 1–3 is so small that verbal estimates show almost 0% error, with error increasing rapidly for numbers beyond 3.

Nonetheless, despite these objections, both behavioral and neurocognitive research suggests that, at least in some cases, adults may represent and process small numerosities differently from large

numerosities. For example, adults can report the numerosity of an array consisting of four dots via analog magnitudes (Cordes et al., 2001), and they can also name it by recognizing its pattern, an example of subtizing (e.g., in a square pattern as shown on the face of a die; Mandler & Shebo, 1982). In addition, adults can subitize individual objects separated in space, either alone, or in a field of distracters, but when items are difficult to individuate (e.g., concentric circles), the subitizing strategy fails, leading adults to either estimate or carefully count the items, even for small sets (Trick & Pylyshyn, 1994).

Beyond the perceptual context, tasks vary in terms of the demands they place on working memory and attention, which may also influence which system adults deploy to process small sets (see Hyde, 2011 for review). For example, in a task testing adults' ability to detect changes in numerosity, converging behavioral and neural evidence showed that subjects represented the items as *individuals* when the set was presented within their focus of spatial attention or when attentional load was low, consistent with the use of the OTS. In contrast, subjects' performance was ratio-dependent when the set was presented outside their focus of attention or when attentional load was high (dual tasks), consistent with the use of the AMS (Hyde & Wood, 2011). Thus, for small sets, if each item is easily individuated and processing resources are sufficient, the OTS may be involved, otherwise, the magnitude of the set will be represented in the AMS (Hyde, 2011). Together, such findings suggest that adults may be able to flexibly recruit one or both systems across a variety of situations.

Our view, the *developmental hypothesis*, argues that although the AMS and OTS may coexist throughout the lifespan, they interfere with each other only early on in development. The logic of this proposal lies in the fact that variability in AMS representations is much greater early in development, with precision increasing markedly from infancy to early childhood, and continuing to increase throughout childhood into adulthood (Brannon, Suanda, & Libertus, 2007; Halberda & Feigenson, 2008; Lipton & Spelke, 2003; Xu & Spelke, 2000). Thus, in contrast to adults' AMS representations, which are remarkably precise in the small number range (Gallistel & Gelman, 2005), infants' AMS representations are remarkably imprecise.[1] As a result, infants may not use AMS representations for small sets until their precision increases enough to provide reliable estimates within the small number range. Indeed, evidence reviewed below suggests that infants may not use the AMS for small sets when conditions afford representation by the OTS. In the following section, we first describe evidence that infants possess both systems, and then discuss in detail the variety of situations in which infants seem to use the OTS instead of the AMS to represent small sets.

Infant quantity representations

Infant studies provide a unique opportunity to examine the origins and development of the two core mechanisms and how they come to interact in adulthood. Although a great many infant studies reveal the signature characteristics of the AMS (i.e., approximate and ratio-dependent quantity representations), there are several recent findings that are not easily explained by the AMS, showing instead the signature properties associated with the OTS. Indeed, the strongest evidence for the OTS having a critical role in numerical processing is found in developmental data, and particularly in young infants and in paradigms in which they must visually track small sets of moving objects through occlusion.

The AMS in infants

Using a variety of research methods, developmental psychologists have investigated how infants represent discrete numerosities and continuous quantities. Similarity in the performance of infants, adults, and nonhuman animals on tasks engaging the AMS strongly suggests both the phylogenetic and ontogenetic continuity of the underlying processes and mechanisms. We begin by reviewing evidence that infants use the AMS to discriminate, order, and perform simple arithmetic on numerosities, focusing primarily on recent research that incorporated stringent controls for non-numerical properties of the stimuli (e.g., surface area, density, rate, etc.).

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[1] One AMS model assumes that the numerosity of a set of items is computed by dividing the total area of the items by inter-item distance of items (Barth et al., 2003; Church & Broadbent, 1990). Mathematically, estimates of these variables are less reliable for small sets than for large (Wood & Spelke, 2005; Xu, 2003).

Building on earlier studies of numerical discrimination in infants (e.g., Antell & Keating, 1983; Starkey & Cooper, 1980; Strauss & Curtis, 1981; Van Loosbroek & Smitsman, 1990), the first studies to provide solid evidence for the AMS in infants were conducted by Xu and her colleagues. Using a visual habituation paradigm, Xu and Spelke (2000) and Xu, Spelke, and Goddard (2005) demonstrated that 6-month-old infants discriminated 8 from 16 dots and 16 from 32 dots, but not 8 from 12, or 16 from 24. Thus, they discriminated quantities that differed by a 1:2 ratio, but not a 2:3 ratio. Such ratio-dependent performance shows that like nonhuman animals and human adults, human infants' large number discrimination abilities follow Weber's law. Importantly, infants at this same age show the same discrimination function – success with 1:2 ratios, and failure with 2:3 ratios – when numerical information is presented in audition (i.e., sequences of sounds), in both the small (vanMarle & Wynn, 2009) and large number range (Lipton & Spelke, 2003). The fact that the discrimination function is identical for both small and large numbers of auditory stimuli is telling. Because the OTS is a visual mechanism, it is not likely to underlie the enumeration of auditory stimuli. The successful discrimination of small numbers of sounds therefore shows that the AMS can and does represent small values, even in infancy.

According to the accumulator model (Meck & Church, 1983), numbers are not the only quantities represented by magnitudes, continuous quantities such as durations also share the same representational format (Gallistel & Gelman, 2000, 2005; Gibbon, 1977). For example, classic experiments by Meck and Church (1983) showed several strong similarities in rats' ability to represent time and number, including that the discrimination functions for the two dimensions were nearly identical (i.e., superimposable). Inspired by this, a study by vanMarle and Wynn (2006) examined whether the same is true for infants. They found that infants can indeed discriminate durations, and crucially, they exhibited the same discrimination function as for number – success with 1:2, but not 2:3 ratios – providing more evidence for a common underlying representational mechanism.

An important discovery, now well established, is the finding that the precision of infants' analog representations (for both number and duration) improves substantially over the first year of life, and continues to improve throughout childhood and into adulthood. For number, infants can discriminate at a ratio of 1:3 at birth (Izard et al., 2009), 1:2 by 5–7 months of age (Brannon et al., 2007; Libertus & Brannon, 2010; McCrink & Wynn, 2007; vanMarle & Wynn, 2009; Wood & Spelke, 2005; Wynn, Bloom, & Chiang, 2002; Xu & Spelke, 2000; Xu et al., 2005), 2:3 by 9 months (Brannon et al., 2007; Libertus & Brannon, 2010; Lipton & Spelke, 2003, 2004; Xu & Arriaga, 2007; Xu & Spelke, 2000), and 3:4 by 3 to 4 years of age (Halberda & Feigenson, 2008) (see Cantrell & Smith, 2013 for review). By adulthood, humans can reliably discriminate numbers with at least a 7:8 ratio (Barth et al., 2003) and possibly up to a 9:10 or 10:11 ratio (Halberda & Feigenson, 2008). Although not tested for all the same ages as numerical discrimination, the same pattern appears to hold for duration and for enumerating non-object entities like actions, with infants succeeding at 1:2 ratios at 6 months and at 2:3 ratios by 9 months of age (Lipton & Spelke, 2003; vanMarle & Wynn, 2006; Wood & Spelke, 2005). The relative imprecision of the AMS early in development, and especially over the first year of life, raises the possibility that OTS representations may actually be preferable to AMS representations when conditions allow. If so, then one would expect the OTS and AMS to be in competition more frequently in younger compared to older individuals, which seems to be the case.

Infants not only use the AMS to discriminate quantities, but also recognize ordinal relations between quantities. Similar to research with rhesus monkeys (Brannon & Terrace, 1998, 2000), Brannon (2002) showed that 11-month-old infants habituated to ascending or descending numerical sequences (e.g., 2–4–8, or 9–6–3) dishabituated to sequences with the reversed order, even when novel numerosities were used in the test sequences (Brannon, 2002). Following this study, Suanda, Tompson, and Brannon (2008) showed that 9-month-olds detected such ordinal changes when number was confounded with individual and summed surface area (e.g., the stimuli in a larger set also had larger individual and summed surface area). And yet another study found that 7-month-olds successfully detected reversed numerical order, even with the stimuli's non-numerical quantity properties such as surface area were controlled (Picozzi, de Hevia, Girelli, & Macchi-Cassia, 2010). Notably, this last study differed from Brannon (2002) in two important ways: it involved only large numerosities (e.g., 6–12–24, or 4–8–16) rather than including both small and large numbers (e.g., 2–4–8), and it provided featural cues which helped distinguish sequences across trials (e.g., varied object shapes

within ordinal sequences and changed colors across sequences). Together, these results suggest that young infants' understanding of ordinal relationships can be facilitated given supportive conditions. Cantrell and Smith (2013) recently summarized studies on infants' numerical representations and suggested that they are more robust when number is confounded with other continuous quantities such as contour length, surface area, density and so on (e.g., more items indicates longer accumulative contour length). This makes sense because these dimensions are often confounded in the natural environment. A set of 10 apples is not only twice as numerous as a set of 5 apples, but it also contains roughly twice as much apple 'stuff' (i.e., volume), twice as much redness (i.e., surface area), etc. It would be peculiar indeed if a core mechanism that evolved to help animals forage (Beran, 2007; Gallistel, 1990; Spelke & Kinzler, 2007) did not take advantage of this natural covariance.

In addition to simply detecting ordinal relationships, infants can also use this information to guide their behavior in ordinal choice tasks. After seeing different numbers of food items dropped into two opaque cups (e.g., 4 vs. 8 or 5 vs. 10), 10-to 12-month-olds spontaneously crawled towards the cup with more food items (vanMarle, 2013; vanMarle & Wynn, 2011). Another study explored what discrimination function obtained for infants' ordinal judgments and found that at this same age, infants reliably chose the larger of two hidden quantities when they differed by a 2:3 ratio (4 vs. 6), but not a 3:4 ratio (6 vs. 8) (vanMarle, Mou, & Seok, 2013), which maps onto the successful performance of 9-month-olds at a 2:3 ratio for auditory and visual number discrimination (Lipton & Spelke, 2003; Xu & Arriaga, 2007; Xu & Spelke, 2000) and duration discrimination (Brannon et al., 2007).

Similar to adults and nonhuman animals, infants can also compute the results of arithmetic operations (Kobayashi, Hiraki, Mugitani, & Hasegawa, 2004; McCrink & Wynn, 2004). For example, McCrink and Wynn (2004) showed 9-month-old infants animated movies depicting simple addition and subtraction events. In the addition events, infants first saw a set of five objects come on screen and subsequently be hidden behind an occluder. Next, another group of five objects came on screen and moved, one-by-one, behind the occluder (i.e., 5 + 5). Finally, the occluder was removed to reveal either five objects (unexpected outcome) or ten objects (expected outcome). Infants in the subtraction condition saw events in which 10 objects were initially hidden, and then 5 moved out from behind the occluder and off screen (i.e., 10 − 5). Finally, the occluder was removed to reveal 5 (expected) or 10 (unexpected) objects. Infants in both conditions looked longer at the unexpected outcome, suggesting that they detected the incorrect numerical result of addition and subtraction operations. Because the number of items involved in the events was well beyond the capacity limit of the OTS, these data provide evidence that the AMS underlies arithmetical abilities in preverbal infants (McCrink & Wynn, 2004).

So far, we have reviewed evidence that infants discriminate quantities, detect ordinal relationships, make ordinal judgments, and perform arithmetic operations. In all these cases, infants' performance varies as a function of the ratio between the comparison quantities, reflecting Weber's Law, and thus implicating the AMS. But ratio-dependent performance is not the only hallmark of the AMS. As mentioned above, another important characteristic is that the representations are abstract. One way in which the representations are abstract is that they are not tied to any particular sensory modality. Although early studies attempting to show that infants can detect numerical correspondence across modalities produced mixed findings (Moore, Benenson, Reznick, Peterson, & Kagan, 1987; Starkey, Spelke, & Gelman, 1983, 1990; see also Mix, Levine, & Huttenlocher, 1997), many recent studies using more ecologically valid stimuli provide clear evidence that infants do detect such correspondences (e.g., vision, audition, tactile; Feigenson, 2011; Feron, Gentaz, & Streri, 2006; Izard et al., 2009; Jordan & Brannon, 2006; Kobayashi, Hiraki, & Hasegawa, 2005), and even combine information across modalities. For example, a study by Kobayashi et al. (2004) presented 5-month-old infants with "addition" events in which the objects made a sound upon impacting the stage floor. After seeing one object, which became occluded, and then hearing one sound, infants expected to see two objects when the occluder was removed, and looked longer when only one was revealed. Thus, infants in the first half of their first year of life were able to add one object and one sound and expect two objects to result.

Importantly, the precision of infants' cross-modal numerical discrimination is ratio-dependent and as precise as their unimodal discrimination. For example, newborn infants successfully detected numerical correspondences when the visual and auditory stimuli differed by a 1:3 ratio (6 vs. 18), but not a 1:2 ratio (4 vs. 8) (Izard et al., 2009). However, by 6-months, infants predicted the number

of items they should see based on the number of tones they heard when the two comparison numbers differ by a 1:3 and a 1:2 ratio (4 vs. 12 and 4 vs. 8), but not a 2:3 ratio (4 vs. 6) (Feigenson, 2011). This discrimination function maps directly onto that found for unimodal performance described above, where infants require a 1:3 ratio at birth, but can discriminate 1:2 ratios by 6 months of age.

This body of work provides strong evidence that human infants represent quantities as analog magnitudes and these representations are approximate, ratio-dependent, and abstract, suggesting that the AMS is used across ages and species to discriminate, order and perform arithmetical computations. Despite this, there are numerous findings that are not easily explained by the AMS.

The OTS in infants

The results from several recent studies suggest that infants may process small numbers differently than large numbers in some contexts. Two lines of evidence support this view. First, studies using manual search tasks clearly show the capacity limit of the OTS (Barner, Thalwitz, Wood, Yang, & Carey, 2007; Feigenson & Carey, 2003, 2005). In one such study, 14-month-old infants saw one or more objects hidden in an opaque box and then a subset of the objects were taken out (e.g., 3 objects were hidden but only 2 retrieved), then infants were allowed to search the box. Compared to a baseline condition in which all three objects had been retrieved, infants searched longer when one object remained in the box, but only when there were no more than three objects hidden in the original set. When four objects were hidden, and only three retrieved, infants did not search for the remaining object, suggesting they had failed to represent sets larger than three (Feigenson & Carey, 2003). This capacity limit is also seen in ordinal choice tasks. For example, Feigenson, Carey, and Hauser (2002) gave 10- to 12-month-olds a choice between two hidden sets of crackers. Infants reliably chose the greater amount when choosing between 1 vs. 2, and 2 vs. 3 crackers, but were at chance when either set had more than 3 crackers. Thus, they chose randomly when the comparison was 2 vs. 4, 3 vs. 4, and even 1 vs. 4, even though the ratio was highly discriminable (Feigenson & Carey, 2005; Feigenson, Carey, & Hauser, 2002).

Second, infants' discrimination of small visual sets is not ratio-dependent like it is for large sets. As mentioned above, infants in a habituation procedure successfully discriminated large numbers of dots (e.g., 4 vs. 8, 8 vs. 16; Xu & Spelke, 2000), but in the same procedure, using the same stimuli and controls, they failed to discriminate two small numbers (e.g., 1 vs. 2, Xu et al., 2005) even though the ratio (1:2) was identical. Conversely, although 6-month-olds fail to discriminate large numbers differing by a 2:3 ratio (e.g., 8 vs. 12; 16 vs. 24; Xu & Spelke, 2000; Xu et al., 2005), several studies show them successfully discriminating 2 from 3 items (e.g., Feigenson, Carey, & Hauser, 2002; Strauss & Curtis, 1981; Wynn, 1996). Moreover, this dissociation is seen not only in discriminating numerosities within single sensory modalities (e.g., vision or audition), but also in matching numerosities across modalities: While 6-month-olds failed to match large numbers at a 2:3 ratio (4 vs. 6; Feigenson, 2011), 5- to 7-month-olds in most intermodal studies successfully match small numbers at a 2:3 ratio (2 vs. 3: Feron et al., 2006; Kobayashi et al., 2005; Starkey et al., 1983, 1990), suggesting that infants are not using the AMS to enumerate the stimuli in these studies. Another interpretation of these findings has been proposed by Jordan and colleagues whose work suggests that the precision of infants' and children's AMS representations is increased when they are provided redundant information across sensory modalities (e.g., seeing 3 faces and hearing 3 voices, Jordan & Brannon, 2006; a ball making sounds with every bounce, Jordan, Suanda, et al., 2008). Although this is a possibility, the fact that the information from different modalities is not usually temporally synched in these studies casts doubt on this explanation.

Cross-boundary comparisons and the "boundary effect"

The best evidence that infants use two different mechanisms is recent work showing they successfully discriminate exclusively small (<4) and exclusively large (>4) sets, but fail to discriminate sets falling on different sides of the boundary (Table 3). In the ordinal choice procedure described above, 10- to 12- month-old infants reliably chose the larger of two hidden amounts when the sets were both large, 5 vs. 10 (vanMarle & Wynn, 2011) and 4 vs. 8 (vanMarle, 2013), but failed in two cross-boundary conditions, 2 vs. 4 and 2 vs. 8 (vanMarle, 2013). Together with similar cross-boundary failures in the studies described above (2 vs. 4 and 3 vs. 6; Feigenson, Carey, & Hauser, 2002), these results suggest that even at 1 year of age, infants may not be able to compare numbers across the boundary. These

Table 2
Examples of animal studies examining whether various species' performance in numerical comparison tasks is more consistent with the AMS or the OTS.

Studies	Species	Stimuli	AMS or OTS or both?	Comments
Agrillo, Dadda, and Bisazza (2007)	Mosquitofish (*Gambusia holbrooki*)	Shoals of mosquitofish	Both	Succeeded with large and small numbers, but Weber fraction differed for small and large sets
Piffer, Agrillo, and Hyde (2012)	Guppies (*Poecilia reticulata*)	Shoals of guppies	Both	Needed larger ratios to overcome the boundary effect
Bisazza et al. (2010)	Guppies (*Poecilia reticulata*)	Shoals of guppies	OTS	newborns succeeded in small number range, but failed in large number comparisons until at least 20 days of age
Uller, Jaeger, Guidry, and Martin (2003)	Salamanders (*Plethodon cinereus*)	Discrete food items	OTS	Failed to compare large numbers, and Weber fraction differed for small and large sets
Rugani et al. (2008)	Chicks (*Gallus gallus*)	Discrete nonfood objects	OTS	Failed to compare large numbers, and Weber fraction differed for small and large sets
Rugani et al. (2013)	Chicks (*Gallus gallus*)	Discrete nonfood objects	AMS	Succeeded in comparing numbers across the boundary
vanMarle et al. (2006)	Capuchin monkeys (*Cebus apella*)	Discrete and continuous food items	AMS	The discriminability was the same for both discrete and continuous quantities
Beran (2008)	Rhesus monkeys (*Macaco mulatto*) & capuchin monkeys (*Cebus apella*)	2-D dot arrays on computer	AMS	Ratio-dependent performance throughout the number range
Beran (2001, 2004)	Chimpanzees (*Pan troglodytes*)	Discrete food items	AMS	Ratio-dependent performance throughout the number range
Tomonaga (2008)	Chimpanzees (*Pan troglodytes*)	2-D dot arrays on computer	AMS	Ratio-dependent performance throughout the number range
Ward and Smuts (2007)	Dogs (*Cants lupusfamiliaris*)	Discrete food items	AMS	Ratio-dependent performance throughout the number range

failures are especially striking because infants of this same age can discriminate exclusively large sets differing by a 2:3 ratio (4 vs. 6) in this same paradigm (vanMarle, Mou, & Seok, 2013).

Similar failures have been reported in habituation paradigms where 5-month-olds successfully discriminated large numbers of actions (i.e., a puppet jumping 4 vs. 8 times), but not small numbers (i.e., 2 vs. 4 jumps), even though the ratio (1:2) was the same in both cases (Wood & Spelke, 2005). In addition, a recent study testing newborn infants' intermodal matching with small numbers demonstrated that newborns discriminated and matched the number of human faces they saw with the number of voices they heard in a 1 vs. 2 comparison, but not in a 2 vs. 3 or even a 1 vs. 3 comparison, which is a ratio that we know is discriminable at birth (Coubart, Izard, Spelke, Marie, & Streri, 2013). The authors interpreted this pattern as evidence that the boundary between small and large numbers for newborns is 2 (compared to 3 for older infants), and suggested that newborn infants cannot make cross-boundary comparisons across modalities. Such failures are not limited to studies using atypical stimuli (actions, Wood & Spelke, 2005; intermodal stimuli, Coubart et al., 2013); even with commonly used visual displays, Xu (2003) and Xu et al. (2005) reported that 6-month-old infants failed to discriminate 1 from 2 and 2 from 4 dots.

This *boundary effect* presumably reflects the capacity limit of infants' OTS, and failures to compare small and large numbers strongly suggests that infants are not representing small and large numbers within a single mechanism. As Anderson and Cordes (2013) have discussed, infants' ordinal abilities also provide indirect evidence to support the two-system view. As mentioned above, when both small and large numbers were involved in ordinal sequences (e.g., 2–4–8), infants younger than 11 months

Table 3

Summary of infant studies testing cross-boundary (i.e., small vs. large) numerical operations. Rows in bold indicate studies in which infants successfully made cross-boundary comparisons.

Studies	Age	Task type	Stimulus attributes						Procedure	Successfully cross boundary?
		Looking time/action	Visual/ auditory	2D/3D	Moving/ static	Continuous quantities controlled?	Identical objects?		Simultaneous/ sequential	
Feigenson and Carey (2003)	14m	Action	Vis	3D	Moving	No	Yes		Sim/Seq	No
Feigenson and Carey (2005)	12m	Action	Vis	3D	Moving	No	Yes		Sim/Seq	No
Feigenson, Carey, and Hauser (2002)	10/12m	Action	Vis	3D	Moving	No	Yes		Seq	No
vanMarle (2013)	10/12m	Action	Vis	3D	Moving	No	Yes		Seq	No
Wood and Spelke (2005)	6m	LT	Vis	3D	Moving	Yes	Yes		Seq	No
Xu (2003)	6m	LT	Vis	2D	Static	Yes	Yes		Sim	No
Xu et al. (2005)	6m	LT	Vis	2D	Static	Yes	Yes		Sim	No
Coubart et al. (2013)	Newborn	LT	Intermodal Vis/Aud	2D	Static	–			Sim	No
Brannon (2002)	9m	LT	Vis	2D	Static	Yes	Yes		Sim	No
Suanda et al. (2008)	**9m**	**LT**	**Vis**	**2D**	**Static**	**No**	**Yes**		**Sim**	**Yes**
Starr et al. (2013)	**6m**	**LT**	**Vis**	**2D**	**Static**	**Yes**	**Yes**		**Sim**	**Yes**
Cordes and Brannon (2009)	**7m**	**LT**	**Vis**	**2D**	**Static**	**Yes**	**Yes**		**Sim**	**Yes**
vanMarle and Wynn (2009)	**7m**	**LT**	**Aud**	**–**	**–**	**Yes**	**No**		**Seq**	**Yes**
Wynn et al. (2002)	**5m**	**LT**	**Vis**	**2D**	**Moving**	**Yes**	**Yes**		**Sim**	**Yes**

of age failed to detect the reversal of the sequences (Brannon, 2002; Suanda et al., 2008). However, when only large numbers were involved (e.g., 6–12–24), even much younger infants succeeded (e.g., 8-month-olds, de Hevia & Spelke, 2010; 7-month-olds, Picozzi et al., 2010).

Such findings provide support for the view that the OTS is routinely used to represent small numerosities in infancy (Feigenson & Carey, 2003, 2005; Feigenson, Carey, & Hauser, 2002; vanMarle, 2013; Xu, 2003; Xu et al., 2005). The implication is that the manner in which infants represent and compare small numbers (as sets of individuals that can be put in one-to-one correspondence) and the way in which they represent large numbers (as analog magnitudes with cardinal values) are so different that infants fail to compare small and large numbers, even when the difference is very large and known to be discriminable (e.g., Feigenson, Carey, & Hauser, 2002; vanMarle, 2013; Xu, 2003).

It is notable that the boundary effect appears most often in tasks in which infants must track sets of 3-dimensional objects as they move and undergo occlusion. These are precisely the conditions in which the OTS should be engaged (Kahneman et al., 1992; Pylyshyn & Storm, 1988; Scholl, 2001), conditions in which attention is required to keep track of individual objects over time, and in which infants are expected to act on the objects (ordinal choice and manual search paradigms), which may further accentuate the individuality of each item in the set. In addition, subjects in ordinal choice tasks receive only a single trial, which may increase the likelihood of finding the set size signature of the OTS because each infant can only get the trial "right" or "wrong". A multiple trial procedure would provide a more sensitive measure of proportion correct, which might reveal reliable differences as a function of comparison ratio, even in the small number range. Although it is challenging to obtain multiple trials per infant in the ordinal choice task due to perseveration (vanMarle, unpublished data), this issue has been discussed in the animal literature where researchers have noted that multiple trial tasks are more likely to produce the ratio signature of the AMS, while single trial tasks are more likely to show the set size signature of the OTS (vanMarle et al., 2006; also see Anderson & Cordes, 2013 for review).

Nonetheless, though sparse, there are instances in which infants succeed in making cross-boundary comparisons. (See Table 3 for a list of studies testing cross-boundary comparisons organized by type of stimuli, paradigm, etc., and whether infants succeeded or failed in the comparison.) And, as the reader will notice, the majority of cross-boundary successes occur in studies using 2-dimensional stimuli presented as a single array, with looking time as the dependent measure, such that infants are not required to act on the stimuli. For example, Cordes and Brannon (2009) tested 7-month-olds in a habituation study in order to explore the effects of ratio on cross-boundary comparisons. Using typical 2-dimensional dot displays controlled for non-numerical variables (e.g., surface area, density), they showed that infants failed when the ratio was 1:2 (2 vs. 4 and 3 vs. 6), consistent with previous findings with infants of roughly this same age (Xu, 2003; Xu et al., 2005). However, using the same stimuli and procedure, infants successfully discriminated displays differing by a 1:4 ratio (1 vs. 4 and 2 vs. 8). Cordes and Brannon suggested two possible explanations. One was that infants represented the small arrays with the OTS and the large arrays with the AMS, but converted the OTS representations into AMS representations, allowing successful comparison and discrimination. On this account, the conversion process resulted in AMS representations with additional error, hence the need for a larger ratio. Alternatively, infants may have used the AMS for both the small and large arrays, but given the relative imprecision of AMS representations for small numbers, the OTS was preferred until the difference reached a critical ratio. As the authors suggest, when this critical ratio is met (1:4 in this case), the AMS representations are precise enough to successfully compete with the OTS, allowing successful discrimination across the boundary. Ongoing studies in our laboratory are testing which of these two possibilities may be accurate, but to date, both alternatives remain feasible.

Another, more recent study showing successful cross-boundary discrimination tested 6-month-old infants in a change detection task. Starr, Libertus, and Brannon (2013) presented infants with two simultaneous 2-dimensional displays, each displaying an array of dots that blinked on and off at a constant rate. One of the image streams displayed a constant number of elements while the other changed number with each onset (non-numerical properties were controlled). Under these conditions, infants successfully discriminated exclusively small (1 vs. 2), exclusively large (4 vs. 8), and cross-boundary sets (2 vs. 4). Interestingly, infants failed to discriminate exclusively small sets when they differed by a 2:3 ratio (2 vs. 3), suggesting they were using the AMS even in the small number range. This is inconsistent with the latter of the two possibilities raised to explain Cordes and Brannon's (2009)

findings (the critical-ratio proposal) since the infants were able to make a cross-boundary discrimination at a 1:2 ratio.

According to Starr et al., the discrepant results are likely attributable to methodological differences. In particular, they suggest that the change detection task places relatively substantial demands on working memory, which may prevent the recruitment of the OTS. And in addition, the relative complexity of the stimuli (changing displays rather than static displays, as in Xu, 2003) may have made it difficult to individuate the items within a set, leading to the engagement of the AMS (see also Hyde & Spelke, 2011). As noted by Starr et al., this explanation may account for previous findings in which 5-month-old infants successfully discriminated 2 from 4 moving groups of dots (Wynn et al., 2002). Although one might expect object motion to engage the OTS, in Wynn, Bloom, & Chiang's (2002) study, the stimuli were such that either the number of items within each group (two groups of four items) or the number of groups (four groups of two items) exceeded the capacity limit of the OTS, which may also have led infants to use the AMS, resulting in successful cross-boundary discrimination.

Finally, one other study showing successful cross-boundary discrimination is vanMarle and Wynn (2009), in which 7-month-old infants reliably discriminated 2 from 4 tones in an auditory habituation task. This is easily explained, however; while the AMS is characteristically amodal, the OTS is a mechanism of *visual* attention and should not be recruited to represent auditory individuals. Still, it is not the case that auditory information cannot be bound to OTS representations. In a study by Kobayashi et al. (2005), infants were initially familiarized to animated displays in which objects dropped one at a time onto a surface, making a sound with each impact. At test, the entire motion sequence was occluded, but infants still heard the impact sounds (either 2 or 3 sounds). Finally, the occluder was removed to reveal either two or three objects. Six-month-old infants in this study discriminated consistent and inconsistent outcomes, looking longer when hearing two impacts but three objects were revealed, or when hearing three impacts but only two objects were revealed. The fact that infants of this age are limited to discriminating items at a 1:2 ratio with the AMS suggests they were instead using the OTS. If so, infants apparently were able to create object indexes on the basis of the auditory information, leading to the expectation of a particular number of objects behind the screen.

Jordan, Clark, and Mitroff (2010) described a similar finding in adults using the "object reviewing" paradigm (Kahneman & Treisman, 1984; Kahneman et al., 1992). In their study, subjects were faster to respond when they heard auditory stimuli that conceptually matched and shared a spatial location with the original object, suggesting that object indexes initially assigned on the basis of visual information can later be accessed via corresponding auditory information (Jordan et al., 2010). Although findings such as these may seem inconsistent with the view of the OTS as a strictly visual mechanism, some have argued that object tracking representations ('object files') may be just one component of a more general category of 'event files', which bind information across domains (visual, motor, auditory, etc.), linking information about perceptual events and relevant actions (Hommel, 1998, 2004; see also Kubovy & Van Valkenburg, 2001 and Shinn-Cunningham, 2008). Indeed, a study exploring congenitally blind individuals' ability to subitize tactile stimuli showed faster and more accurate performance naming the number of fingers touched when 1–3 fingers had been touched than when 4–9 fingers were touched, suggesting vision is not necessary for the development of subitization (Ferrand, Riggs, & Castronovo, 2010).

The two-system view gains further support from a recent ERP study by Hyde and Spelke (2011) showing that distinct brain regions were involved when 6- to 7.5-month-olds detected a numerical change in small sets and large sets. The peak value of firing in the parietal region was modulated by the ratio between two large, but not small numbers, while the peak value in the occipital-temporal region was related to the absolute difference between two small, but not large numbers (but see Izard, Dehaene-Lambertz, & Dehaene, 2008). This result is consistent with findings in adults (Hyde & Spelke, 2009), and again, supports the existence of two distinct representational systems.

Moving beyond the either/or debate

In the introduction, we outlined various manifestations of the two-system hypothesis. One possibility, that the OTS and AMS are limited to representing small and large numbers, respectively, clearly cannot be true. Although the OTS, by definition, is indeed limited to representing small sets, there is

ample evidence that the AMS represents numbers throughout the number range in human adults (Cantlon & Brannon, 2006; Cordes et al., 2001; Whalen et al., 1999) and infants (Cordes & Brannon, 2009; Starr et al., 2013; vanMarle & Wynn, 2009; Wynn et al., 2002), as well as nonhuman animals (e.g., Beran, 2001, 2004, 2008; Beran et al., 2011; Cantlon & Brannon, 2006; Jones & Brannon, 2012; Tomonaga, 2008; vanMarle et al., 2006).

A second possibility is that the OTS and the AMS both represent small sets and compete throughout the lifespan and across species. In support of this view, there are numerous studies showing the AMS is ubiquitous throughout the animal kingdom, and throughout development in humans (for reviews, see Beran, 2008; Brannon, 2006; and Gallistel, 1990). However, although there are many studies suggesting that the OTS plays some role in adults' small number representations (e.g., Dehaene & Cohen, 1994; Ferrand et al., 2010; Kaufman et al., 1949; Mandler & Shebo, 1982; Revkin et al., 2008; Riggs et al., 2006; Trick & Pylyshyn, 1993, 1994; see Trick, 2008 for review), these studies use a limited set of paradigms and dependent measures, and critically, none to our knowledge have shown the boundary effect as seen in infants, suggesting that in adults, the systems coexist in ways that are flexible, rather than antagonistic.

As noted earlier, Kaufman et al.'s (1949) findings suggesting that small numbers are processed differently than large numbers have been called into question (Balakrishnan & Ashby, 1992; Gallistel & Gelman, 2005). And more recent studies by Whalen et al. (1999) and Cordes et al. (2001) show continuity throughout the number range. The best evidence that the OTS plays a role in enumerating small sets in adults come from work by Trick and colleagues (Trick, 2008; Trick et al., 1996; Trick & Pylyshyn, 1994; Trick et al., 2003). Trick and Pylyshyn (1994), for example, showed that adults' ability to subitize items was compromised when the items were difficult to individuate (i.e., static displays with concentric circles). The authors interpreted this as evidence that spatial attention is necessary for subitization and that the ability relies on a preattentive indexing mechanism (FINSTs) similar to the OTS. Another study showed that RT slopes were different for subitizing (1–4) and counting ranges (6–9), for both static and moving stimuli, and with heterogeneity of the items speeding enumeration in the counting range, but not the subitizing range (Trick, 2008). It is important to note, however, that not only was the range of values extremely limited in these studies (usually 1–9), but also that subjects were told to emphasize accuracy. Because subjects had an unlimited amount of time to respond, they likely counted (subvocally or otherwise) for the larger numbers, rather than estimating them. Thus, these studies did not actually compare subitizing and estimation (which relies on the AMS), and so did not actually compare small and large number *estimation*.

Many other adult studies suffer from these and similar limitations. For example, subjects are often presented with only a limited range of numbers (usually fewer than 20, cf. Revkin et al., 2008), and in most cases are asked to verbally name the sets. Asking subjects to name Arabic numerals sets such studies well apart from infant studies, all of which use nonsymbolic stimuli and response measures. Notably, the adult studies that have used nonverbal responses (e.g., Cordes et al., 2001; Whalen et al., 1999), and are thus more comparable to studies with infants, showed no discontinuity between small and large numbers.

In line with the scant data showing a role for the OTS in adults' enumeration, there is very little evidence showing that nonhuman animals use the OTS to enumerate small sets. As with infants, the most compelling evidence comes from studies showing a failure to compare small and large sets. Such a finding was reported by Hauser, Carey, and Hauser (2000). In an ordinal choice procedure, rhesus monkeys were given a choice between two hidden quantities of food items (just like infants in Feigenson, Carey, & Hauser, 2002 and vanMarle, 2013). They reliably chose the larger amount when comparing 1 vs. 0, 1 vs. 2, 2 vs. 3, 3 vs. 4, but not 4 vs. 5 or 5 vs. 6, or even 4 vs. 6, 4 vs. 8, or 3 vs. 8, despite the favorable ratios. The authors claimed that the pattern reflected the set size signature of the OTS (a limit of 4 items), arguing that monkeys failed whenever the number of items in either set exceeded four. And true enough, the monkeys showed striking failures at favorable ratios (4 vs. 6, 4 vs. 8, and 3 vs. 8), despite success with small numbers (2 vs. 3). Clearly, this pattern is more consistent with the OTS than the AMS. However, the monkeys did show successful performance in a 3 vs. 5 comparison, a cross-boundary condition, and at least one recent attempt to replicate the findings in a prosimian primate species have shown clear evidence of the AMS using the same single trial, ordinal

choice procedure. In Jones and Brannon (2012), lemurs succeeded at a 1:3 ratio, but not a 1:2 ratio, with exclusively small sets, exclusively large sets, and cross-boundary sets.

Beyond the findings with nonhuman primates, other nonhuman species (honeybees: Gross et al., 2009; horses: Uller & Lewis, 2009; salamanders: Uller, Jaeger, Guidry, & Martin, 2003) have shown performance consistent with the OTS. However, Uller and colleagues (Uller & Lewis, 2009; Uller et al., 2003) used the same single trial ordinal choice task as Hauser et al. (2000). Because this task involves a single trial, and requires subjects to track moving objects through occlusion, it presents animals with what are arguably ideal conditions for engaging the OTS, leaving it an open question whether these animals might use the AMS to represent small sets in other contexts.

In contrast to the limited support for the OTS, there is substantial evidence that a variety of nonhuman species routinely use the AMS to represent small sets as well as large sets. Studies with rhesus macaques (*Macaca mulatta*), capuchin monkeys (*Cebus apella*), and chimpanzees (*Pan troglodytes*) reveal the ratio signature for both small and large number comparisons (Beran, 2001, 2004, 2008; Beran et al., 2011; Tomonaga, 2008; vanMarle et al., 2006), and studies with fish (*Poecilia reticulata*) (Piffer, Agrillo, & Hyde, 2012) and chicks (Rugani, Cavazzana, Vallortigara, & Regolin, 2013) show success with cross-boundary comparisons. Beyond making simple numerical comparisons, rhesus monkeys' and pigeons' ability to order numerosities also suggests the use of a single representational system. After learning to order small numbers, training spontaneously transfers to novel large numbers, and their performance in both ranges varies as a function of ratio (Cantlon & Brannon, 2006; Scarf, Hayne, & Colombo, 2011). Across several studies, animals' performance in learning a particular ordinal position in a series does not differ for ordinal positions in the small and large number range (e.g., the third vs. the sixth location) (rats, Davis & Bradford, 1986; Suzuki & Kobayashi, 2000; Clarks nutcrackers, Rugani, Kelly, Szelest, Regolin, & Vallortigara, 2010; chicks, Rugani, Regolin, & Vallortigara, 2007, 2011; bees, Dacke & Srinivasan, 2008). And chicks are able to perform arithmetic involving both small and large sets (Rugani, Fontanari, Simoni, Regolin, & Vallortigara, 2009) (see Table 2 for a non-exhaustive list of animal studies providing evidence for one or both of the mechanisms). Thus, overall, the evidence that the OTS and AMS compete throughout the lifespan and across species in such a way as to make small and large numbers incomparable, as seen in infants, is quite weak.

Instead, we take the position that although the OTS and AMS are both functional across species and across the lifespan, the two systems interfere with each other predominantly in early development. The boundary effect is a reflection of this competition. More than just being inconsistent with the use of the AMS, the boundary effect represents a pattern of performance that is fundamentally maladaptive. Failure to choose the greater of two quantities of food in real life situations would clearly confer a disadvantage on infants. And according to the empirical data, this maladaptive behavior is surprisingly long-lived, lasting up to at least a year of age (and perhaps as much as 2 years, vanMarle, Seok, & Mou, 2013). Such failures to discriminate small and large sets, even when the difference between sets is very favorable (e.g., 2v8), to our knowledge, has not been documented in adults.

The fact AMS representations are remarkably imprecise early in life (Halberda & Feigenson, 2008) suggests a possible explanation for this mysterious pattern of performance. Because the OTS provides precise representations for small sets (up to 2 for newborns, 3 for infants aged 10- to 12-months, and 4 for adults), it may be preferable to use the OTS until the AMS is able to represent small sets with reasonable precision. In support of this notion is the fact that not only do we see evidence of the OTS under conditions that would be considered ideal (i.e., when infants must track 3-D visual objects that undergo occlusion, Feigenson & Carey, 2003, 2005; Feigenson, Carey, & Hauser, 2002; vanMarle, 2013), but it also appears under conditions which seemingly should engage the AMS (e.g., looking time tasks, tasks with static arrays of 2-dimensional elements; Cordes & Brannon, 2009; Kobayashi et al., 2005; Starkey & Cooper, 1980; Starkey et al., 1983, 1990; Strauss & Curtis, 1981; Wood & Spelke, 2005; Wynn, 1996; Xu, 2003). This suggests that the gain in precision within the small number range is more important (from an evolutionary standpoint) than being able to compare small and large sets in the first year or two of life. This could perhaps reflect a greater likelihood of being faced with small rather than large sets, though whether this is true of infants' actual experience in natural environments (particularly those inhabited by our distant ancestors) is an empirical question.

The *developmental hypothesis* also gains support from the animal literature. Despite the dearth of evidence for the OTS in the many studies exploring nonhuman animals' enumeration abilities, few

of these studies have tested newborn or even juvenile animals. At least two that have do indeed show competition between the OTS and AMS, as found in work with human infants. For example, Bisazza, Piffer, Serena, and Agrillo (2010) took advantage of guppies' tendency to want to be near the larger of two shoals of fish. By manipulating the number of fish in two available shoals, Bisazza et al. found that newborn guppies were limited to discriminating between small numbers, reliably choosing to be near the larger shoal when comparing 1 vs. 2, 2 vs. 3, and 3 vs. 4, but failing (spending equal time with both shoals) when comparing 4 vs. 5 and 5 vs. 6, as well as two large number comparisons with larger ratios (4 vs. 8 and 4 vs. 12). Further experiments showed that the ability to discriminate large numbers did not emerge until the fish were juveniles, and the exact age at which it emerged was a function of experience seeing groups of fish. Specifically, the guppies became able to make a large number comparison (4 vs. 8) at 20 days of age if raised in groups, but not until 40 days of age if raised in pairs. Another study tested chicks' ability to discriminate numerosities and found that they could successfully differentiate 1 vs. 2 and 2 vs. 3, but not 3 vs. 4, 4 vs. 5, or 4 vs. 6 (Rugani, Regolin, & Vallortigara, 2008). Taken together, these data are consistent with the idea that the young of at least two nonhuman animal species may show the boundary effect as seen in human infants.

Of course, our view does not imply that young infants will always use the OTS for small sets and the AMS for large sets. Clearly, the data suggest that the engagement of either mechanism depends on several factors, including the nature of the stimuli and the task demands (e.g., action or looking time). Other factors that seem to impact the AMS and OTS differently are the heterogeneity of the stimuli and whether the stimuli are controlled for non-numerical properties. In general, controlling for continuous extent (e.g., equating test displays for surface area, contour length, density, etc.) appears to undermines processing by the OTS, but leaves the AMS unaffected (Xu & Spelke, 2000; cf. Cantrell & Smith, 2013). For example, in looking time studies, infants sometimes fail to discriminate 1 vs. 2 items when continuous extent is controlled (Feigenson, Carey, & Spelke, 2002; Xu et al., 2005). And, when continuous extent is pitted against number in small sets, infants may respond to changes in continuous extent, and not number (Clearfield & Mix, 1999, 2001; Feigenson, Carey, & Spelke, 2002; Mix, Huttenlocher, & Levine, 2002; but see Cordes & Brannon, 2008, 2009).

To complicate matters further, Feigenson and colleagues showed that the homogeneity or heterogeneity of the items in a set interacts with effects of controlling for continuous extent. Specifically, 7-month-old infants' failed to discriminate 1 from 2 identical objects when continuous extent was controlled, but succeeded in the same discrimination when the objects had different features (Feigenson & Carey, 2005; Feigenson, Carey, & Spelke, 2002). Feigenson and colleagues argued that when faced with small sets of identical objects, the OTS computes continuous extent and not number, but computes number and not extent when faced with objects whose features vary (Feigenson, 2005). The reason behind this tendency is that for heterogeneous sets, the contrasting object features may facilitate the creation and/or maintenance of representations for each distinct object in the set. For homogeneous sets, even though distinct object indexes are initially assigned to each object, infants may simply extract the common featural properties, and discard the individual tokens, leading to a failure to discriminate small homogeneous sets (Feigenson, 2005).

One context in which extracting common features and discarding the number of individuals may be advantageous is when selecting between two quantities of food, such as in the ordinal choice task. Both infants (Feigenson & Carey, 2005; Feigenson, Carey, & Hauser, 2002) and chimpanzees (Beran, Evans, & Harris, 2008) will select the container with the most food, even if it has the smaller number of items (e.g., 1 huge cracker vs. 2 tiny crackers). This strategy makes sense when the stimuli are food items, as it is clearly more adaptive to maximize the total amount of food one obtains, not the number of food items (Beran et al., 2008; Feigenson et al., 2004). Interestingly, in a search task with non-food items, infants ignored continuous extent, and responded instead on the basis of number (Feigenson & Carey, 2003). Thus, even in infants the OTS is able to guide responses based on what information (continuous extent or number) is most relevant to the task.

One final puzzle that is germane to both the AMS and OTS is whether and how they represent empty sets (i.e., '0'). Historically, the concept of 'zero' did not appear until quite late in the development of mathematics, and was only reluctantly accepted as a number on par with the positive integers (Brainerd, 1979; Dantzig, 1930; Seife, 2000). One of the first cultures to use zero was the Babylonians (∼1500 BCE), but it was only used as a placeholder marking the absence of a value in symbolic

notation (e.g., 2013 has no value in the "hundreds" column). It was not until later that the Greeks began using zero, putting it to the same use, and several more centuries before mathematicians in India elevated it to a true number to be used in mathematical operations (Bialystok & Codd, 2000; Menninger, 1992; Merritt & Brannon, 2013). Ontongentically, the concept of zero follows a similarly protracted development relative to the positive integers. According to Wellman and Miller (1986), when young children first learn to recognize the symbol for zero, '0', they do not understand what it means. After some time, they come to understand that it means "none" or "nothing", but without understanding that it is a number with a value that can be ordered on a number line. Finally, by about age 6 they come to understand it as a number like the other integers, and can correctly report that it is smaller than '1'.

Why is zero so difficult? One reason may be that neither the OTS nor the AMS can represent empty sets (Gallistel & Gelman, 1992; Wynn, 1995a, 1995b; Wynn & Chiang, 1998). From a purely logical standpoint, it does not make sense to routinely represent empty sets. For example, when you walk into your house, you may (implicitly or explicitly) notice that there are four people in the living room, or about 100 toys scattered about your son's bedroom. However, you would not likely notice that there were zero bears in the kitchen, or zero Ferris wheels in your backyard. Indeed, it is impossible to represent all the empty sets you encounter because there are infinitely many of them.

The proposal that neither the OTS nor the AMS represents empty sets stems from evidence that infants have difficulty computing the outcome of simple addition/subtraction operations when the correct result is zero. Following the classic study by Wynn (1992), Wynn and Chiang (1998) used the same addition and subtraction paradigm to test 8-month-olds' responses to $1 - 1 = 1$ (magic appearance) and $0 + 1 = 1$ (expected appearance) events, and found that infants looked equally at the two outcomes. This finding is peculiar given that even younger infants (5 months) succeeded with subtractions such as $2 - 1 = 2$ or 1 (Koechlin, Dehaene, & Mehler, 1997; Wynn, 1992). To explain infants' failure, Wynn and Chiang (1998) suggested that neither mechanism is capable of producing a representation for zero. For the AMS, an empty accumulator simply indicates that nothing has been counted yet. If nothing has been counted, then no representation is output and the mismatch between the resulting number and the expected number cannot be detected. The same basic reasoning was applied to the OTS. Infants faced with a $1 - 1 = 1$ situation initially assign an index for the original object, but then unassign it following the subtraction, leaving no active indexes. Thus, when the result (1 object) is revealed, there is no representation to be put into one-to-one correspondence with the visible set, and thus no mismatch is detected. Interestingly, older infants succeed in a 0 vs. 4 comparison in the ordinal choice task (Feigenson & Carey, 2005), which is inconsistent with this view. However, infants may simply ignore the empty bucket, leaving open the question of whether they are actually representing zero in that case.

Despite the difficulties infants have in representing zero, children and adults show evidence of representing zero along the same continuum as the positive integers. From 4 years of age, children are able to order zero correctly in relation to the positive integers in a nonsymbolic task and their performance shows the distance effect, suggesting that they have started to integrate zero in the numerical continuum (Merritt & Brannon, 2013). In addition, animal studies show that rhesus monkeys can match empty sets in a match-to-sample task, and also touch two dot arrays (set sizes 1–12) in ascending or descending order even when a (previously untrained) zero set is introduced (Merritt, Rugani, & Brannon, 2009), suggesting that they can recognize the cardinal and ordinal properties of zero. However, even extensively trained animals still have difficulties in flexibly applying the symbolic number zero, suggesting that they treat zero differently from other numbers (Biro & Matsuzawa, 2001; Pepperberg, 2006). Clearly further work is needed before we understand this important aspect of numerical knowledge.

Conclusions

The two core systems, analog magnitudes and object tracking, have different signature characteristics. The evidence reviewed here suggests that the systems coexist across ages and in many nonhuman animal species. However, although they are both present, they seem to compete for representing

small sets primarily early in development, as evidenced by the boundary effect seen in infants, but not adults.

We are just beginning to explore how and when each system is engaged, but there is a great deal that we still do not understand with respect to how the systems may (or may not) interact. In this review, we emphasized the coexistence of the two systems in human infants and that their deployment seems to depend largely on experimental context. However, it is still unclear whether the two systems are typically activated simultaneously, with one trumping the other in a given context, or whether just one becomes engaged at a time. In addition, the boundary effect may reflect a developmentally significant limitation in which the representations are initially incommensurable (vanMarle, Seok, & Mou, 2013), causing infants to either see the forest or the trees, but not both (Spelke, 2011). To date, we know little about when and how infants finally overcome this limitation and begin to successfully compare sets across the boundary. Some researchers believe that language plays a critical role in integrating the two systems, though how exactly this might unfold is unknown (Spelke, 2011).

An ongoing study in our lab is testing older infants' ability to compare small and large numbers to determine at what age infants begin to compare small and large sets. The results suggest that the ability does not develop until after 18 months of age, and possibly as late as 24 month of age (vanMarle, 2013). Once this is determined, it will become important to explore *how* infants breach this important limitation. There are at least two possibilities that should be examined. One is that the two systems may become able to "talk" to each other. That is, infants may become able to compare OTS representations to AMS representations. This seems unlikely given that OTS representations do not specify the cardinality of a set, and AMS representations, by definition, are continuous and lack information about the enumerated individuals, making one-to-one correspondence impossible. A more plausible alternative is that both systems may be activated in the task, in both younger and older infants (and beyond infancy), but that OTS representations "trump" the AMS representations early in development. Thus, with maturation, the AMS representations may become "stronger", due to increasing fidelity of the representations, allowing both small and large quantities to be represented and compared within a single system.

Understanding the roles that the two systems play in infants' numerical reasoning may also help us determine which system provides the underlying representations onto which children map their verbal number labels when they learn to count. Current research suggests that both mechanisms may play a role, though the issue remains hotly debated (Benoit, Lehalle, & Jouen, 2004; Carey, 2004; Gallistel & Gelman, 1992; Gelman & Cordes, 2001; Gilmore, McCarthy, & Spelke, 2007; Le Corre & Carey, 2007). As it stands, neither system alone can provide a compelling account of the phenomena. Instead, given that the two systems coexist in infants and young children, it is entirely possible that they both contribute to the mapping of verbal number words onto their underlying mental representations. The role of language in the development of the number concept is therefore an important area for future research (Spelke & Tsivkin, 2001).

Besides behavioral studies on infants' numerical representations, very few studies to date have explored the neural mechanisms underlying the two systems in human infants (but see Hyde & Spelke, 2011; Izard et al., 2008). Due to practical and technical limitations, we know very little about maturation of the underlying neural systems and how increasing experience may improve infants' numerical abilities. Advances in technology will no doubt open up many avenues for exploring how the neural circuitry underlying quantity representation changes with age and how these changes relate to the developmental changes seen in behavioral tasks. Imaging studies can also shed light on whether the brain areas involved in quantity representation are the same across development and across species, as suggested by the behavioral evidence. Such knowledge will greatly improve our understanding of the origins and the development of these two systems.

Having more than one representational system functioning in a cognitive domain is not unique to the core domain of numerical cognition. Recently, Spelke (2011) proposed that nonhuman animals and human children may reason within the core domain of spatial cognition by using two distinct systems, one responding to distance and direction information in 3D contexts, and the other responding to distance and angle in 2D contexts. More generally, the well-known overlapping waves model of cognitive development emphasizes the coexistence and competition of multiple representations or strategies that children can use to process information and solve problems (Siegler, 1996). Studying

infants provides unique opportunities to observe the initial states and interactions of the two systems and how they change over time. Future research will continue to shed light on these issues, providing a better understanding of the foundations of numerical cognition.

Acknowledgments

References

Agrillo, C., Dadda, M., & Bisazza, A. (2007). Quantity discrimination in female mosquitofish. *Animal Cognition, 10*, 63–70.

Allan, L. G., & Gibbon, J. (1991). Human bisection at the geometric mean. *Learning and Motivation, 22*, 39–58.

Alvarez, G. A., & Cavanagh, P. (2004). The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychological Science, 15*, 106–111.

Alvarez, G. A., & Franconeri, S. L. (2007). How many objects can you track? Evidence for a resource-limited tracking mechanism. *Journal of Vision, 7*, 1–10.

Anderson, U. S., & Cordes, S. (2013). 1 < 2 and 2 < 3: Nonlinguistic appreciations of numerical order. *Frontiers in Psychology, 4*. http://dx.doi.org/10.3389/fpsyg.2013.00005.

Ansari, D., Lyons, I. M., van Eimeren, L., & Xu, F. (2007). Linking visual attention and number processing in the brain: The role of the temporo-parietal junction in small and large symbolic and nonsymbolic number comparison. *Journal of Cognitive Neuroscience, 19*, 1845–1853.

Antell, S. E., & Keating, D. P. (1983). Perception on numerical invariance in neonates. *Child Development, 54*, 695–701.

Balakrishnan, J. D., & Ashby, F. G. (1992). Subitizing: Magical numbers or mere superstition? *Psychological Research, 54*, 80–90.

Barner, D., Thalwitz, D., Wood, J., Yang, S., & Carey, S. (2007). On the relation between the acquisition of singular-plural morpho-syntax and the conceptual distinction between one and more than one. *Developmental Science, 10*, 365–373.

Barth, H., Kanwisher, N., & Spelke, E. (2003). The construction of large number representations in adults. *Cognition, 86*, 201–221.

Barth, H., La Mont, K., Lipton, J., Dehaene, S., Kanwisher, N., & Spelke, E. (2006). Nonsymbolic arithmetic in adults and young children. *Cognition, 98*, 199–222.

Barth, H., La Mont, K., Lipton, J., & Spelke, E. (2005). Abstract number and arithmetic in preschool children. *Proceedings of the National Academy of Sciences, 102*, 14116–14121.

Benoit, L., Lehalle, H., & Jouen, F. (2004). Do young children acquire number words through subitizing or counting? *Cognitive Development, 19*, 291–307.

Beran, M. J. (2001). Summation and numerousness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 115*, 181–191.

Beran, M. J. (2004). Chimpanzees (*Pan troglodytes*) respond to nonvisible sets after one-by-one addition and removal of items. *Journal of Comparative Psychology, 118*, 25–36.

Beran, M. J. (2007). Rhesus monkeys (*Macaca mulatta*) enumerate large and small sequentially presented sets of items using analog numerical representations. *Journal of Experimental Psychology: Animal Behavior Processes, 33*, 42–54.

Beran, M. J. (2008). Monkeys (*Macaca mulatta* and *Cebus apella*) track, enumerate, and compare multiple sets of moving items. *Journal of Experimental Psychology: Animal Behavior Processes, 34*, 63–74.

Beran, M. J. (2010). Chimpanzees (*Pan troglodytes*) accurately compare poured liquid quantities. *Animal Cognition, 13*, 641–649.

Beran, M. J. (2012). Quantity judgments of auditory and visual stimuli by chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes, 38*, 23–29.

Beran, M. J., Decker, S., Schwartz, A., & Schultz, N. (2011). Monkeys (*Macaca mulatta and Cebus apella*) and human adults and children (*Homo sapiens*) enumerate and compare subsets of moving stimuli based on numerosity. *Frontiers in Comparative Psychology, 2*. Article 61.

Beran, M. J., Evans, T. A., & Harris, E. H. (2008). Perception of food amount by chimpanzees based on the number, size, contour length, and visibility of items. *Animal Behaviour, 75*, 1793–1802.

Beran, M. J., Johnson-Pynn, J. S., & Ready, C. (2011). Comparing children's *Homo sapiens* and chimpanzees' *Pan troglodytes* quantity judgments of sequentially presented sets of items. *Current Zoology, 57*, 419–428.

Beran, M. J., Taglialatela, L. A., Flemming, T. M., James, F. M., & Washburn, D. A. (2006). Nonverbal estimation during numerosity judgments by adult humans. *Quarterly Journal of Experimental Psychology (Colchester), 59*, 2065–2082.

Bialystok, E., & Codd, J. (2000). Representing quantity beyond whole numbers: Some, none, and part. *Canadian Journal of Experimental Psychology, 54*, 117–128.

Biro, D., & Matsuzawa, T. (2001). Use of numerical symbols by the chimpanzee (*Pan troglodytes*): Cardinals, ordinals, and the introduction of zero. *Animal Cognition, 4*, 193–199.

Bisazza, A., Piffer, L., Serena, G., & Agrillo, C. (2010). Ontogeny of Numerical Abilities in Fish. *PLoS One, 5*, e15516.

Brainerd, C. J. (1979). *The origins of the number concept*. New York: Praeger.

Brannon, E. M. (2002). The development of ordinal numerical knowledge in infancy. *Cognition, 83*, 223–240.

Brannon, E. M. (2006). The representation of numerical magnitude. *Current Opinion in Neurobiology, 16*, 222–229.

Brannon, E. M., & Merritt, D. (2011). Evolutionary foundations of the Approximate Number System. In S. Dehaene & E. M. Brannon (Eds.), *Space, time, and number in the brain: Searching for the foundations of mathematical thought*. London: Elsevier.

Brannon, E. M., & Roitman, J. (2003). Nonverbal representations of time and number in non-human animals and human infants. In W. Meck (Ed.), *Functional and neural mechanisms of interval timing* (pp. 143–182). New York: CRC Press.

Brannon, E. M., Suanda, U., & Libertus, K. (2007). Temporal discrimination increases in precision over development and parallels the development of numerosity discrimination. *Developmental Science, 10*, 770–777.

Brannon, E. M., & Terrace, H. S. (1998). Ordering of the numerosities 1–9 by monkeys. *Science, 282*, 746–749.

Brannon, E. M., & Terrace, H. S. (2000). Representation of the numerosities 1–9 by Rhesus Monkeys (*Macaca mulatta*). *Journal of Experimental Psychology: Animal Behavior Processes, 26*, 31–49.

Brannon, E. M., & Terrace, H. S. (2002). The evolution and ontogeny of ordinal numerical ability. In M. Bekoff (Ed.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 197–204). Cambridge, MA, US: MIT Press.

Cantlon, J. F. (2012). Math, monkeys, and the developing brain. *Proceedings of the National Academy of Sciences, 109*, 10725–10732.

Cantlon, J. F., & Brannon, E. M. (2006). Shared system for ordering small and large numbers in monkeys and humans. *Psychological Science, 17*, 401–406.

Cantlon, J. F., & Brannon, E. M. (2007). Basic math in monkeys and college students. *PLoS Biology, 5*, 2912–2919.

Cantlon, J. F., Platt, M., & Brannon, E. M. (2009). Beyond the number domain. *Trends in Cognitive Sciences, 13*, 83–91.

Cantrell, L., & Smith, L. B. (2013). Open questions and a proposal: A critical review of the evidence on infant numerical abilities. *Cognition, 128*, 331–352.

Carey, S. (2004). Bootstrapping and the origins of concepts. *Daedalus*, 59–68.

Carey, S. (2009). *The origin of concepts*. New York: Oxford University Press.

Carey, S., & Xu, F. (2001). Infants' knowledge of objects: Beyond object files and object tracking. *Cognition, 80*, 179–213.

Castelli, F., Glaser, D. E., & Butterworth, B. (2006). Discrete and analogue quantity processing in the parietal lobe: A functional MRI study. *Proceedings of the National Academy of Sciences, USA, 103*, 4693–4698.

Cheries, E. W., Mitroff, S. R., Wynn, K., & Scholl, B. J. (2009). Do the same principles constrain persisting object representations in infant cognition and adult perception?: The cases of continuity and cohesion. In B. Hood & L. Santos (Eds.), *The origins of object knowledge* (pp. 107–134). USA: Oxford University Press.

Clearfield, M. W., & Mix, K. S. (1999). Number versus contour length in infants' discrimination of small visual sets. *Psychological Science, 10*, 408–411.

Clearfield, M. W., & Mix, K. S. (2001). Infant use continuous quantity – not number – to discriminate small visual sets. *Journal of Cognition and Development, 2*, 243–260.

Cordes, S., & Brannon, E. M. (2008). Quantitative competencies in infancy. *Developmental Science, 11*, 803–808.

Cordes, S., & Brannon, E. M. (2009). Crossing the divide: Infants discriminate small from large numerosities. *Developmental Psychology, 45*, 1583–1594.

Cordes, S., Gallistel, C. R., Gelman, R., & Latham, P. (2007). Nonverbal arithmetic in humans: Light from noise. *Perception and Psychophysics, 69*(7), 1185–1203.

Cordes, S., Gelman, R., Gallistel, C. R., & Whalen, J. (2001). Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. *Psychonomic Bulletin & Review, 8*, 698–707.

Coubart, A., Izard, V., Spelke, E. S., Marie, J., & Streri, A. (2013). Dissociation between small and large numerosities in newborn infants. *Developmental Science*. http://dx.doi.org/10.1111/desc.12108.

Dacke, M., & Srinivasan, M. V. (2008). Evidence for counting in insects. *Animal Cognition, 11*, 683–689.

Dale, C. L. (2000). Range effects in repetitive time production. *Dissertation Abstracts International: The Sciences and Engineering, 61*, 5033.

Dantzig, T. (1930). *Number: The language of science*. New York: The Macmillan Company.

Davis, H., & Bradford, S. A. (1986). Counting behavior by rats in a simulated natural environment. *Ethology, 73*, 265–280.

de Hevia, M. D., & Spelke, E. S. (2010). Number-space mapping in human infants. *Psychological Science, 21*, 653–660.

Dehaene, S. (1997). *The number sense: How the mind creates mathematics*. New York: Oxford University Press.

Dehaene, S. (2009). Origins of mathematical intuitions: The case of arithmetic. *Annals of the New York Academy of Sciences, 1156*, 232–259.

Dehaene, S., & Changeux, J. (1993). Development of elementary numerical abilities: A neuronal model. *Journal Cognitive Neuroscience, 5*, 390–407.

Dehaene, S., & Cohen, L. (1994). Dissociable mechanisms of subitizing and counting: Neuropsychological evidence from simultanagnosic patients. *Journal of Experimental Psychology: Human Perception & Performance, 20*, 958–975.

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology, 20*, 487–506.

Einstein, A. (1950). *Out of my later years*. London: Thames and Hudson.

Feigenson, L. (2005). A double-dissociation in infants' representations of object arrays. *Cognition, 95*, B37–B48.

Feigenson, L. (2011). Predicting sights from sounds: 6-Month-olds' intermodal numerical abilities. *Journal of Experimental Child Psychology, 110*, 347–361.

Feigenson, L., & Carey, S. (2003). Tracking individuals via object-files: Evidence from infants' manual search. *Developmental Science, 6*, 568–584.

Feigenson, L., & Carey, S. (2005). On the limits of infants' quantification of small object arrays. *Cognition, 97*, 295–313.

Feigenson, L., Carey, S., & Hauser, M. D. (2002). The representations underlying infants' choice of more: Object files vs. analog magnitudes. *Psychological Science, 13*, 150–156.

Feigenson, L., Carey, S., & Spelke, E. (2002). Infants' discrimination of number vs. Continuous extent. *Cognitive Psychology, 44*, 33–66.

Feigenson, L., Dehaene, S., & Spelke, E. S. (2004). Core systems of number. *Trends in Cognitive Sciences, 8*, 307–314.

Feron, J., Gentaz, E., & Streri, A. (2006). Evidence of amodal representation of small numbers across visuo-tactile modalities in 5-month-old infants. *Cognitive Development, 21*, 81–92.

Ferrand, L., Riggs, K. J., & Castronovo, J. (2010). Subitizing in congenitally blind adults. *Psychonomic Bulletin & Review, 17*, 840–845.

Flombaum, J. I., Junge, J. A., & Hauser, M. D. (2005). Rhesus monkeys (*Macaca mulatta*) spontaneously compute addition operations over large numbers. *Cognition, 97*, 315–325.

Flombaum, J. I., Scholl, B. J., & Santos, L. R. (2009). Spatiotemporal priority as a fundamental principle of object persistence. In B. Hood & L. Santos (Eds.), *The origins of object knowledge* (pp. 135–164). USA: Oxford University Press.

Fontanari, L., Rugani, R., Regolin, L., & Vallortigara, G. (2011). Object individuation in 3-day-old chicks: Use of property and spatiotemporal information. *Developmental Science, 14*, 1235–1244.

Gallistel, C. R. (1990). *The organization of learning.* Cambridge, MA: MIT Press.

Gallistel, C. R. (2007). Commentary on Le Corre & Carey. *Cognition, 105*, 439–445.

Gallistel, C. R., & Gelman, R. (1992). Preverbal and verbal counting and computation. *Cognition, 44*, 43–74.

Gallistel, C. R., & Gelman, R. (2000). Non-verbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences, 4*, 59–65.

Gallistel, C. R., & Gelman, R. (2005). Mathematical cognition. In K. Holyoak & R. Morrison (Eds.), *The Cambridge handbook of thinking and reasoning* (pp. 559–588). New York: Cambridge University Press.

Gallistel, C. R., King, A., & McDonald, R. (2004). Sources of variability and systematic error in mouse timing behavior. *Journal of Experimental Psychology: Animal Behavior Processes, 30*, 3–16.

Gelman, R., & Cordes, S. (2001). Counting in animals and humans. In E. Dupoux (Ed.), *Language, brain, and cognitive development: Essays in honor of Jacques Mehler* (pp. 279–303). Cambridge, MA: MIT Press.

Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review, 84*, 279–325.

Gibbon, J., Fairhurst, S., & Goldberg, B. (1997). Cooperation, conflict and compromise between circadian and interval clocks in pigeons. In C. M. Bradshaw & E. Szabadi, et al. (Eds.), *Time and behavior: Psychological and neurobehavioural analyses advances in psychology* (pp. 329–384). Amsterdam, Netherlands: North-Holland/Elsevier Science Publishers.

Gilmore, C. K., McCarthy, S. E., & Spelke, E. S. (2007). Symbolic arithmetic knowledge without instruction. *Nature, 447*, 589–591.

Gross, H. J., Pahl, M., Si, A., Zhu, H., Tautz, J., & Zhang, S. W. (2009). Number-based visual generalisation in the honeybee. *PLoS One, 4*, e4263.

Halberda, J., & Feigenson, L. (2008). Developmental change in the acuity of the "Number Sense": The approximate number system in 3-, 4-, 5-, 6-year-olds and adults. *Developmental Psychology, 44*, 1457–1465.

Hauser, M. D., Carey, S., & Hauser, L. B. (2000). Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings of the Royal Society of London: Biological Sciences, 267*, 829–833.

Hommel, B. (1998). Event files: Evidences for automatic integration of stimulus-response episodes. *Visual Cognition, 5*, 183–216.

Hommel, B. (2004). Event files: Feature binding in and across perception and action. *Trends in Cognitive Sciences, 8*, 494–500.

Hyde, D. (2011). Two systems of non-symbolic numerical cognition. *Frontiers in Human Neuroscience, 5*, 150.

Hyde, D. C., & Spelke, E. S. (2009). All numbers are not equal: An electrophysiological investigation of small and large number representations. *Journal of Cognitive Neuroscience, 21*, 1039–1053.

Hyde, D. C., & Spelke, E. S. (2011). Neural signatures of number processing in human infants: Evidence for two core systems underlying numerical cognition. *Developmental Sciences, 14*, 360–371.

Hyde, D. C., & Wood, J. N. (2011). Spatial attention determines the nature of nonverbal number representation. *Journal of Cognitive Neuroscience, 23*, 2336–2351.

Izard, V., Dehaene-Lambertz, G., & Dehaene, S. (2008). Distinct cerebral pathways for object identity and number in human infants. *PLoS Biology, 6*, 275–285.

Izard, V., Sann, C., Spelke, E. S., & Streri, A. (2009). Newborn infants perceive abstract numbers. *Proceedings of the National Academy Sciences, USA, 106*, 10382–10385.

Jevons, W. S. (1871). The power of numerical discrimination. *Nature, 3*, 281–282.

Jones, S. M., & Brannon, E. M. (2012). Prosimian primates show ratio dependence in spontaneous quantity discriminations. *Frontiers in Comparative Psychology, 3*. Article 550.

Jordan, K. E., & Brannon, E. M. (2006). The multisensory representation of number in infancy. *Proceedings of the National Academy of Sciences, USA, 103*, 3486–3489.

Jordan, K. E., Brannon, E. M., Logothetis, N. K., & Ghazanfar, A. A. (2005). Monkeys match the number of voices they heat to the number of faces they see. *Current Biology, 15*, 1034–1038.

Jordan, K. E., Clark, K., & Mitroff, S. R. (2010). See an object, hear an object file: Object correspondence transcends sensory modality. *Visual Cognition, 18*, 492–503.

Jordan, K. E., MacLean, E. L., & Brannon, E. M. (2008). Monkeys match and tally quantities across senses. *Cognition, 108*, 617–625.

Jordan, K. E., Suanda, S. H., & Brannon, E. M. (2008). Intersensory redundancy accelerates preverbal numerical competence. *Cognition, 108*, 210–221.

Kahneman, D., Treisman, A., & Gibbs, B. J. (1992). The reviewing of object files: Object-specific integration of information. *Cognitive Psychology, 24*, 174–219.

Kahneman, D., & Treisman, A. (1984). Changing views of attention and automaticity. In R. Parasuraman, D. R. Davies, & J. Beatty (Eds.), *Variants of attention* (pp. 29–61). New York: Academic Press.

Kaufman, E. L., Lord, M. W., Reese, T. W., & Volkmann, J. (1949). The discrimination of visual number. *American Journal of Psychology, 62*, 498–525.

King, A. S., McDonald, R., & Gallistel, C. R. (2001). Screening for mice that remember incorrectly. *International Journal of Comparative Psychology, 14*, 232–257.

Kobayashi, T., Hiraki, K., & Hasegawa, T. (2005). Auditory-visual intermodal matching of small numerosities in 6-month-old infants. *Developmental Science, 8*, 409–419.

Kobayashi, T., Hiraki, K., Mugitani, R., & Hasegawa, T. (2004). Baby arithmetic: One object plus one tone. *Cognition, 91*, B23–B34.

Koechlin, E., Dehaene, S., & Mehler, J. (1997). Numerical transformations in five month old human infants. *Mathematical Cognition, 3*, 89–104.

Kubovy, M., & van Valkenburg, D. (2001). Auditory and visual objects. *Cognition, 80*, 97–126.

Le Corre, M., & Carey, S. (2007). One, two, three, four, nothing more: An investigation of the conceptual sources of the verbal counting principles. *Cognition, 105*, 395–438.

Leslie, A. M., Xu, F., Tremoulet, P., & Scholl, B. (1998). Indexing and the object concept: Developing 'what' and 'where' systems. *Trends in Cognitive Sciences, 2*, 10–18.

Libertus, M. E., & Brannon, E. M. (2010). Stable individual differences in number discrimination in infancy. *Developmental Science, 13*, 900–906.

Lipton, J. S., & Spelke, E. S. (2003). Origins of number sense: Large number discrimination in human infants. *Psychological Science, 14*, 396–401.

Lipton, J. S., & Spelke, E. S. (2004). Discrimination of large and small numerosities by human infants. *Infancy, 5*, 271–290.

Mandler, G., & Shebo, B. J. (1982). Subitizing: An analysis of its component processes. *Journal of Experimental Psychology: General, 111*, 1–22.

McCrink, K., & Wynn, K. (2004). Large-number addition and subtraction by 9-month-old infants. *Psychological Science, 15*, 776–781.

McCrink, K., & Wynn, K. (2007). Ratio abstraction by 6-month-old infants. *Psychological Science, 18*, 740–746.

Meck, W. H., & Church, R. M. (1983). A mode control model of counting and timing processes. *Journal of Experimental Psychology: Animal Behavior Processes, 9*, 320–334.

Mendes, N., Rakoczy, H., & Call, J. (2008). Ape metaphysics: Object individuation without language. *Cognition, 106*, 730–749.

Menninger, K. (1992). In Z. Ziffer (Trans.), *Number words and number systems.* New York: Dover.

Merritt, D. J., & Brannon, E. M. (2013). Nothing to it: Precursors to a zero concept in preschoolers. *Behavioural Processes, 93*, 91–97.

Merritt, D. J., Rugani, R., & Brannon, E. M. (2009). Empty sets and the representation of number in macaques. *Journal of Experimental Psychology: General, 138*(2), 258–269.

Mitroff, S. R., & Alvarez, G. A. (2007). Space and time, not surface features, underlie object persistence. *Psychonomic Bulletin & Review, 14*, 1199–1204.

Mix, K., Huttenlocher, J., & Levine, S. (2002). Multiple cues for quantification in infancy: Is number one of them? *Psychological Bulletin, 128*, 278–294.

Mix, K. S., Levine, S. C., & Huttenlocher, J. (1997). Numerical abstraction in infants: Another look. *Developmental Psychology, 33*, 423–428.

Moore, D., Benenson, J., Reznick, J. S., Peterson, P., & Kagan, J. (1987). Effect of auditory numerical information on infants' looking behavior: Contradictory evidence. *Developmental Psychology, 23*, 665–670.

Moyer, R. S., & Landauer, T. K. (1967). The time required for judgments of numerical inequality. *Nature, 215*, 1519–1520.

Nieder, A., & Dehaene, S. (2009). Representation of number in the brain. *Annual Review in Neuroscience, 32*, 185–208.

Nieder, A., & Miller, E. K. (2003). Coding of cognitive magnitude: Compressed scaling of numerical information in the primate prefrontal cortex. *Neuron, 37*, 149–157.

Nieder, A., & Miller, E. K. (2004). A parieto-frontal network for visual numerical information in the monkey. *Proceedings of the National Academy of Sciences of the USA, 101*, 7457–7462.

Parkman, J. M. (1971). Temporal aspects of digit and letter inequality judgments. *Journal of Experimental Psychology, 91*, 191–205.

Pepperberg, I. M. (2006). Grey parrot (*Psittacus erithacus*) numerical abilities: Addition and further experiments on a zero-like concept. *Journal of Comparative Psychology, 120*, 1–11.

Piazza, M. (2010). Neurocognitive start-up tools for symbolic number representations. *Trends in Cognitive Sciences, 14*, 542–551.

Piazza, M., Giacomini, E., Le Bihan, D., & Dehaene, S. (2003). Single-trial classification of parallel pre-attentive and serial attentive processes using functional magnetic resonance imaging. *Proceeding of the Royal Society Biological Sciences, 270*, 1237–1245.

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron, 44*, 547–555.

Piazza, M., Mechelli, A., Price, C., & Butterworth, B. (2006). Exact and approximate judgments of visual and auditory numerosity: An fMRI study. *Brain Research, 1106*, 177–188.

Picozzi, M., de Hevia, M. D., Girelli, L., & Macchi-Cassia, V. (2010). Seven-month-old infants detect ordinal numerical relationships within temporal sequences. *Journal of Experimental Child Psychology, 107*, 359–367.

Piffer, L., Agrillo, C., & Hyde, D. C. (2012). Small and large number discrimination in guppies. *Animal Cognition, 15*, 215–221.

Plaisier, M. A., Tiest, W. M. B., & Kappers, A. M. L. (2010). Range dependent processing of visual numerosity: Similarities across vision and haptics. *Experimental Brain Research, 204*, 525–537.

Platt, J., & Johnson, D. (1971). Localization of position within a homogeneous behavior chain: Effects of error contingencies. *Learning and Motivation, 2*, 386–414.

Pylyshyn, Z. W. (1989). The role of location indexes in spatial perception: A sketch of the FINST spatial-index model. *Cognition, 32*, 65–97.

Pylyshyn, Z. W. (1994). Some primitive mechanisms of spatial attention. *Cognition, 50*, 363–384.

Pylyshyn, Z. W. (2001). Visual indexes, preconceptual objects, and situated vision. *Cognition, 80*, 127–158.

Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spatial Vision, 3*, 179–197.

Rakitin, B. C., Hinton, S. C., Penney, T. B., Malapani, C., Gibbon, J., & Meck, W. H. (1998). Scalar expectancy theory and peak-interval timing in humans. *Journal of Experimental Psychology: Animal Behavior Processes, 24*, 1–19.

Revkin, S. K., Piazza, M., Izard, V., Cohen, L., & Dehaene, S. (2008). Does subitizing reflect numerical estimation? *Psychological Sciences, 19*, 607–614.

Richard, A. M., Luck, S. J., & Hollingworth, A. (2008). Establishing object correspondence across eye movements: Flexible use of spatiotemporal and surface feature information. *Cognition, 109*, 66–88.

Riggs, K. J., Ferrand, L., Lancelin, D., Fryziel, L., Dumur, G., & Simpson, A. (2006). Subitizing and tactile perception. *Psychological Science, 17*, 271–272.

Roberts, S. (1982). Cross-modal use of an internal clock. *Journal of Experimental Psychology: Animal Behavior Process, 8*, 2–22.

Rugani, R., Cavazzana, A., Vallortigara, G., & Regolin, L. (2013). One, two, three, four, or is there something more? Numerical discrimination in day-old domestic chicks. *Animal Cognition.* http://dx.doi.org/10.1007/s10071-012-0593-8.

Rugani, R., Vallortigara, G., & Regolin, L. (2013). Numerical abstraction in young domestic chicks (*Gallus gallus*). *PLoS ONE, 8*, e65262. http://dx.doi.org/10.1371/journal.pone.0065262.

Rugani, R., Fontanari, L., Simoni, E., Regolin, L., & Vallortigara, G. (2009). Arithmetic in newborn chicks. *Proceedings of the Royal Society: Biological Sciences, 276*, 2451–2460.

Rugani, R., Kelly, D. M., Szelest, I., Regolin, L., & Vallortigara, G. (2010). Is it only humans that count from left to right? *Biology Letters, 6*, 290–292.

Rugani, R., Regolin, L., & Vallortigara, G. (2007). Rudimental numerical competence in 5-day-old domestic chicks (*Gallus gallus*): Identification of ordinal position. *Journal of Experimental Psychology Animal Behavior Processes, 33*, 21–31.

Rugani, R., Regolin, L., & Vallortigara, G. (2008). Discrimination of small numerosities in young chicks. *Journal of Experimental Psychology. Animal Behavior Processes, 34*, 388–399.

Rugani, R., Regolin, L., & Vallortigara, G. (2011). Summation of large numerousness by newborn chicks. *Frontier in Psychology*, 2.

Santos, L. R., Barnes, J. L., & Mahajan, N. (2005). Expectations about numerical events in four lemur species (*Eulemur fulvus, Eulemur mongoz, Lemur catta*, and *Varecia rubra*). *Animal Cognition, 8*, 253–262.

Scarf, D., Hayne, H., & Colombo, M. (2011). Pigeons on par with primates in numerical competence. *Science, 334*, 1664.

Scholl, B. J. (2001). Objects and attention: The state of the art. *Cognition, 80*, 1–46.

Scholl, B. J., & Leslie, A. M. (1999). Explaining the infant's object concept: Beyond the perception/cognition dichotomy. In E. Lepore & Z. Pylyshyn (Eds.), *What is cognitive science?* (pp 26–73). Oxford: Blackwell.

Seife, C. (2000). *Zero: The biography of a dangerous idea*. New York: Penguin Books.

Shinn-Cunningham, B. G. (2008). Object-based auditory and visual attention. *Trends in Cognitive Sciences, 12*, 182–186.

Siegler, R. S. (1996). *Emerging minds: The process of change in children's thinking*. New York: Oxford University Press.

Spelke, E. S. (2000). Core knowledge. *American Psychologist, 55*, 1233–1243.

Spelke, E. S. (2011). Natural number and natural geometry. In E. Brannon & S. Dehaene (Eds.), *Attention and performance. Space, time and number in the brain: Searching for the foundations of mathematical thought* (Vol. 24, pp. 287–317). Oxford, United Kingdom: Oxford University Press.

Spelke, E. S. (2004). Core knowledge. In N. Kanwisher & J. Duncan (Eds.), *Attention and performance. Functional neuroimaging of visual cognition* (Vol. 20, pp. 29–56). Oxford, UK: Oxford University Press.

Spelke, E. S., & Kinzler, K. (2007). Core knowledge. *Developmental Science, 10*, 89–96.

Spelke, E. S., & Tsivkin, S. (2001). Initial knowledge and conceptual change: Space and number. In M. Bowerman & S. Levinson (Eds.), *Language acquisition and conceptual development*. Cambridge, UK: Cambridge University Press.

Starkey, P., & Cooper, R. G. (1980). Perception of numbers by human infants. *Science, 210*, 1033–1035.

Starkey, P., Spelke, E. S., & Gelman, R. (1983). Detection of intermodal numerical correspondences by human infants. *Science, 222*, 179–181.

Starkey, P., Spelke, E., & Gelman, R. (1990). Numerical abstraction by human infants. *Cognition, 36*, 97–127.

Starr, A. B., Libertus, M. E., & Brannon, E. M. (2013). Infants show ratio dependent discrimination regardless of set size. *Infancy*, 1–15.

Strauss, M. S., & Curtis, L. E. (1981). Infant perception of numerocity. *Child Development, 52*, 1146–1152.

Suanda, S. H., Tompson, W., & Brannon, E. M. (2008). Changes in the ability to detect ordinal numerical relationships between 9 and 11 months of age. *Infancy, 13*, 308–337.

Suzuki, K., & Kobayashi, T. (2000). Numerical competence in rats (*Rattus norvegicus*): Davis and Bradford (1986) extended. *Journal of Comparative Psychology, 114*, 73–85.

Taves, E. H. (1941). Two mechanisms for the perception of visual numerousness. *Archives of Psychology, 37*, 1–47.

Thompson, R. F., Mayers, K. S., Robertson, R. T., & Patterson, C. J. (1970). Number coding in association cortex of the cat. *Science, 168*, 271–273.

Tomonaga, M. (2008). Relative numerosity discrimination by chimpanzees (*Pan troglodytes*): Evidence for approximate numerical representations. *Animal Cognition, 11*, 43–57.

Trick, L. M. (2008). More than superstition: Differential effects of featural heterogeneity and change on subitizing and counting. *Perception and Psychophysics, 70*, 743–760.

Trick, L. M., Audet, D., & Dales, L. (2003). Age differences in enumerating things that move: Implications for the development of multiple-object tracking. *Memory and Cognition, 31*, 1229–1237.

Trick, L. M., Enns, J. T., & Brodeur, D. A. (1996). Life-span changes in visual enumeration: The number discrimination task. *Developmental Psychology, 32*, 925–932.

Trick, L. M., & Pylyshyn, Z. W. (1993). What enumeration studies can show us about spatial attention: Evidence for limited capacity preattentive processing. *Journal of Experimental Psychology: Human Perception & Performance, 19*, 331–351.

Trick, L. M., & Pylyshyn, Z. W. (1994). Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. *Psychological Review, 101*, 80–102.

Uller, C., Carey, S., Hauser, M., & Xu, F. (1997). Is language needed for constructing sortal concepts? A study with non-human primates. In E. Hughes et al. (Eds.), *Proceedings of the twenty-first Boston University conference on language development*. Sommerville, MA: Cascadilla Press.

Uller, C., Jaeger, R., Guidry, G., & Martin, C. (2003). Salamanders (*Plethodon cinereus*) go for more: Rudiments of number in an amphibian. *Animal Cognition, 6*, 105–112.

Uller, C., & Lewis, J. (2009). Horses (*Equus caballus*) select the greater of two quantities in small numerical contrasts. *Animal Cognition, 12*, 733–738.

Vallortigara, G., Chiandetti, C., Rugani, R., Sovrano, V. A., & Regolin, L. (2010). Animal cognition. *Wiley Interdisciplinary Reviews: Cognitive Science, 1*, 882–893.

Van Loosbroek, E., & Smitsman, A. W. (1990). Visual perception of numerosity in infancy. *Developmental Psychology, 26*, 911–922.

vanMarle, K. (2013). Different mechanisms underlie infants' representation of small and large numbers in an ordinal choice task. *Journal of Experimental Child Psychology, 114*, 102–110.

vanMarle, K., Aw, J., McCrink, K., & Santos, L. R. (2006). How capuchin monkeys (*Cebus apella*) quantify objects and substances. *Journal of Comparative Psychology, 120*, 416–426.

vanMarle, K., Mou, Y., & Seok, J. (2013). Infants' ordinal judgments show ratio signature for large numbers (in preparation).

vanMarle, K., Seok, J., & Mou, Y. (2013). Overcoming the boundary effect: When can infants successfully compare small and large sets? Manuscript in preparation.

vanMarle, K., & Wynn, K. (2006). 6-Month-old infants' use analog magnitudes to represent duration. *Developmental Science, 9*, F41–F49.

vanMarle, K., & Wynn, K. (2009). Infants' auditory enumeration: Evidence for analog magnitudes in the small number range. *Cognition, 111*, 302–316.

vanMarle, K., & Wynn, K. (2011). Tracking and quantifying objects and non-cohesive substances. *Developmental Science, 14*(3), 5020515.

Walsh, V. (2003). A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends of Cognitive Sciences, 7*, 483–488.

Ward, C., & Smuts, B. B. (2007). Quantity-based judgments in the domestic dog (*Canis lupus familiaris*). *Animal Cognition, 10*, 71–80.

Warren, H. C. (1897). The reaction time of counting. *Psychological Review, 4*, 569–591.

Wellman, H. M., & Miller, K. F. (1986). Thinking about nothing: Developmental concepts of zero. *British Journal of Developmental Psychology, 4*, 31–42.

Whalen, J., & West, V. (2001). Why should you count on subitizing: Evidence from count and estimating. Psychonomics Society Abstracts, No 453, p. 66.

Whalen, J., Gallistel, C. R., & Gelman, R. (1999). Nonverbal counting in humans: The psychophysics of number representation. *Psychological Science, 10*, 130–137.

Wood, J., & Spelke, E. (2005). Infants' enumeration of actions: Numerical discrimination and its signature limits. *Developmental Science, 8*, 173–181.

Wynn, K. (1992). Addition and subtraction by human infants. *Nature, 358*, 749–750.

Wynn, K. (1995a). Infants possess a system of numerical knowledge. *Current Directions in Psychological Science, 4*, 172–177.

Wynn, K. (1995b). Origins of numerical knowledge. *Mathematical Cognition, 1*, 35–60.

Wynn, K. (1996). Infants' individuation and enumeration of actions. *Psychological Science, 7*, 164–169.

Wynn, K., Bloom, P., & Chiang, W. C. (2002). Enumeration of collective entities by 5-month-old infants. *Cognition, 83*, B55–B62.

Wynn, K., & Chiang, W. (1998). Limits of infants' knowledge of objects: The case of magical appearance. *Psychological Science, 9*, 448–455.

Xu, F. (2003). Numerosity discrimination in infants: Evidence for two systems of representations. *Cognition, 89*, B15–B25.

Xu, F., & Arriaga, R. I. (2007). Number discrimination in 10-month-old infants. *British Journal of Developmental Psychology, 25*, 103–108.

Xu, F., & Carey, S. (1996). Infants' metaphysics: The case of numerical identity. *Cognitive Psychology, 30*, 111–153.

Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition, 74*, B1–B11.

Xu, F., Spelke, E. S., & Goddard, S. (2005). Number sense in human infants. *Developmental Science, 8*, 88–101.