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The Small-Large Divide: A Case of Incompatible Numerical Representations in Infancy

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Abstract

Converging evidence in the field of numerical cognition suggests that humans and non-human animals have access to two distinct systems for representing number, an exact object-file system that can precisely track a small number of items and an approximate number system used to represent large sets. In this chapter, we review behavioral and neuroscientific evidence indicating that these distinct systems are evolutionarily ancient, emerge early in the lifespan, and do so in a linguistic-free capacity. We discuss those circumstances under which infants overcome the representational incompatibilities presented by the interaction of these two systems, characterizing those circumstances that promote the employment of a single system for representation across small and large sets. Finally, we address the question of how, over the course of development, we overcome these discrimination difficulties, presenting two hypotheses to account for this change.

Keywords: numerical cognition, approximate number system, analog magnitudes, object files, number discrimination, infant cognition

Introduction

The importance of understanding the developmental origins of our numerical abilities has recently been highlighted by studies suggesting that primitive abilities for tracking numerical information serve as the preverbal foundations for formal mathematics. Individual differences in the sensitivity of these preverbal abilities may contribute to children's initial learning of formal mathematical symbols and their meaning (e.g., Arabic numerals) and contribute to variation in mathematical outcomes in adults (e.g., Bonny & Lourenco, 2013; Geary, 2011; Geary, Hoard, Nugent, & Bailey, 2013; Halberda & Feigenson, 2008; Jordan, Kaplan, Ramineni, & Locuniak, 2009; LeFevre, Fast, Skwarchuk, Smith-Chant, & Bisanz, 2010; Libertus, Odic, & Halberda, 2012), although the relative importance of preverbal and verbal numerical processing is debated (De Smedt, Noel, Gilmore, & Ansari, 2013). Importantly, this relationship appears to be causal, at least in some domains of formal mathematics, such that arithmetic processing is improved following training on approximate numerical estimation (e.g., Hyde, Khanum, & Spelke, 2014; Park & Brannon, 2013), and is evident prior to formal mathematical experience, with preverbal numerical abilities in infancy and early childhood predicting math achievement several years later (Libertus, Feigenson, & Halberda, 2011, 2013; Starr, Libertus, & Brannon, 2013b; vanMarle, Chu, Li, & Geary, 2014). Given that math achievement upon entering school is strongly predictive of math achievement throughout later schooling (e.g., Duncan et al., 2007; Geary, 2013), it is critical that we understand the origins of these numerical abilities in order to target educational outcomes long before children reach the classroom.

A substantial corpus of work accumulated over the past 40+ years has unveiled striking similarities in the ways that numerical information is processed across phylogeny and ontogeny (see Anderson & Cordes, 2013; Cantlon, Platt, & Brannon, 2009; Gallistel, 1990). For example, data from infants, children, adults, and non-human animals consistently point to the existence of two distinct systems for tracking set sizes, one specifically dedicated to precisely tracking small sets of items (≤ 3;

referred to as the object-file system), and a second system responsible for representing all set sizes in an approximate manner (referred to as either the analog magnitude or approximate number system (ANS)). Despite notable parallels observed across development, robust differences in the way infants deal with the interface of these two numerical systems may point to qualitative distinctions in the way that number is processed throughout development. In this chapter, we will review the evidence for these two systems across development and across species while attempting to answer open questions regarding how humans progress from a state of representational incompatibility, in which infants are generally incapable of comparing small and large sets due to qualitatively distinct representational systems, to a numerically fluid state, in which small and large set sizes are given equal treatment, just a few years later.

Distinct systems of representation: Evidence of continuity across development and phylogeny

Converging evidence suggests that humans and non-human animals have access to two distinct systems for representing number (see Feigenson, Dehaene, & Spelke, 2004 and Cordes & Brannon, 2008b for reviews). The first is a noisy, analog magnitude system used for representing number in an approximate manner (also termed the approximate number system [ANS]; Barth, La Mont, Lipton, Dehaene, Kanwisher, & Spelke, 2006; Brannon & Terrace, 1998; Cantlon & Brannon, 2006; Cordes & Gelman, 2005; Cordes, Gelman, Gallistel, & Whalen, 2001; Dehaene, 1997; Gallistel & Gelman, 2000; Meck & Church, 1983; Whalen, Gallistel, & Gelman, 1999; Xu & Spelke, 2000). Importantly, the signature characteristic of the ANS is its adherence to Weber's law, such that the ease with which two set sizes are discriminated is dependent upon their ratio, not absolute difference (e.g., Halberda & Feigenson, 2008). That is, the speed and accuracy of discriminating sets of 8 and 6 items is the same as that for discriminating sets of 16 and 12 items (3:4 ratio in both cases; Barth et al., 2006). Evidence for a ratio-dependent ANS system has been found in humans throughout the lifespan, but also in nonhuman animals including primates (e.g., chimpanzees; *Pan troglodyte*; Beran & Beran, 2004; Beran, Evans, & Harris, 2008; lemurs: *Lemur catta, Eulemur mongoz, Eulemur macaco flavifrons*; Jones, Pearson, DeWind, Paulsen, Tenekedjieva, & Brannon, 2013; macaques: *Macaca mulatta*; Jones et al., 2013; orangutans;

Pongo pygmaeus; Call, 2000; Hanus & Call, 2007), elephants (*Loxodonta Africana*; Perdue, Talbot, Stone, & Beran, in press), birds (e.g., African grey parrots; *Psittacus erithacus;* Al Ain, Giret, Grand, Kreutzer, & Bovet, 2009; Bogale, Kamata, Mioko, & Sugita, 2011; Zorina & Smirnova, 1996), dogs (*Canis lupus familiaris;* coyote: *Canis latrans*; Baker, Shivik, & Jordan, 2011; Ward & Smuts, 2007), bears (*Ursus americanus*; Vonk & Beran, 2012), sea lions (*Otaria flavescens*; Abramson, Hernandez-Lloreda, Call, & Colmenares, 2011), salamanders (*Caudata plethodon*; Krusche, Uller, & Dicke, 2010), and even fish (*Gambusia affinis*; Agrillo, Piffer, & Bisazza, 2010; Agrillo, Piffer, Bisazza, & Butterworth, 2012; *Xiphophorus helleri;* Buckingham, Wong, & Rosenthal, 2007; *Poecilia reticulata;* Piffer, Agrillo, & Hyde, 2011; for a review see Anderson & Cordes, 2013; Cantrell & Smith, 2013).

Developmental data from both animals and humans suggest that the precision of ANS representations increases with age, such that the numerical ratio of discriminability approaches one over the course of development, with the greatest changes early in life (e.g., Bisazza, Piffer, Serena, & Agrillo, 2010; Halberda & Feigenson, 2008; Libertus & Brannon, 2010; Lipton & Spelke, 2003). Specifically, whereas newborn humans require as much as a 3-fold change in number to notice a change (e.g., 4 vs. 12), 6-months-olds are able to detect a 2-fold (but not a 1.5-fold) change (e.g., 4 vs. 8, 8 vs. 16, 16 vs. 32) and 9- to 10-month olds notice even smaller numerical changes (1.5-fold change; e.g., 8 vs. 12; Brannon, Abbot, & Lutz, 2004; Cordes & Brannon, 2008a; Izard, Sann, Spelke, & Streri, 2009; Lipton & Spelke, 2003, 2004; Wood & Spelke, 2005; Xu, 2003; Xu & Arriaga, 2007; Xu & Spelke, 2000; Xu, Spelke, & Goddard, 2005), with this precision continuing to increase into adulthood, such that adults discriminate a 1.14-fold (7:8) change in magnitude (Halberda & Feigenson, 2008). A similar progression in ANS acuity has been found in nonhuman animals, such that 1-day old guppies are unable to discriminate a 2-fold difference in number (4 vs. 8), but by their 40^{th} day of life, they do so reliably (Bisazza et al., 2010).

The second system implicated in numerical tasks, the object-file system, is an exact, one-to-one representational system that can only be used to track a small number of visual items (1-3 or 4; Carey & Xu, 2001; Dehaene, 1997; Feigenson, Carey, & Hauser, 2002; Feigenson et al., 2004; Hyde & Wood, 2011; Leslie, Xu, Tremoulet, & Scholl, 1998; Simon, 1997). In contrast to the ANS, this system of parallel individuation has an absolute set size limit (e.g., Alvarez & Cavanaugh, 2004; Alvarez & Franconeri, 2007). Evidence suggests that human infants can hold exactly three or less items in working memory when making numerical discriminations (Carey & Xu, 2001; Feigenson, 2008; Feigenson et al., 2004; Hyde & Wood, 2011; Jordan & Brannon, 2006; Uller, Carey, Huntley-Fenner, & Klatt, 1999; Xu, 2003). Similarly, human adults simultaneously track up to 4 or 5 items before working memory becomes overly taxed (e.g., Awh, Vogel, & Oh, 2006; Feigenson & Yamaguchi, 2009; Halberda, Simons, & Wetherhold, submitted; Klahr, 1973; Luck & Vogel, 1997; Luria & Vogel, 2011; Piazza, Giacomini, Bihan, & Dehaene, 2003; Scholl & Pylyshyn, 1999; Trick & Pylyshyn, 1994; Vogel, Woodman, & Luck, 2001; Zosh & Feigenson, 2012; Zosh, Halberda, & Feigenson, 2011). Moreover, data from non-human animals also reveal precise tracking of small sets of items (Agrillo et al., 2012; Bisazza et al., 2010; Hauser, Carey, & Hauser, 2000; Hunt, Low, & Burns, 2008; Piffer et al., 2011; Uller & Lewis, 2009; Uller, Jaeger, Guidry, & Martin, 2003).

Notably, the object file system is posited to be a function of the visual attention system and as such, it is only employed when tracking visual objects (i.e., not sounds; vanMarle & Wynn, 2009, but see Mou & vanMarle, 2013). The object file system was originally conceptualized within the adult visual attention literature, where striking demonstrations revealed differences in the way adults tracked a small compared to a large number of objects. In a classic example, adult observers were briefly shown a sample array consisting of 1-12 colored squares and then saw a test array and were asked to identify whether the sample array differed from the test array in the color of one of the squares (Luck & Vogel, 1997). When arrays of 1-3 items were presented, subjects demonstrated perfect performance. However, performance declined systematically as a function of set size once the number of items in the array increased from 4 to 12. Furthermore, this decline in accuracy was not due to verbal working memory nor to any limitations in overall processing as subjects showed no difference in performance when given more time to view the sample array. Therefore, performance accuracy varied as a function of set size specifically due to a difference in demands on working memory for dealing with small sets (<4) compared to large sets (>3; Luck & Vogel, 1987).

Importantly, although the object file system likely evolved for non-numerical processing – because it involves the tracking of individual items and, unlike the ANS, does not implicitly represent the items in a numerical fashion (i.e., as a collection with a cardinal value) – the system has been implicated in numerical tasks across the lifespan. Object file representations have been implicated in visual enumeration in adulthood, where small sets (4 or fewer items) are generally enumerated effortlessly, accurately, and quickly ("subitized"), whereas the enumeration of larger groups invokes an effortful, slower, and error-prone process of verbal counting (Balakrishnan & Ashby, 1982; Piazza, Mechelli, Butterworth, & Price, 2002; Trick, Enns, & Brodeur, 1996; Trick & Pylyshyn, 1993, 1994). Similarly, human infants also appear to show a numerical advantage in the small number range, such that infant data reveal finer-grained numerical discriminations than predicted by the ANS when sets fall exclusively within the small number range (3 or fewer). For example, although 6-month olds robustly fail to discriminate large sets differing by only a 2:3 ratio (e.g., 4 vs 6; 8 vs. 12, 16 vs. 24; Lipton & Spelke, 2003, 2004; Wood & Spelke, 2005; Xu, 2003; Xu & Arriaga, 2007; Xu & Spelke, 2000; Xu, Spelke, & Goddard, 2005), when sets are small (<4), they succeed in doing so under certain circumstances (2 vs. 3; e.g., Antell & Keating, 1983; Bijeljac-Babic, Bertoncini, & Mehler, 1993; Cordes & Brannon, 2009b; Jordan, Suanda, & Brannon, 2008; Kobayashi, Hiraki, & Hasegawa, 2005; see Cordes & Brannon, 2008b for review). Furthermore, similar small set numerical discrimination advantages have been demonstrated in non-human animals (guppies, *Poecilia reticulata*: Bisazza et al., 2010; mosquitofish, *Gambusia holbrooki*; Agrillo, Dadda, Serena, & Bisazza, 2008; chicks, *Gallus gallus*: Rugani, Regolin, & Vallortigara, 2008; dogs, *Canus lupus familiaris*: Bonanni, Natoli, Cafazzo, & Valsecchi, 2011; primates, *Macaca mulatta*; Hauser et al., 2000)

Consistent with the behavioral data, neuroscientific evidence has also reveal clear differences in how we process small and large sets. Notable differences in both the location and timing of brain activation have been demonstrated as a function set size (Ansari, Lyons, van Eimeren, & Xu, 2007; Hyde & Spelke, 2009, 2011, 2012; see Buhusi & Cordes, 2011). For example, imaging studies with human adults have revealed that processing of small non-symbolic (i.e., arrays of 1-3 dots) sets (but not symbolic number, i.e., Arabic numerals), results in activation of an area of the brain associated with visual attention (right temporo-parietal junction or rTPJ). In contrast, less activity in this area (presumably resulting in greater suppression of object file representations) was associated with faster numerical judgments involving large sets (Ansari et al., 2007; see also Hyde & Spelke, 2012). Moreover, event-related potential studies (ERP, tracking the timing of electrical activity in the brain) have revealed passive viewing of small sets in both human adults and infants to evoke earlier activity, with the magnitude of the activity dependent upon the *absolute* size of the set (regardless of the size of previously viewed sets). In contrast, ERPs associated with viewing large sets were slightly later and dependent upon the *relative* magnitude of the set (compared to other sets; Hyde & Spelke, 2009; 2011). In sum, the neuroscientific data corroborate behavioral findings to suggest small sets are processed in a very different manner than large sets across the lifespan.

Evidence for two systems in infancy

As described above, both behavioral and neuroscientific investigations indicate humans throughout the lifespan and non-human animals have access to two distinct systems used for representing numerical quantity: an exact object-file system used to precisely track items within small sets (<4), and an approximate number system used to represent all natural numbers. However, arguably the strongest evidence to date of these two distinct systems emerges from work with human infants, where numerical discrimination data robustly violate Weber's Law when one of the sets involved is small, in two different regards. First, as alluded to above, infant discriminations of small sets are reported to be more precise than dictated by Weber's Law under certain circumstances. Second, discriminations of small sets from large ones yield robust failures, despite seemingly facile discrimination ratios.

Small versus small discriminations

Consistent with the exact nature of object-file representations, data reveal infant discriminations of exclusively small sets (1-3 items) can be more precise than predicted by Weber's Law. For example, 6-month olds robustly fail to discriminate a 2:3 ratio (e.g., 6 vs. 9) of change in number for large sets, yet they notice the difference between sets of 2 and 3 items (also a 2:3 ratio, but involving exclusively small sets; Cordes & Brannon, 2009b; Jordan et al., 2008; Xu & Spelke, 2000). Importantly, however, infants' success at discriminating among small sets is found only under certain circumstances in which tasks include multi-modal input or when redundant visual information is provided (Cantrell & Smith, 2013). For example, when infants are placed in a situation in which they must match the number of sounds they hear to the number of items they see, they detect a mismatch between 2 sounds and 3 objects and vice versa (Jordan et al., 2008; Kobayashi et al., 2005; Starkey, Spelke, & Gelman, 1983, 1990). Moreover, when habituated to purely visual arrays in which continuous quantities (surface area, contour) are held constant in habituation, young infants notice the difference between 2 and 3 items (Antell & Keating, 1983; Cordes & Brannon, 2009b) [1]. Importantly, however, when continuous quantities vary from trial-to-trial in habituation (thus preventing infants from using surface area as a cue for discrimination), 6-month olds fail to detect even a 1:2 ratio change in number (1 versus 2 items; Xu et al., 2005). This finding is particularly surprising given that similar-aged infants have no difficulty in detecting a 1:2 ratio change in number across stimuli varying in continuous quantities when sets are exclusively large (e.g., 8 vs. 16; Lipton & Spelke, 2003; Wood & Spelke, 2005; Xu, 2003; Xu & Spelke, 2000; Xu et al., 2005). In sum, unlike the ubiquitous ability to compare large sets using the ANS, infant abilities to detect numerical changes for exclusively small sets within the object file system appear to be highly contingent upon task variables.

The small-large divide

Even more striking evidence in favor of the two-systems account in infancy is the finding of robust discrimination failures when comparing small (<4) and large (≥4) sets, despite a favorable ratio of discriminability (e.g., Cordes & Brannon, 2009a; Feigenson & Carey, 2003, 2005; Feigenson et al., 2002; Lipton & Spelke, 2004; vanMarle, 2013; Wood & Spelke, 2005; Xu, 2003; see also Mou & vanMarle, 2013). For example, although looking time measures reveal that infants as young as 6-months reliably

[1] The need for redundant visual information has provided the basis for the Signal Clarity Hypothesis (Cantrell & Smith, 2013) discussed later in this chapter.

discriminate 1:2 ratio changes in number for large sets (e.g., 4 vs. 8, 16 vs. 32; e.g., Xu & Spelke, 2000), when presented with a similar 1:2 ratio change in number crossing the small-large divide (e.g., 2 vs. 4 or 3 vs. 6), they repeatedly fail on these discriminations (Cordes & Brannon, 2009a; Lipton & Spelke, 2004; Wood & Spelke, 2005; Xu, 2003). Similarly, paradigms involving more active infant responses (such as searching for toys placed within a box or crawling to a container with a greater number of food items) reveal successful discrimination between 1 vs. 2, 2 vs. 3, and 4 vs. 8 items, but not between 2 vs. 4 and 3 vs. 6 items (Feigenson & Carey, 2003, 2005; Feigenson & Halberda, 2004; Feigenson et al., 2002; vanMarle, 2013). In fact, using these active response measures, even when the ratio between the to-be-enumerated numbers is relatively large (e.g., 1 vs. 4), infants still fail to spontaneously detect which of two sets contains more items (Feigenson & Carey, 2003, 2005; Feigenson et al., 2002; vanMarle, 2013; but see Cordes & Brannon, 2009a).

Tracking small sets with the ANS: Exceptions to the rule

Although evidence for small-large discrimination failures supports the notion of an incompatibility between ANS and object file systems in infancy (also see Mou & vanMarle, 2013), a handful of studies report successful discrimination between small and large sets (Cordes & Brannon, 2009a; Cantrell, Boyer, Cordes, & Smith, submitted; Hyde & Spelke, 2011; Starr et al., 2013a; vanMarle & Wynn, 2009; Wynn, Bloom & Chiang, 2004). What circumstances give rise to infant abilities to cross the small-large numerical divide? And, more importantly, what do these findings tell us about these two systems in infancy?

Although the behavioral pattern of infant discriminations suggests that infants exclusively employ object files to represent small sets (up to 3 items) while solely invoking the ANS for larger sets, empirical evidence indicates that they in fact have access to ANS representations for small and large sets alike, at least under certain circumstances. For example, when presented with *non-visual* numerical sets (i.e., sounds), infant numerical discriminations are ratio-dependent, consistent with an ANS signature, even for discriminations involving small sets. That is, 7-month old successfully detect the difference between 2 and 4 *tones* (1:2 ratio change), but not between 2 and 3 (2:3 ratio; vanMarle & Wynn, 2009). Importantly, this finding is consistent with claims that object files are a component of the visual attention system, and thus are not invoked for tracking auditory stimuli, leaving ANS representations as the sole cognitive system available for tracking small sets. Therefore, in contrast to other small-large discrimination failures with visual sets, ratio-dependent numerical discriminations involving auditory sets strongly suggest that infants, much like older children, adults, and non-human animals (Brannon & Terrace, 1998; Cantlon & Brannon, 2006; Cordes et al., 2001; Meck & Church, 1983; Moyer & Landauer, 1967; Ward & Smuts, 2007), have access to ANS representations all the way down the number line.

Provided evidence that infants have access to ANS representations for small sets, it is somewhat surprising that object file representations are consistently invoked when infants confront small visual sets. If these representations result in discrimination failures, one might question why they have evolved to be the preferred system of representation for small sets early in development. An ecological account may posit that in the first year of life, the tracking of small sets is much more important to the young infant than the tracking of large sets. Whereas in natural contexts, infants may encounter large groups of objects (e.g., toys in the room), by far, the most important items to track are those that provide food and comfort to the infant – that is, the set of people in the room. Moreover, the members of this set are not necessarily interchangeable, such that e.g., Dad may provide a different source of nourishment and comfort than Mom. Therefore, being able to attend to the total number of individuals in the set (e.g., people in the room), as well as to store information such as the location and salient characteristics of each individual belonging to that set (i.e., know where Mom is sitting) may be considered much more relevant to preverbal infants than an abstract ability to compare small and large sets. Unlike the ANS, which only provides a summary representation of a set (i.e., the total number of items present), object files can be used to store not only the location of an object, but also salient characteristics of the object, even in infancy (e.g., remembering a triangle is at Location 1 and a circle is at Location 2; Feigenson, 2005; Kaldy & Leslie, 2003). Thus, it seems that the tracking demands of the infant's environment may naturally give rise to an overarching preference towards object file representations.

In addition to specific ecological demands, the significant difference in representational precision afforded by the object file system compared with the ANS system may also account for a bias towards object file representations early in development. Whereas the object file system allows for the *precise, exact* tracking of individual items, the ANS is an *approximate, noisy* system. Evidence of a numerical discrimination advantage for small sets in infancy (such that infants succeed on finer-grained discriminations in the small number range compared to the large number range), suggest that object files offer a relatively higher level of precision than the ANS in infancy (e.g., Antell & Keating, 1983; Cordes & Brannon, 2009b; Kobayashi et al., 2005; Jordan et al., 2008). Evidence of increasing precision in the ANS across development (e.g., Lipton & Spelke, 2003, Halberda & Feigenson, 2008) also indicates that, particularly in infancy, ANS representations are somewhat unreliable. Thus, object files may simply provide infants with a more reliable means for tracking objects, and as such, have evolved to be the preferred system for representation for small sets.

Consistent with this precision hypothesis are cases in which infants succeed in small-large discriminations following experimental manipulation of the relative precision of the two systems. The handful of cases in which infants have been shown to succeed on small-large discriminations of visual sets generally fall under two categories of circumstances: either (1) stimuli are presented in such a way as to allow ANS representations to provide reliable, clear information (Cantrell & Smith, 2013; Cantrell et al., submitted; Cordes & Brannon, 2009a) or (2) object file representations are made less reliable by taxing working memory (Hyde & Spelke, 2011; Starr et al., 2013a; Wynn, Bloom, & Chiang, 2002).

(1) Signal clarity of the ANS

When numerical information tracked via the ANS can provide a clear, reliable signal, ANS representations may predominate over the object-file system. That is, young infants may fail to compare small and large sets on the basis of number when sets differ by a 2-fold ratio (i.e., 3 vs. 6 or 2 vs. 4; Cordes & Brannon, 2009a; Xu, 2003), yet this may be because this ratio change in number is near the limits of their ability to discriminate. Thus, while the ANS may be able to detect a change in number, the signal is fairly weak and unreliable, resulting in reliance upon precise object files in this case. In contrast, 7-month olds have been shown to successfully compare numbers across the small-large boundary when the sets vary by a four-fold change in magnitude (i.e., 1 vs. 4 or 2 vs. 8; Cordes & Brannon, 2009a). That is, when provided a greater ratio of numerical change, the ANS unequivocally detects the change and produces a clear strong signal that overrides the information provided by object files representations. A similar pattern has been found for at least one non-human species (guppy, *Poecilia reticulata*). Piffer et al. (2011) demonstrated that guppies can succeed at a comparison between large numbers (5 vs. 10), small numbers (3 vs. 4), but not small-large comparisons close in magnitude (3 vs. 5). However, increasing the distance between the small and large numbers resulted in successful discrimination across the small-large boundary (3 vs. 6, 3 vs. 7, 3 vs. 9; Piffer et al., 2011). Results such as these have been explained in terms of the signal strength of the ANS. In particular, it is posited that ANS magnitudes trump object file ones when the magnitude of the ratio between the small and large set exceeds some threshold criterion, such that ANS representations provide strong, clear, and precise information regarding changes in set sizes (Cordes & Brannon, 2009a).

Similarly, when numerical stimuli are designed in such a way as to present numerical information with reduced noise by providing redundant perceptual information across displays, numerical discrimination is facilitated across the small-large divide (Cantrell et al., submitted; Cantrell & Smith, 2013). Cantrell et al. (submitted) habituated 9-month-old infants to arrays of 2 or 4 items in which, unlike standard practice in the field of numerical cognition (i.e., Xu & Spelke, 2000), continuous quantitative variables such as surface area, density, and contour, were held constant throughout habituation (i.e., in Xu & Spelke's design, infants were habituated to displays containing the same number of dots (e.g., 8), yet surface area of the dots varied dramatically (5-fold) across habituation; in contrast, in Cantrell et al's design, both surface area and number remained constant across habituation). When numerical information co-varied with continuous perceptual information in habituation, infants successfully discriminated between arrays of 2 and 4 items, and in a second experiment, between arrays of 3 and 4 items. Importantly, the change in cumulative surface area from habituation to test was significantly smaller than has been shown to be detectable by infants of this age (1:2 or 2:3 ratio; Cordes & Brannon, 2008a, 2011), indicating that increases in infant looking time must have been partly accounted for by an attention to numerical changes in their task. That is, consistent with the Signal Clarity Hypothesis (Cantrell & Smith, 2013), redundancy in number and other continuous dimensions across habituation reduced noise in the infants' ANS representations, allowing for the formation of a strong, clearer signal. In contrast to studies in which continuous variables varied throughout habituation (e.g., Cordes & Brannon, 2009 a, b; Xu, 2003; Xu et al., 2005), Cantrell and colleagues (submitted; Cantrell & Smith, 2013) posit that infants in their study were sensitive to statistical information during habituation, resulting in a lower noise-to-signal ratio. This clearer signal allowed them to pick out the relevant numeric properties of the stimuli more quickly and discriminate much smaller ratios than previously demonstrated, especially those that cross the small-large boundary (e.g., 2 vs. 4, 3 vs. 6; Cordes & Brannon, 2009a, b; Xu, 2003; Xu et al., 2005). In a similar vein to the finding of successful discrimination of greater ratios crossing the small-large boundary (Cordes & Brannon, 2009a), the precision of infants' representations appear to vary as a function of the clarity of the information provided by the numerical displays.

(2) Taxed working memory

Alternatively, when individual items within a small set become difficult to track via object files, ANS representations may become the default system for infants' numerical representations. Data indicate that the memory demands of a given task may influence recruitment of the ANS for tracking small sets (also see Mou & vanMarle, 2013). Hyde and Spelke (2009, 2011) found that infants' and adults' neural signatures of processing small (<4) versus large (≥4) numerical arrays were best characterized by the object file and approximate number systems, respectively. But, importantly, neural signatures associated with the ANS were obtained when processing small sets in the context of high memory load requirements (Hyde & Wood, 2011). According to Hyde (2011), when items are presented under conditions that allow individuation, they are represented as distinct mental items, not as numerical magnitudes; however, when items are presented outside one's attentional limits (e.g., too many, too close together, display time too brief, high memory or attentional load, etc.), they are represented as mental magnitudes (e.g., Burr, Anobile, & Turi, 2011; Burr, Turi, & Anobile, 2010; Hyde & Wood, 2011; Piazza et al., 2002, 2003). To this end, this system is affected by the limits of attention and working memory, suggesting the object file system is automatically recruited for numerical discriminations when representing exclusively small sets for visual stimuli low in cognitive load, but does not remain a "default" when small numbers are presented outside the limits of the brain's ability to encode them precisely and accurately (Hyde, 2011; Hyde & Wood, 2011; see also Mou & vanMarle, 2013). Similar to the proposal that object files are automatically recruited for the representation of small sets unless there is a clear ANS signal for small quantities (Cantrell & Smith, 2013; Cordes & Brannon, 2009a), data from Hyde and colleagues likewise suggest the ANS may be used to represent small quantities when attentional and working memory manipulations degrade the precision of the object-file system.

Consistent with this view, Starr et al. (2013a) found that 6-month-old infants successfully discriminate sets of 2 from 4 using a change-detection paradigm. This paradigm, originally designed to assess working memory in infancy (Ross-Sheehy, Oakes, & Luck, 2003), involves presenting infants two side-by-side movies simultaneously. One movie (the non-changing display) shows images containing the same number of items (e.g., 4 items), but changing in surface area, density, contour, and configuration every 500 ms. The second movie (the changing display) is similar, except displays alternate between two set sizes (e.g., sets of 2 and 4) every 500 ms. yet continuous extent continues to vary across displays, making it an unreliable cue for discrimination. The assumption of the change detection paradigm is that infants prefer to look to things that change, and thus will preferentially attend to the numerically changing display *if they detect the numerical changes involved* (Libertus & Brannon, 2010). Because change detection paradigms require infants to recognize a change in number across rapidly changing and dynamic visual images, this particular paradigm is thought to tax working memory to a greater extent than standard habituation paradigms, making it difficult to attend to individual items within each set and limiting the recruitment of object files (Starr et al., 2013a). In fact, across all numerical comparisons tested using this paradigm to date (1 vs. 3, 1 vs. 2, 2 vs. 3, 2 vs. 4 plus larger sets e.g., 10 vs. 20), infants' performance exhibits ratio-dependence (Starr et al., 2013a; Libertus & Brannon, 2010), the signature of the ANS. These findings, consistent with Hyde's (2011) hypothesis, suggest that different working memory demands may selectively recruit the ANS (during high cognitive load) over the object file system (Hyde, 2011; Hyde & Wood, 2011; Mou & vanMarle, 2013; Starr et al., 2013a; Wynn, Bloom, & Chiang, 2002).

In sum, although human infants demonstrate striking failures to discriminate between small (<4) and large (>3) sets, the few circumstances under which they have succeeded in doing so are consistent with the idea that infants employ ANS representations for small sets when (1) ANS signals are strong and (2) object file signals are weak, such as when working memory is taxed. Thus, it appears that ANS and object files can both simultaneously be used to represent small sets, but it is the relative precision (i.e., signal strength) of the two systems that determines which system will drive responses. At least in infancy, it appears that object files generally provide a stronger clearer signal over the ANS, resulting in a greater reliance upon this system for representing small sets. We next turn to the question of when, and importantly, *how,* during the course of development, we overcome this dependency on the object file system for representing small sets, such that older children reliably discriminate small from large sets without error.

Overcoming the small-large divide

Despite the fact that infants typically fail to discriminate between small and large sets early in infancy, ample evidence demonstrates that children and adults do not. The earliest reported evidence of reliable discrimination of 2 from 4 visual items (without taxing working memory) is 3 years of age (e.g., Cantlon, Safford, & Brannon, 2010). So, how is it that, over the course of early human development, young children overcome the discrimination difficulties posed by the two-system interaction? Almost no research has examined the development of this understanding in toddler-hood (i.e., between 15-35 months; but see Barner, Thalwitz, Wood, Yang, & Carey, 2007; see also Mou & vanMarle for a review). This section considers the ontongenetic continuity of this representational interaction by addressing how children eventually come to reliably discriminate small sets from large ones. We propose two noncompeting hypotheses regarding the mechanism(s) responsible for this change over the course of development: (1) children's acquisition of numerical language and (2) increasing precision in the ANS.

Children's acquisition of numerical language

One observable cognitive change between infancy and early childhood is the acquisition of language, and, specifically relevant to the current discussion, the acquisition of numerical language. Several distinct lines of research suggest that children – at approximately 2 years of age – have begun to learn the number word list, and have begun to understand the cardinal meanings associated with the first few words in the list (e.g., Condry & Spelke, 2008; Gallistel & Gelman, 1992; Wynn, 1990, 1992). Additionally, at this same time, children begin to appropriately use the plural form of nouns around 22-24 months of age (Barner et al., 2007). Thus, it is quite possible that this newly acquired ability to talk about small and large set sizes using a common system - number words - may facilitate thinking about these numbers as belonging to a common integrated system. In fact, the idea that the way we talk about number impacts numerical abilities is not a new one; it has long been reported that differences in the way number is referred to within a language (spoken or signed) may promote (or hinder) the acquisition of other numerical abilities (e.g., Geary, Bow-Thomas, Liu, & Siegler, 1996; Miller & Stigler, 1987; Leybaert & Van Cutsem, 2002). On this linguistic account, children may develop an ability to represent small and large sets via yet another representational system – verbal language.

One line of research suggests children's developing understanding of singular and plural sets expressed through numerical language may foster success on small-large discriminations, particularly on 1 vs. 4 comparisons. Barner et al. (2007) found that children succeed in discriminating exclusively small sets (1 vs. 3) between the ages of 14- to 18-months, but could not yet compare sets such as 1 vs. 4 at this age (e.g., Feigenson & Carey, 2003, 2005). However, around 22-24-months of age, children begin to succeed in these discriminations, with the timing of this coinciding with the onset of plural word production in spoken language. The authors posit that the ability to verbally express the distinction between a single item ("a") compared to many items ("some") provides cues to children as to how many items are being enumerated (Barner et al., 2007; Wood, Kouider, & Carey, 2009). Thus, the researchers suggest that the child's developing singular-plural morphology aids them in making a previously difficult discrimination by making the distinction between the sets more salient to them (Barner et al., 2007; Li, Ogura, Barner, Yang, & Carey, 2009). Although a positive correlation exists between the acquisition of plural nouns and children's successes in certain small-large discriminations, it is not the entire story. That is, 22-24 month olds, who have begun to produce plural nouns, continue to fail on 2 vs. 4 numerical discriminations (Barner et al., 2007), suggesting that the singular/plural distinction alone cannot account for the acquisition of the ability to compare small and large sets.

Instead of highlighting the use of plural vs. singular nouns, children's abilities to successfully compare small and large sets during toddler-hood and early childhood may be the result of the acquisition and use of number words – and, eventually, an understanding of the cardinalities associated with those words. Children begin to produce number words at approximately 2 years of age (Wynn, 1992), yet just as young children can recite the alphabet before they can read or write, young children can count out loud before they understand what those number words really mean (e.g., Condry & Spelke, 2008; Gallistel & Gelman, 1992; Wynn, 1990). In time, though, children come to understand the meaning behind those number words that they can recite out loud, and, more importantly, they learn that reciting those words in sequence (i.e., counting) constitutes a reliable strategy for determining the cardinality of a set ("the Cardinal Principle;" Gelman & Gallistel, 1978). In this regard, verbal counting may provide children with an alternative and exact system for representing small and large numbers alike along a single continuum, allowing them to bridge the gap between salient preverbal representation systems. Thus, numerical language may provide a third integrated and reliable system for representing number that children begin to rely upon when tracking differences among set sizes.

Importantly, it should be pointed out that although the acquisition of the count list does generally coincide with the onset of small-large discrimination successes (roughly around 3 years of age for both; e.g., Cantlon et al, 2010; Le Corre & Carey, 2007), more data are necessary to determine the viability of this account. If this is the case, then small-large discrimination successes should correlate with counting abilities, and moreover, providing linguistic support in the form of counting during small-large discrimination tasks should promote performance on these tasks. These are questions for future research.

Increasing precision in the ANS across development

Although children's acquisition of numerical language may afford them an alternative form of representation by which to learn about numbers, it may also be the case that improvements in precision in the ANS may allow them to overcome discrimination failures across small and large sets. In fact, one of the most recognized changes in the way we process numerical information between infancy and childhood – and even into adulthood – is the increasing precision of the ANS. Newborns can discriminate a 3-fold change in number (e.g., Izard et al., 2009), 6-month olds a 2-fold change (e.g., Xu & Spelke, 2000), 9-month olds a 1.5-fold change (Wood & Spelke, 2005), 3-year olds a 1.3-fold change, and so on, such that adults generally discriminate a 1.14-change in number (Halberda & Feigenson, 2008). Importantly, consistent with the modality-independence of the ANS, a similar developmental change in precision has been observed for numerical information presented in the auditory domain (Barth, La Mont, Lipton, & Spelke, 2005; Barth et al., 2006; Barth, Spelke, & Beckmann, 2007; Lipton & Spelke, 2003, 2004). This increasing precision over the course of development, coupled with the idea that signal strength may contribute to the pattern of successes and failures observed for small-large discriminations in infancy, support the idea that increased precision may result in stronger signal strength of the ANS, leading to a greater reliance upon the ANS for comparing small and large sets in the preschool years.

Although ample evidence suggests that the ANS increases in precision into adulthood – both across sensory modalities and possibly across species (see Anderson & Cordes, 2013 for review) – the mechanisms driving these changes are not fully understood. Research reveals that ANS training can lead to improvements in precision, suggesting more generally that children's repeated use of the ANS contributes to this improvement. ANS acuity has been demonstrated to improve with practice in adulthood and in children with mathematical difficulties (DeWind & Brannon, 2012; Wilson, Dehaene, Pinel, Revkin, Cohen, & Cohen, 2006). Moreover, ANS training may even selectively improve symbolic exact addition and subtraction (Hyde, Khanum, & Spelke, 2014; Park & Brannon, 2013), indicating that enhanced ANS acuity may acutely boost performance for some types of formal mathematics problems. Training has also been shown to improve ANS acuity in guppies (*Poecilia reticulate*; Piffer, Miletto, Petrazzini, & Agrillo, 2013). Moreover, controlled experiments with guppies have also shown that ecologically salient environmental factors may similarly influence precision of the ANS across development, such that guppies (*Poecilia reticulate*) raised in large social groups are able to discriminate a 1:2 ratio change in large sets earlier than those raised in pairs (Bisazza et al., 2010), suggesting that more than just acute training may impact precision of the ANS. In sum, although much research already suggests that training and other experiences can lead to enhancements in ANS acuity, more work is needed to determine the potential lasting support this may have on the developing ANS.

To conclude, evidence suggests that the ANS is less salient early in development and that early tracking of small sets in the visual domain may defer to the object file system, with the ANS emerging as the dominant system of number representation with age, maturation, and even experience. Furthermore, recent research suggests that ANS acuity is fairly malleable, such that training paradigms improve not only ANS acuity itself, but also performance on tests of symbolic arithmetic. Although data to date do not distinguish whether ANS acuity training may be the source of the developmental change observed in small-large discriminations, future research should explore this possibility.

Open questions and future directions

In sum, a robust pattern of failures to discriminate small from large sets has been documented, supporting claims that infants have access to two distinct systems for representing number. Evidence suggests that, like children, adults, and non-human animals, infants eventually overcome this incompatibility of representations when ANS representations of small sets are given priority over object file ones. Little research to date, however, has explored when and how children overcome this incompatibility but we have proposed two potential mechanisms to account for this developmental change; namely, (1) numerical language (offering a third, alternative form of representing number along an integrated continuum) and (2) increased precision of the ANS (resulting in a stronger ANS signal and decreased reliance on object files). To conclude, we pose some open questions and future directions to further explore the circumstances contributing to small-large discrimination successes in infancy and early toddlerhood.

What parameters help infants succeed at small-large comparisons?

Evidence from infants' successful discrimination of exclusively small sets may shed light on future avenues of investigation. Specifically, evidence for successful discrimination of exclusively small sets (1-3 items) from infant looking-time studies (for review see Cantrell & Smith, 2013) comes primarily from paradigms in which numerical information is presented cross-modally (e.g., Feron, Gontaz, & Streri, 2006; Kobayashi et al., 2005; Jordan & Brannon, 2006; Starkey, Spelke, & Gelman, 1983, 1990) or when infants use item-specific cues, such as perceptual variability, to individuate the items to be enumerated (Feigenson, 2005). For example, researchers found that 6-month-olds expect the number of sounds of an object dropping when hitting the stage to match the number of objects seen behind an occluder (Kobayashi et al., 2005), while 5-month-olds successfully discriminated a difficult ratio (2:3) in a cross-modal transfer task between tactile and visual information (Feron et al., 2006). Similarly, 7-month-olds tracked number across the small number range when items were heterogeneous (i.e., varying in color, pattern, texture), but not homogeneous (i.e., all the same shape and color), suggesting the item variability may also facilitate infants' discrimination of small numbers (Feigenson, 2005; Tremoulet, Leslie, & Hall, 2001; Wilcox, 1990). Stimulus heterogeneity similarly has been shown to enhance 3-10 year old children's numerical discrimination performance, (Posid, Huguenel, & Cordes, in preparation; but see Cantlon, Fink, Safford, & Brannon, 2007). Together, data suggest that cross-modal input and perceptual variability in the form of set heterogeneity may in fact facilitate an early attention to number and thus selectively recruit the ANS for abstract numerical representation. Future research should examine the impact of these two variables on infants' abilities to compare small and large sets. Moreover, if cross-modal input and perceptual variability promote attention to numerical differences, then large number discriminations may also be enhanced under these conditions, such that infants may successfully discriminate finer ratios than found with visual sets alone.

Is the small-large incompatibility receptive to feedback or training?

Finally, another avenue for future research examining the small-large divide in infancy is to examine how training of the ANS may impact young toddler abilities to discriminate small from large. If it really is the case that increased ANS acuity is the driving force behind children's increasing reliance upon ANS representations (resulting in successful small-large comparisons), then earlier improvements in the ANS should promote earlier acquisition of small-large discriminations. If it is possible to shape ANS acuity as early as infancy, then this may provide a clear way to identify whether ANS acuity is the mechanism of change in the observed pattern of small-large discriminations across development.

Conclusions

We have considered the question of phylogenetic and ontogenetic continuity of the two-system hypothesis for representing quantities and specifically addressed the issue of how and under what circumstances children come to exclusively rely on the ANS for numerical comparisons. Consistent with data revealing an early reliance on the object-file system in human infant studies, we posit that the ANS may be suppressed for the visual tracking of a small number of items relative to the object file system, but eventually emerges as the dominant system for tracking and representing number with increasing age, maturation, and experience. We discussed evidence suggesting that when the ANS is invoked to represent small sets, infants generally succeed in discriminating small and large sets, including much finer ratios than previously demonstrated (Cantrell et al., 2013). Finally, we proposed some open questions and future directions for distinguishing between these accounts, in order to clarify when and how infants may distinguish between small and large sets, and what mechanisms may facilitate this distinction.

This review demonstrates parallels in the way that numerical information is processed across phylogeny and ontogeny. The importance of this line of research has been highlighted recently be several studies indicating that the ability to precisely discriminate sets of items predicts math achievement across the lifespan, even when assessed as early as infancy (e.g., Halberda & Feigenson, 2008; Libertus et al., 2011, 2012, 2013; Lyons & Beilock, 2009, 2011; Starr et al., 2013b; but see De Smedt et al., 2013).

Importantly, this relationship appears to be causal, such that approximate number training improves some aspects of formal mathematical processing (e.g., Park & Brannon, 2013). Therefore, numerical abilities as they appear in infancy may facilitate some aspects of children's formal mathematics learning and competence. If this is the case, understanding how infants successfully attend to number and why they may not be able to do so under certain circumstances may shed light on the origins of one potential preverbal precursor to formal mathematical abilities.

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