Numerosity representation is encoded in human subcortex

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Certain numerical abilities appear to be relatively ubiquitous in the animal kingdom, including the ability to recognize and differentiate relative quantities. This skill is present in human adults and children, as well as in nonhuman primates and, perhaps surprisingly, is also demonstrated by lower species such as mosquitofish and spiders, despite the absence of cortical computation available to primates. This ubiquity of numerical competence suggests that representations that connect to numerical tasks are likely subserved by evolutionarily conserved regions of the nervous system. Here, we test the hypothesis that the evaluation of relative numerical quantities is subserved by lower-order brain structures in humans. Using a monocular/dichoptic paradigm, across four experiments, we show that the discrimination of displays, consisting of both large (5–80) and small (1–4) numbers of dots, is facilitated in the monocular, subcortical portions of the visual system. This is only the case, however, when observers evaluate larger ratios of 3:1 or 4:1, but not smaller ratios, closer to 1:1. This profile of competence matches closely the skill with which newborn infants and other species can discriminate numerical quantity. These findings suggest conservation of ontogenetically and phylogenetically lower-order systems in adults' numerical abilities. The involvement of subcortical structures in representing numerical quantities provokes a reconsideration of current theories of the neural basis of numerical cognition, inasmuch as it bolsters the cross-species continuity of the biological system for numerical abilities.

subcortex | numerical cognition | vision | development | phylogeny

Humans exhibit remarkable mathematical abilities. Many of today's students readily master difficult mathematical constructs, the knowledge of which is based on the very early developing appreciation of numerosity. In the adult human brain, the parietal cortex plays a central role in the representation and processing of number. More specifically, in many neuroimaging studies, bilateral intraparietal sulcus has been implicated in numerical tasks such as exact calculation and arithmetic problem solving (1–6), and additional evidence for the necessary role of parietal cortex comes from patients who exhibit selective number-processing deficits following a parietal lesion (7, 8). A finer division between the hemispheres suggests that the left and right parietal cortices themselves exhibit relative specialization; the right parietal cortex appears to be engaged to a greater extent in more intuitive numerical approximation (2, 9, 10), whereas the left parietal cortex is engaged to a great degree in more precise arithmetic or symbolic mathematical tasks (1, 3, 11). Furthermore, the connectivity between the two hemispheres is correlated with performance on nonsymbolic arithmetic tasks (12). Thus, areas of the parietal cortex appear to play a critical role in mathematical abilities. The cortex, however, is far from mature at birth and follows a developmental trajectory that coincides with developing number skills in growing children (13).

The ontogenetic emergence of numerical skills follows a reasonably well-established trajectory with an initial ability to approximate numerical quantity nonverbally, followed, over the course of early childhood, with the development of increasingly precise representations of numerical values, including a symbolic number system that allows children to conceive of numerical information as Arabic numerals or number words (14–16). The

early ability to distinguish two nonsymbolic quantities, for example, in the context of a display of varying numbers of dots potentially forms the foundation for developing math abilities akin to the "number sense" (17). This suggests that our analog number system is best described as one that tracks relative quantities, and that it can be bootstrapped during schooling when more discrete mathematical abilities are acquired (but see ref. 18). In the earlier stages of development, the number system is thought to operate with rather coarse representations, and differentiation of nonsymbolic quantities is largely dependent on ratios (19). As development proceeds, however, the system becomes more finely tuned to smaller differences in quantities. Consistent with this, infants as young as 48 h are able to differentiate ratios of 3:1 but not 2:1 (20), and, as they age, children show increasingly precise abilities: at 6 mo, they can distinguish ratios of 2:1, and by 9 mo, ratios of 3:2 (21, 22). They eventually reach competencies for ratios 4:3 by 3 y, 6:5 by 6 y, and 8:7 and more difficult ratios by adulthood (23–26). Furthermore, the ability to discriminate nonsymbolic number in childhood is predictive of later numerical discrimination abilities (27, 28).

There has been long-standing debate regarding the origins of these numerical abilities. Some have suggested that the endowment of a number system is innate and present from birth (29). Evidence to support this claim comes from studies showing that young children (22, 30–32) and adults in cultures without any training in mathematics (33–35) perform many numerical tasks with ratios of sufficiently large numbers independent of controlled nonnumeric properties such as size or density. Similar

Significance

Despite major neuroanatomical differences, adults, infants, nonhuman primates, and invertebrates possess the ability to evaluate relative quantities. Humans' ability starts with coarse granularity (distinguishing ratios of numerical quantities of 3:1 or larger), but this becomes increasingly precise over development. This series of experiments demonstrates a role of the subcortex in discriminating numerosities in larger (4:1 or 3:1), but not in smaller ratios. These findings map onto the precision with which newborns evaluate number. Combined with evidence from the development of numerical skills, this study implicates the human subcortex as a possible source of core number knowledge that is both related to phylogenetic numerical competence and serves as the foundation on which more complex ontogenetic numerical skills may be built.

abilities have been noted in nonhuman primates (36, 37), and the presence of age- and species-invariant number ability suggests that the core knowledge, which underlies coarse numerical processing, may be ontogenetically and phylogenetically conserved in primates.

Even more surprising, different species of fish also appear to have coarse number representations. Mosquitofish can perform various numerical tasks including picking larger shoals (38), choosing more companions (39) or mates (40), or discriminating larger quantities (41), and guppies have been shown to differentiate ratios with levels of precision similar to that of undergraduate college students (42). Moreover, number processing is not restricted to vertebrates as both honeybees (43) and spiders (44) possess some ability to process number, as well. Taken together, the evidence from the nonprimate literature suggests that the ability to process number may be relatively ubiquitous in the animal world. Of interest, these numerical feats are accomplished by animals without well-developed cerebral cortices, and the intraparietal sulcus (see ref. 45), heavily implicated in human and nonhuman primate numerical cognition (15, 46, 47), is entirely absent in some of these species. Number processing in these species, therefore, likely relies on older, more evolutionarily conserved regions of the nervous system. Of interest, analogously, computational models provide evidence that visual number judgments are possible even with relatively small networks (48, 49).

One candidate region that might serve the phylogenetic bridge is human subcortex, a region largely neglected in contemporary research of numerical cognition. The involvement of subcortical structures in coarse numerical representation provokes a reconsideration of current theories of number perception, which are reliant on cortical-level processing, inasmuch as it bolsters the cross-species continuity of the biological system for numerical knowledge. In the current work, we hypothesize the presence of a coarse subcortical number processor that makes contributions to numerical processing, independently of cortex, thereby serving as the link between lower- and higher-order species. Specifically, we expect the subcortical mechanism to respond selectively to nonsymbolic quantities (here, dot arrays) given that symbolic manipulation of quantities is uniquely human and likely requires cortical contributions. Moreover, we predict that subcortical contributions to number processing will be ratio dependent as young children evince numerical abilities that are themselves ratio dependent (20–22).

To explore the possible contribution of subcortical structures to number processing in humans, we exploit a psychophysical method that allows us to differentiate between cortical vs. subcortical, monocular visual signals before layer IV of primary visual cortex (50–52). Before this layer, the monocular signals of the visual system are propagated by separate sets of neurons, but beyond layer IV, signals from each eye are no longer segregated, and, because there are relatively few monocular neurons beyond area V1, activation of extrastriate areas is not eye dependent (52). The current work takes advantage of this prestriate separation of signals. We report data from four experiments using a Wheatstone stereoscope (Fig. 1) in which we evaluate performance of judgments on two (numerical) stimuli presented sequentially to the same eye (monocular presentation) relative to two stimuli presented sequentially to different eyes (dichoptic presentation). Any differences in performance in the monocular over dichoptic conditions can be interpreted as arising as a function of the prestriate, subcortical system.

The first experiment involved participants making same–different identity judgments on sequentially presented stimuli, and examined, at the outset, whether a difference in monocular vs. dichoptic conditions was evident for dot displays, number forms, or false font number forms. In light of the observed performance advantage for dot displays under monocular vs. dichoptic conditions, the next two experiments required participants to make numerosity judgments (number of dots comparison) with displays
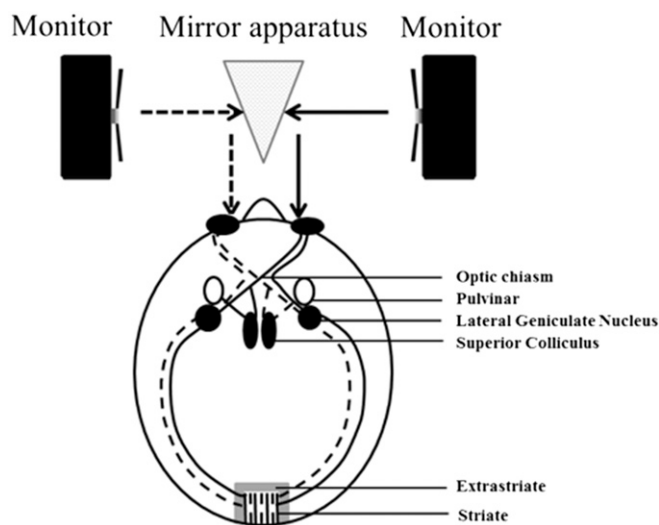

Fig. 1. A schematic depiction of the experimental apparatus and visual pathways from the eyes to the brain. Each monitor delivers visual information to a different eye. The visual information first passes through monocularly segregated subcortical regions (left eye, dashed lines; right eye, solid lines), which is then projected to the pulvinar, lateral geniculate nucleus (LGN), and superior colliculus en route to the striate and then dichoptic extrastriate regions. Reprinted with permission from ref. 76.

of larger (range, 10–32 dots; experiment 2) and smaller (subitizing range, 1–4 dots; experiment 3) numbers of dots. The final, fourth experiment replicates and confirms the previous findings but does so equating response probability for ratio on each trial. Together, these experiments elucidate the ratio-dependent nature of monocular, subcortical contributions in human adults.

Experiment 1

This experiment tests the hypothesis that the subcortex contributes selectively to the processing of stimuli containing nonsymbolic numerical information but not to the processing of symbolic numerical stimuli [Arabic numerals (Num)] or to nonnumeric stimuli [false fonts, made from scrambled recombined elements of Arabic numerals (Snum)]. This hypothesis follows from the intuitive notion that complex symbol manipulation is relatively unique to the human species and that if the proposed subcortical mechanism does indeed link humans to other species, especially lower-order species, with respect to number processing, the mechanism should be specific to nonsymbolic forms of number. In this experiment, two displays, which were either the same or different, were presented sequentially to the same eye or dichoptically, with the first display to one eye and the second display to the other eye. In both conditions, the first eye was selected to be left or right with equal probability, and trials from the two conditions were randomly interleaved. Participants made a two-alternative forced-choice decision using one of two keys. A schematic of the task procedure is shown in Fig. 2A.

Regarding task difficulty, the overall median accuracy and RT were 97.9% and 635 ms. The results from this experiment are summarized in Fig. 2B. We used inverse efficiency (IE) as the dependent variable because the task likely affects both accuracy and reaction time (RT). Additionally, participants may make speed/accuracy trade-offs such that one measure would not completely describe the effects induced by the manipulation (note also that accuracy itself is high in almost all conditions). The IE score (expressed in milliseconds) is equal to the mean RT divided by the proportion of correct responses, calculated separately for each condition and each participant. Lower values on this measure indicate better performance (53).
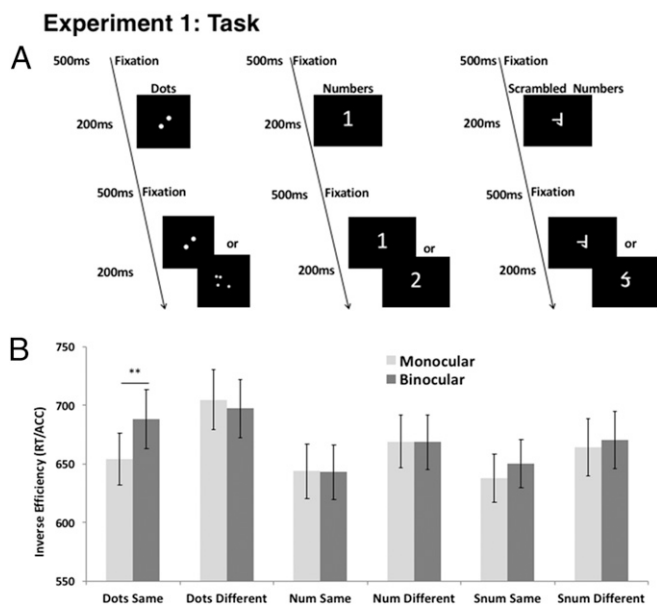
Experiment 1: Task

Fig. 2. (A) A schematic depiction of the procedure in experiment 1. Each trial consisted of two stimuli that were sequentially presented either monocularly or dichoptically. Stimuli consisted of dots, Arabic numerals, or scrambled numbers. Participants were instructed to indicate whether the stimuli were identical or not using a binary button response. (B) Experiment 1 results: Mean IE as a function of identity for dots, number forms (Num), and scrambled numbers (Snum). Error bars reflect 1 SE. Lower values indicate better performance. **$P = 0.001$.

Mauchly's test indicated that the assumption of sphericity was valid [$X^2_{(2)} = 0.82$; $P = 0.66$] in this experiment. A repeated-measures ANOVA conducted with stimulus type, identity (same/different), and ocularity (monocular/dichoptic) as within-subject factors revealed a significant three-way interaction [$F_{(2,60)} = 3.67$ and $P = 0.03$]. There was also a significant identity by ocularity interaction [$F_{(1,30)} = 4.49$; $P = 0.04$], but not a stimulus type by ocularity interaction [$F_{(2,60)} = 2.34$; $P = 0.10$]. There were significant main effects of stimulus type [$F_{(2,60)} = 4.54$; $P = 0.01$], identity [$F_{(1,30)} = 12.1$; $P = 0.002$], and a marginally significant effect of ocularity [$F_{(1,30)} = 3.37$; $P = 0.07$]. There were marginally significant three-way interactions when using accuracy, $F_{(1.67,50.1)} = 2.40$; $P = 0.10$ [sphericity violated, $X^2_{(2)} = 8.48$; $P = 0.01$; Huynh–Feldt correction, $\varepsilon = 0.83$], or RT, $F_{(2,60)} = 2.86$; $P = 0.07$ alone [sphericity valid, $X^2_{(2)} = 1.65$; $P = 0.43$]. See Fig. S1 A and B.

Further analysis of the data within stimulus type and between identity (as shown in Fig. 2B) revealed the source of the interactions described. Pairwise comparisons between conditions showed that only when the sets of dots were the same was a monocular advantage observed [$t_{(30)} = 3.51$; $P = 0.001$; Cohen's d = 0.25]. There was no reliable monocular facilitation for any of the other conditions: incongruent dots [$t_{(30)} = 0.94$; $P = 0.35$; d = 0.05], congruent Num [$t_{(30)} = 0.11$; $P = 0.911$; d = 0.01], incongruent Num [$t_{(30)} = 0.10$; $P = 0.92$; d = 0.004], congruent Snum [$t_{(30)} = 2.04$; $P = 0.05$; d = 0.10], and incongruent Snum [$t_{(30)} = 0.57$; $P = 0.57$; d = 0.04].

This experiment demonstrates a selective monocular advantage when participants judged the identity of the dot array stimuli presented sequentially to the same eye vs. different eyes in a same/different judgment task. The effect was not present for Arabic numerals or their false-font counterparts.

One obvious explanation for these findings is that the monocular advantage simply results from an identity priming effect and is unrelated to numerical processing: the representation of the input is primed in the subcortical pathway, and, thus, reactivation of the

same pathway by the identical stimulus results in a performance advantage. However, this does not account for the specificity of the results—the monocular advantage was obtained only for the dots and not for the other stimulus types. The specificity of the finding indicates that it is not stimulus repetition per se that gives rise to the monocular advantage; rather, it is the repeated representation of the dot displays that support the facilitation. Taken together, the results suggest that subcortical structures selectively contribute to the processing of stimuli containing nonsymbolic quantity information.

Experiment 2

Thus far, the evidence favors the representation of some properties of dot displays in the monocular visual pathway before striate cortex. In this next experiment, we evaluated whether this representation of the dot displays contains information that can be used to judge numerosity. Also, consistent with the claim that a coarse representation of quantity might be present in lower-order structures, we might expect to see a ratio-dependent effect with greater monocular facilitation for discriminating larger ratios, which require less precision, than smaller ratios. Because many of the findings noted in the Introduction separate large and small quantities (in the subitizing range and beyond the subitizing range), we first test this hypothesis in displays with large numbers of dots, ranging from 8 to 32. A schematic of the task, again using monocular vs. dichoptic presentation, is shown in Fig. 3A. Participants made an explicit evaluation of numerosity by indicating which of two sequentially presented displays contained more dots and indicated their decision using a binary button response. Dot displays contained 8, 11, 16, 22, or 32 dots.

Regarding task difficulty, the overall median accuracy and RT were 96.7% and 543.9 ms. The results are summarized in Fig. 3B. Mauchly's test indicated that sphericity was violated [$X^2_{(9)} = 23.6$; $P < 0.01$], and therefore, the degrees of freedom were corrected in the linear model using Huynh–Feldt correction ($\varepsilon = 0.80$). A repeated-measures ANOVA with ratio and ocularity (monocular/dichoptic) as

Experiment 2: Task

Fig. 3. (A) A schematic depiction of the procedure in experiment 2. Each trial consisted of displays containing two dots that were sequentially presented either monocularly or dichoptically. Participants were instructed to indicate whether the first or second dot display contained more dots using a binary button response. (B) Experiment 2 results: Mean IE as a function of dot ratio. Error bars reflect 1 SE. Lower values indicate better performance. *$P < 0.05$.

within-subjects factors and IE as the dependent measure revealed a significant two-way interaction [$F_{(3.2,80)} = 2.73$; $P = 0.04$]. There was a main effect of ratio [$F_{(2.7,80)} = 115.6$; $P < 0.001$], but no main effect of ocularity [$F_{(1,20)} = 0.001$; $P = 0.97$]. There was no interaction when using either RT, $F_{(4,80)} = 2.02$; $P = 0.09$ [sphericity valid, $X^2_{(9)} = 11.99$; $P = 0.21$], or accuracy, $F_{(2.66,53.2)} = 1.15$; $P = 0.33$, alone [sphericity violated, $X^2_{(9)} = 22.6$; $P < 0.01$; Greenhouse–Geisser correction, $\varepsilon = 0.66$]. See Fig. S2 *A* and *B*.

Further analysis of the data between monocular and dichoptic trials within each ratio revealed a significant monocular advantage for displays with the ratio of 4:1 [$t_{(20)} = 2.39$; $P = 0.02$; d = 0.13], but not with ratios of 3:1 [$t_{(20)} = 1.10$; $P = 0.28$; d = 0.03], 2:1 [$t_{(20)} = 1.69$; $P = 0.10$; d = 0.03], 1.4:1 [$t_{(20)} = 1.03$; $P = 0.31$; d = 0.09], or 1.3:1 [$t_{(20)} = 1.6$; $P = 0.30$; d = 0.08].

When participants were required to evaluate the relative numerosity of two dot arrays outside the subitizing range, they demonstrated a ratio-dependent monocular advantage. Evaluating larger ratios, close to 4:1, revealed better performance under monocular than dichoptic presentation, whereas the evaluation of relatively smaller ratios did not reflect a monocular advantage. Furthermore, this experiment replicated previous findings showing that relative number judgments are easier with larger ratios, and become increasingly difficult as the ratios approach 1:1, potentially indicating a noisy representation of numerosity on a mental number line (14).

These results advance our understanding of the contribution of a subcortical mechanism to numerosity judgments in human adults. Namely, the monocular facilitation is not based on a simple (perceptual) representation of the dot displays but, rather, entails the representation of quantity that permits computations that obey ratio-dependent constraints. These findings were obtained with displays that contained quantities beyond the subitizing range. Because recent evidence suggests that ratio effects might also be found in number evaluations regardless of the range of numbers used (54), the third experiment explores whether similar subcortical facilitation with larger vs. smaller ratios of displays holds when the dot displays contain quantities in the subitizing range.

Experiment 3

If the computation supported by human subcortex is related to that performed by other species, one would expect facilitation for both larger and smaller numbers because other nonprimate species do evince ratio-dependent effects for both small and large numbers (38, 40, 42). In this experiment, participants performed the same task as in experiment 2, but with arrays with small numbers (one to four) of dots. In addition, because participants were able to detect the exact numerosity of one to four dots, we added trials in which participants were required to report whether the number of dots in the first display was the same as in the second display (in addition to trials where the two arrays differed in numerical quantity). The presence of these trials prevented participants from developing a boundary strategy in which they could determine the answer based on the first stimulus alone (e.g., if participants know that the first array contained one dot, the second array would always have more dots). Thus, participants made a three-way forced number evaluation (first display more/second display more/same on both displays) on each trial. These "same" trials, used to prevent the boundary strategy, were excluded from the analysis. A task schematic is shown in Fig. 4*A*.

Regarding task difficulty, the overall median accuracy and RTs were 95.8% and 678.3 ms. The results of experiment 3 are summarized in Fig. 4*B*. Mauchly's test indicated that sphericity was valid [$X^2_{(9)} = 10.4$; $P = 0.31$]. A repeated-measures ANOVA with ratio and ocularity (monocular/dichoptic) as within-subject factors revealed a significant two-way interaction [$F_{(4,72)} = 5.29$;
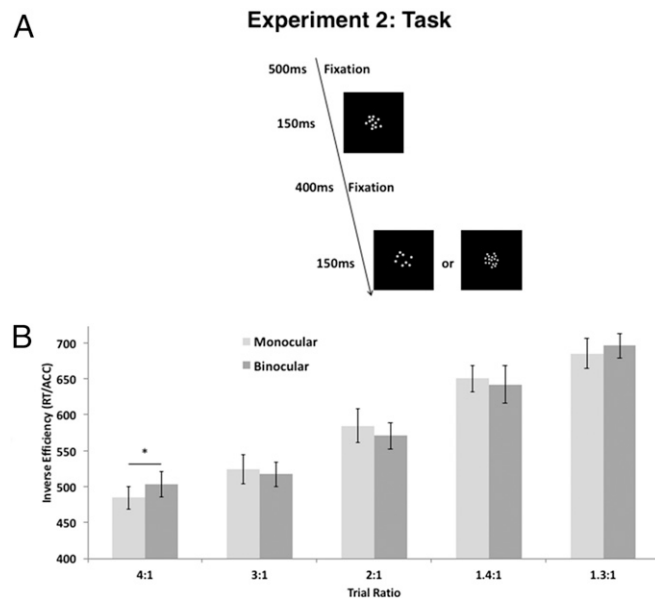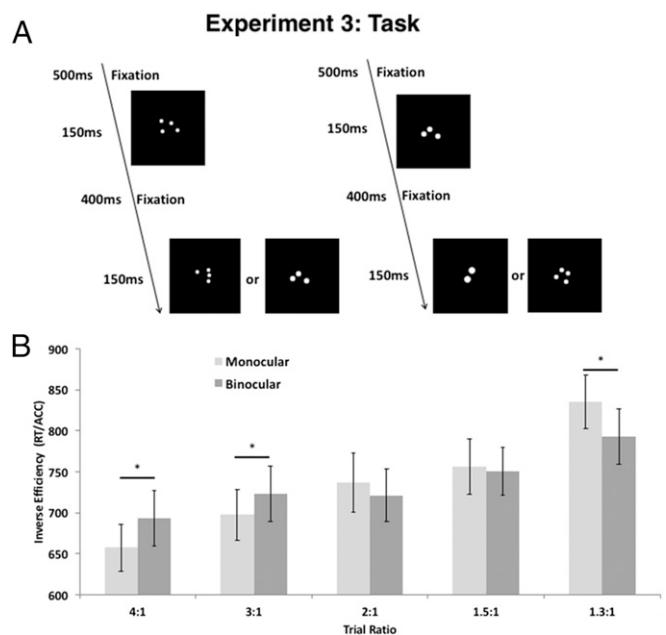

Fig. 4. (*A*) A schematic depiction of the procedure in experiment 3. Each trial consisted of displays containing two dots that were sequentially presented either monocularly or dichoptically. Participants were instructed to indicate whether the first or second dot display contained more dots (*Right*), or whether the two stimuli contained the same number of dots (*Left*) using a three-way button response. (*B*) Experiment 3 results: Mean IE as a function of dot ratio. Error bars reflect 1 SE. Lower values indicate better performance. *$P < 0.05$.

$P = 0.001$]. There was a main effect of ratio [$F_{(4,72)} = 35.4$; $P < 0.001$], with better performance for large than small ratios, but no main effect of ocularity [$F_{(1,18)} = 0.01$; $P = 0.92$]. There was no interaction when using accuracy alone, $F_{(4,72)} = 1.67$; $P = 0.16$ [sphericity valid, $X^2_{(9)} = 4.71$; $P = 0.58$], but was when using RT alone, $F_{(4,72)} = 3.65$; $P < 0.01$ [sphericity valid, $X^2_{(9)} = 7.55$; $P = 0.58$]. See Fig. S3 *A* and *B*.

Further analysis of the data within each ratio and between monocular and dichoptic trials revealed a significant monocular advantage for displays with ratios of 4:1 [$t_{(18)} = 2.30$; $P = 0.03$; d = 0.25] and 3:1 [$t_{(18)} = 2.18$; $P = 0.04$; d = 0.17], but not with smaller ratios of 2:1 [$t_{(18)} = 1.6$; $P = 0.12$; d = 0.10] or 1.5:1 [$t_{(18)} = 0.48$; $P = 0.64$; d = 0.04]. Somewhat surprisingly, in this study, the ratio of 1.3:1 had a significant dichoptic advantage [$t_{(18)} = 2.27$; $P = 0.03$; d = 0.27], a finding that is difficult to interpret and is not observed in any other experiment.

Experiment 3 replicates and extends the findings from experiment 2. Namely, participants exhibited monocular facilitation when evaluating larger, but not smaller, ratios. Here, the effect was found with the same ratio (4:1) as in experiment 2 and with a 3:1 ratio, but with numbers in the subitizing range (one to four dots).

Together, experiments 2 and 3 show that subcortical contributions to the processing of numerosity of dot displays, as reflected by the monocular facilitation, occur in both the subitizing and nonsubitizing ranges and that the facilitation is ratio dependent. Several studies have documented ratio effects in the subitizing range (55–59), but others have found ratio effects only with larger numbers (22, 42) and the emergence of these effects may be experiment- or task-dependent (54). Our findings corroborate previous research showing that ratio effects exist for numerosities both within and beyond the subitizing range, and, in the context of this particular experimental approach, the subcortex appears to represent ratio-dependent numerosity for the evaluation of both small and large numbers.

Experiment 4

In the previous experiments, participants made quantity judgments on displays containing numerosities randomly and equiprobably drawn from a fixed set of numerosities (e.g., 8, 11, 16, 22, or 32 in experiment 2). Thus, the probability of a specific response (e.g., choosing that the first array contains more dots) coincided with the numerical ratio and with the numerosity of the first array itself. For instance, if the first array contained 11 dots (although note that participants were unlikely to apprehend the exact numerosity), there was a higher probability of having a 3:1 ratio (if the second array contains 32 dots) and a higher probability of having "first array contains more" as the correct answer, compare with the case in which the first array contained 16 dots.

It remains a possibility, therefore, that the particular behavioral pattern found only in larger ratios might have been driven by this idiosyncratic stimulus arrangement. Although we have no reason to believe that this particular arrangement would selectively affect only the monocular condition (and not the dichoptic condition), we designed the final experiment such that both responses (first display more/second display more) were equally probable on all trials and for all ratios. Here, the first stimulus always contained 20 dots, whereas the second stimulus contained either a smaller (5, 7, 10, or 15) or larger (27, 40, 60, or 80) number of dots. Each possible second display of dots occurred with equal probability. The procedure was identical to that in experiments 2 and 3. A schematic of the two types of trials is shown in Fig. 5A.

Regarding task difficulty, the overall accuracy and RT were 91.1% and 641 ms. Ratios were calculated using the same approach as in previous experiments. All trials with the same ratio value were analyzed as part of the same condition (for example, trials in which 10 and 40 dots appeared after 20 dots were analyzed under the same ratio condition, 2:1). The results are summarized in Fig. 5B. Mauchly's test indicated that sphericity had been violated ($X^2_{(5)} = 51.6$; $P < 0.01$), and therefore the degrees of freedom in the linear model were corrected using Greenhouse–Geisser estimates of sphericity ($\varepsilon = 0.46$). A repeated-measures ANOVA with ratio and ocularity (monocular/dichoptic) as within-subject factors revealed a nonsignificant two-way interaction [$F_{(1.4,39)} = 2.27$; $P = 0.16$]. There were main effects of both ratio [$F_{(1.4,37)} = 223.3$; $P < 0.001$] and ocularity [$F_{(1,28)} = 9.18$; $P = 0.005$]. There was a trend toward an interaction when using accuracy alone, $F_{(2.13,59.88)} = 2.44$ and $P = 0.09$ [sphericity violated $X^2_{(5)} = 18.5$; $P < 0.01$, Greenhouse–Geisser corrected ($\varepsilon = 0.77$)] and was an interaction when using RT alone, $F_{(3,84)} = 4.69$ and $P < 0.01$ [sphericity valid, $X^2_{(5)} = 2.59$; $P = 0.76$]. See Fig. S4 A and B.

In light of our predictions and the data obtained in earlier experiments, we broke down the trending interaction, as we have done above. Further analysis of the data within each ratio and between monocular and dichoptic trials revealed a significant monocular advantage for ratios of 4:1 [$t(28) = 3.66$; $P = 0.001$; $d = 0.23$] and 3:1 [$t(28) = 2.20$; $P = 0.03$; $d = 0.18$], but not for ratios of 2:1 [$t(28) = 0.32$; $P = 0.75$; $d = 0.01$] or 1.3:1 [$t(28) = 1.94$; $P = 0.06$; $d = 0.27$]. As we elaborate below, the presence of monocular facilitation for the large, but not small, ratio conditions is consistent with the findings of the previous experiments. One unexpected finding was the nearly significant monocular advantage for trials with the ratio of 1.3:1. This effect was not seen in any of the previous studies and does not quite reach statistical significance here. In fact, the opposite findings were obtained in experiment 3: a dichoptic advantage for the same ratio of 1.3:1, but in the subitizing range. Given that this finding did not replicate, and because the opposite result was observed in another experiment, we are not confident of its reliability or interpretation, in contrast with the clear replication of the monocular advantage for large ratios revealed over multiple experiments. However, further research using the paradigm from this experiment will clarify the pattern of monocular facilitation and its dependency on a larger Weber fraction in the subcortex.

Considering that numerosity of a dot array is necessarily correlated with nonnumerical cues of the array, it is worth questioning to what extent the judgments of numerosity may have been driven by the processing of nonnumerical cues as opposed to the processing of numerical information, a notion strongly advocated by a few authors (60, 61). In recent work, an innovative approach has been developed to provide a statistical test of the effects of numerical and nonnumerical magnitudes on behavior or on neural activity (62–65). These studies have demonstrated a large effect of numerosity and minimal, if any, effects of nonnumerical cues (such as surface area, sparsity, or spacing) on behavioral measures of numerosity judgment or on neural activity evoked by passively viewing dot arrays of a wide range of numerosities with no explicit task demands on magnitude. Along with a computational demonstration that an artificial neural network model designed to achieve efficient coding of sensory data successfully retrieves numerosity information as a statistical property of the visual scene (48), these previous empirical findings suggest that it is unnecessary, and even faulty, to assume that numerical information must be derived from nonnumerical information. Most critically, even if nonnumerical cues substantially influence numerosity judgment, such a fact cannot explain the current finding that judging numerosities is selectively facilitated in the monocular, but not dichoptic, condition.

Nevertheless, we conducted an additional analysis on the data from experiment 4 to determine the contribution of each of the magnitude dimensions to participants' behavioral performance on numerosity judgments. Following the analytic approach developed to address this point (64), we modeled each participant's choice behavior as a function of number and of two dimensions orthogonal to number, namely, size and spacing. Size conceptually refers to the dimension that varies in both the surface area
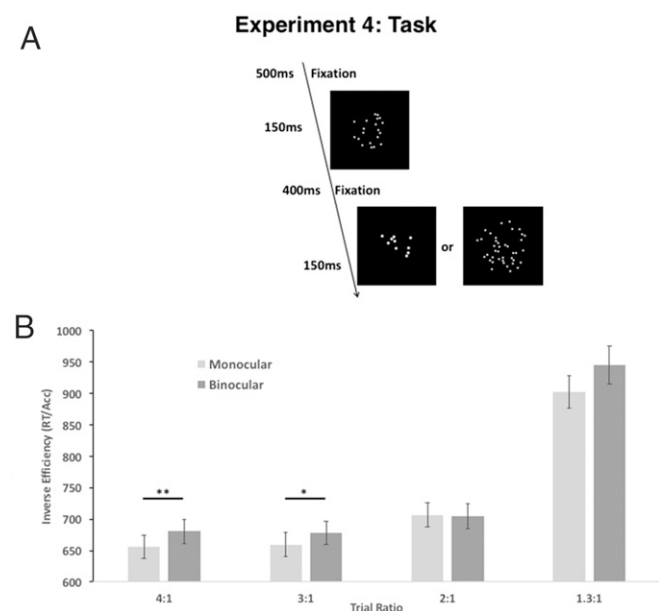
Fig. 5. (A) A schematic depiction of the procedure in experiment 4. Each trial consisted of displays containing two dots that were sequentially presented either monocularly or dichoptically. Participants were instructed to indicate whether the first or second dot display contained more dots using a binary button response. (B) Experiment 4 results: Mean IE as a function of dot ratio. Error bars reflect 1 SE. Lower values indicate better performance. **P = 0.001, *P < 0.05.

of each dot within an array and the total surface area of the array, while holding number constant. Spacing conceptually refers to the dimension that varies in both the density of the array and the area of the invisible circular field within which the dots are drawn (close to convex hull), while holding number constant. Critically, number, size, and spacing make up three orthogonal dimensions, and many nonnumerical dimensions typically discussed in the literature can be expressed as a linear combination of the three dimensions. Thus, besides number, size, and spacing, at least seven nonnumerical dimensions can be expressed as a function of those three dimensions: total perimeter, total surface area, individual surface area, field area, sparsity, coverage, and apparent closeness (see ref. 64 for precise mathematical definitions and derivations of the choice model). After estimating the degree to which number, size, and spacing influence each participant's choice behavior (b_{number}, b_{size}, and $b_{spacing}$ respectively), these β estimates were created to form a β vector for behavior. Then, by calculating the angle between each participant's β vector and the unit vector along numerical and nonnumerical dimensions, we assessed which stimulus dimension best explained behavior (Fig. S5).

We calculated bootstrapped confidence intervals (10,000 samples) on the mean angle, in degrees, between the behavioral β vector and each of nine stimulus parameter vectors across all subjects. This analysis was done separately for monocular and dichoptic trials, and then for all trials together. For monocular trials, analysis yielded the following 95% confidence intervals (in degrees from β vector): number (7.02, 11.0), total perimeter (19.3, 22.6), total surface area (43.9, 47.6), individual surface area (43.9, 47.3), field area (47.8, 53.2), sparsity (37.2, 42.5), coverage (82.5, 85.4), apparent closeness (82.2, 86.0), size (84.9, 87.2), and spacing (80.4, 84.4). For dichoptic trials, analysis yielded the following 95% confidence intervals: number (6.72, 10.1), total perimeter (18.6, 22.6), total surface area (46.1, 50.4), individual surface area (40.2, 44.6), field area (44.1, 48.9), sparsity (41.7, 46.6), coverage (83.4, 86.4), apparent closeness (82.6, 85.1), size (83.1, 86.2), and spacing (83.0, 86.4). For all trials together, analysis yielded the following 95% confidence intervals: number (5.37, 8.31), total perimeter (20.2, 24.5), total surface area (45.2, 48.6), individual surface area (42.0, 45.3), field area (46.2, 50.1), sparsity (40.3, 44.2), coverage (84.9, 87.2), apparent closeness (83.8, 86.5), size (84.8, 87.1), and spacing (83.7, 86.5). In each of these three analyses (monocular, dichoptic, all trials), the mean behavioral vector was closest to the number vector and this angle was clearly smaller than between the behavioral vector and any other stimulus parameter vector. Furthermore, the behavioral vector for every single participant was closest to number. In summary, this analysis clearly shows that the stimulus parameter that best explains the participants' behavior is number, and it does so better than any of the nine other stimulus parameters.

In summary, experiment 4 provides an additional replication of the findings from the previous experiments, in which monocular facilitation was evident for larger but not for smaller ratios. This experiment demonstrated that this monocular advantage held regardless of the probability of a given response. Furthermore, this experiment extended the upper bound of the range of quantities used in previous experiments, from 32 to 80 confirming the generality of the finding across a large range of display sizes. Finally, we confirmed that participants' choices were best explained by number and not by nonnumeric continuous stimulus parameters.

General Discussion
The aim of the current study was to explore the extent to which the adult human subcortex contributes to number processing, specifically numerical quantity evaluation, as measured by performance differences in monocular vs. dichoptic processing in

the context of a stereoscopic experiment. There is mounting evidence demonstrating that children, nonhuman primates, and some lower-order animals, as well, are able to execute numerosity evaluations. Given the difference in brain structures between these groups, some of whose neural structures bear little resemblance to those of adult humans, we hypothesized the existence of a lower-order representation of number, whose homolog might account for the seeming universality of number abilities, and we speculated that the human subcortex might play this role.

The first experiment documented a selective monocular advantage for stimuli containing nonsymbolic numerical information (dot arrays), but not for symbolic number forms or for nonnumeric stimuli. The second experiment revealed that the monocular facilitation with displays of numbers of dots where the quantity falls beyond the subitizing range is ratio dependent: discrimination of numerosity in a larger, 4:1, ratio, but not smaller ratios, elicited the monocular facilitation. The third experiment replicated and extended the findings, again showing facilitation for large ratios but using arrays of dots that fall within the subitizing range. The final experiment replicated, once again, the results from earlier experiments but with displays of dot arrays containing a larger range of numbers, and confirmed that the monocular advantage is present regardless of the exact probabilities of the responses required by the observer, independent of the extent to which participants learned the statistical properties of the responses and independent of any nonnumeric continuous stimulus parameters. Collectively, these experiments uncover the presence of a coarse, ratio-dependent, number-processing system present in the monocular portion of the visual system.

One possible inconsistency in our findings was the significant monocular advantage for identical dot stimuli in the first experiment (ratio equal to 1), but the monocular advantage for large ratios only on subsequent experiments (and not with ratios close to 1). There may be a number of reasons for this difference. There were differences in task instructions between the experiments (number vs. identity evaluation) so participants may have not been specifically tuned to number in the first experiment (for "same" condition, the same stimulus was shown twice). Thus, the pattern of monocular advantage may have been influenced by the task itself (54). Also, there may have been a ratio effect in the first experiment for "different" numbered dot trials, but the experiment contained so few trials of each ratio that such an analysis was not feasible. Moreover, an analysis of the ratio of 1:1 was not possible on subsequent experiments given that there were very few or no trials with such ratio.

We have suggested that the neural mechanism that supports the finding of a monocular advantage might lie in prestriate regions of the visual system, in which the neurons maintain their eye-specific, monocular segregation, before cortex. However, layer 4 of area V1 is composed of some monocular neurons, as well, and so, an alternative possibility is that the results emerge from V1 itself rather than from prestriate subcortical regions. In fact, a recent scalp-electroencephalography study revealed an extremely early-latency encoding of numerical information of a dot array in the visual stream, potentially implicating the role of V1 in numerosity perception (62). Nevertheless, we think this V1 explanation is unlikely in the current study for a host of reasons. The ratio-dependent effect we report is also present in more primitive species, some of whom do not have cortex per se. Also, that the monocular facilitation is observed for the dot patterns but not for other visual stimuli may reflect the greater sensitivity of subcortical structures to low spatial frequency inputs (compared with number form or false font: experiment 1), reflecting the known signature of the subcortical system (66) rather than that of monocular neurons that occupy layer 4 of V1. Indeed, the monocular advantage conferred by the subcortex may even result from propagating low-spatial-frequency information to cortical

number processing or decision making areas, although this appears to be specific for nonsymbolic number stimuli. Last, given what is known about V1, representation of the perceptual patterns of numerals and false number images might also have produced facilitation but this was not the case. In light of the above, the pattern of findings is highly compatible with the function of a prestriate, subcortical structure. Obviously, in the context of this experiment, it is not possible to tag which specific subcortical structure(s) are implicated, and, indeed, this is difficult to do in humans: even functional magnetic resonance imaging, used prolifically to establish brain–behavior relations, is inadequate given the small size and the depth of the various subcortical structures (67).

The findings from this study uncover the contribution of a subcortical number system in human adults. The extent to which this system participates in any of the other (multiple) forms of numerical computation (such as arithmetic) and the relationship between the observed subcortical facilitation and cortical processes remain to be determined. However, several possible alternatives exist. One possibility is that the monocular advantage and its subcortical neural correlate might act independently of cortex, perhaps as an evolutionary vestige, that plays no real functional role in more complex number processing. A second possibility is that, at least in human adults, such computations serve a functional role and signals from these prestriate regions are then propagated for later cortical processing.

An additional (not mutually exclusive) possibility is that this coarse subcortical system plays a key role in the development of number processing during childhood. Our findings demonstrate that facilitation of number processing occurs in a coarse or approximate fashion and that only ratios of 3:1 or 4:1 elicited a reproducible monocular advantage. This same coarse-grain number evaluation was found in infants only 48 h old (20). From just after birth, infants appear able to make cross-modal number evaluations that were also ratio dependent. Using looking time as their dependent measure, Izard et al. (20) found that infants could distinguish quantities whose ratio was at least 3:1, but not smaller. Relatedly, human subcortex has been implicated in these types of cross-modal object detections (68). The presence of such coarse number processing in children suggests that more complex numerical abilities are likely not innate (29) and are certainly not adult-like and, thus, a more basic approximate system such as the one we propose might serve as the basis of the rudimentary skills exhibited by the infants. In line with this idea, a recent developmental electroencephalography study reports little evidence for cortical involvement of numerosity processing in very young children and rather that the cortical mechanism for numerosity perception develops gradually throughout childhood (65). Thus, the numerosity competence of the subcortical mechanism might serve to bootstrap cortical mechanisms early in development.

A similar bootstrapping explanation has been offered for the face-processing skills observed in infancy (for review, see ref. 69). A well-known account of face processing (70) posits two processes: the first is a predisposition in newborns to orient toward faces (termed CONSPEC; face detection, subcortical system), and the second is an acquired specialization for other aspects of face processing (termed CONLEARN; face recognition and processing, cortical system). Although the CONSPEC system may bootstrap cortex and play a disproportionate role in childhood, coarse face-specific representations can still be uncovered in subcortical regions in adulthood (71). The numerosity evaluation ability documented here may be akin to the CONSPEC mechanism in that a rudimentary, evolutionarily conserved system that computes coarse properties of the input may suffice and may be mediated by subcortical systems. The coarse signals computed by these lower-order structures are then propagated to cortex and serve as the training signal for more precise cortical CONLEARN processes, likely resulting

in the well-established contribution of parietal cortex to mathematical skills. The ratio-dependent sensitivity to numerosity of the subcortical system, although key during development, may still be uncovered in adults and may contribute functionally.

Although the evidence presented here does not localize number representation in the subcortex or identify a specific mechanism, it is worth noting that, even when V1 is inactivated, visual input from the superior colliculus can activate neurons in the dorsal visual stream (72, 73). The direct connection of the subcortex to areas of parietal cortex, perhaps even bypassing V1, strongly supports a functional relationship between these two regions and may reflect a candidate conduit through which cortical bootstrapping may occur. A specific instantiation of this might be as follows: there may be coarsely tuned eye-specific numerosity-sensitive neurons in the prestriate visual pathway that propagate number information further up the visual pathway to higher-level number processing areas in parietal cortex. A stimulus could activate prestriate neurons tuned to a specific number and adjacent numbers. Then a second numerical stimulus, if sufficiently smaller or larger (in number) than the first, might activate a second set of neurons independent from the first, thereby enhancing the contrast between stimuli in the prestriate visual regions (the bigger the difference, the stronger the contrast resulting in the ratio effects). This enhanced numerical contrast can then be propagated up to higher-order number processing and decision-making areas of cortex, resulting in monocular facilitation. The same instantiation, may or may not involve primary visual cortex, which has been implicated in number processing previously (62). This mechanism can account for the pattern of results obtained from adult participants and the theoretical pattern of development discussed above. However, this mechanism does not rule out additional mechanistic explanations. If the developmental relationship between subcortex and cortex in the number domain posited here is similar to that in the face domain as described by Johnson (69), the subcortex may serve as the source upon which more general representation or knowledge is constructed across the course of development.

In conclusion, the current set of experiments shows that, in the context of a stereoscopic setting, the adult human subcortex computes quantity, which results in facilitated numerical judgments. This facilitation exhibits ratio dependence and generalizes to both small and large quantities. The numerical representations in the subcortex uncovered here may relate to the ontogenetic developmental knowledge of number and the ubiquitous number knowledge across phylogeny.

Materials and Methods

Our Approach. The current work uses a Wheatstone stereoscope (Fig. 1) to deliver stimuli (such as displays of dots or of number forms). This approach induces the perception of a single, "fused" image when stimuli are presented dichoptically and the participant does not know in which eye the signal originated (74, 75). Because participants do not know in which eye the signal originated, this approach allows us to present sequential stimuli in the same eye or in two eyes separately without the participant perceiving a difference. The logic is as follows: the participants' performance is contrasted under two conditions: first, when two stimuli (for example, two displays containing dots) are presented sequentially to the same eye in a row (monocular condition). In the dichoptic condition, two sequential stimuli are presented to one eye followed by the other eye. If performance is better when the sequential stimuli are presented to a single eye than when stimuli are presented to different eyes, termed "monocular advantage," we can infer neural processing in the monocular portion of visual pathway mediated by subcortical regions. This monocular vs. dichoptic approach has already yielded interesting findings, revealing, for example, better matching of faces, but not of cars or words, under monocular vs. dichoptic conditions (76, 77). Using the same approach, support for subcortical computation has also been uncovered in the domains of perceptual learning (77), spatial attention (78), and multisensory perception (79).

Experiment 1.

Participants. Participants (*n* = 31; female, 20; left-handed, 3; age: mean = 22.6, SD = 8.5) had normal or corrected-to-normal vision and consented to participate in exchange for course credit or payment according to the protocol approved by the Institutional Review Board at Carnegie Mellon University (Institutional Review Board number 00000352).

Stimuli. Stimuli consisted of displays containing one through four dots (Dots), Arabic numerals (1–4) (Num), or scrambled Arabic numerals (Snum) (Fig. 2*A*). The scrambled Arabic numerals were made by extracting the component features of Arabic numerals 1 through 4 and rearranging them such that the resulting stimuli no longer resembled a number but the spatial frequency and number of edges were retained. Both the Num and Snum stimuli were ∼1.91 visual degrees in width and 2.86 visual degrees in height. Numeric dot stimuli contained arrays of one, two, three, or four nonoverlapping dots. The size of individual dots was homogeneous within an array but ranged between 0.27° to 0.53° in diameter across arrays. These dots were randomly drawn within an implicit, invisible circle that ranged between 1.49° and 2.98° in diameter. The minimum distance between any two dots within an array was one-third of the dot diameter. Importantly, these arrays were designed to span equal ranges of numerical and nonnumerical properties (in logarithmic scale) in three orthogonal dimensions: number, size, and spacing, whereby size refers to the surface area of the dots while holding number constant and spacing refers to overall interdot distance while holding number constant. This dot array construction scheme (first introduced in refs. 62 and 64) allows parsing the effects of numerical and nonnumerical visual properties in explaining variations in behavioral performance or neural activation patterns. We used this scheme to provide comparable variations to numerical and nonnumerical properties, although it should be noted that size and spacing of dot arrays show almost negligible influence on behavioral and neural responses to number perception (77, 78). All stimuli were presented on a black background.

Procedure. The same procedure was used across all experiments. The participant's head was stabilized with the aid of a chin and head rest. Two mirrors, one at 45° and one at 135°, each reflecting one of two monitors (55 cm from left or right side of observer), were placed in front of the participant (Fig. 1). Two cardboard dividers were attached to the chin/head rest, blocking the participant's direct view of the monitors, so that the display was only visible in the mirror. Where necessary, before the experiment, the stereoscope was adjusted slightly for each participant to ensure that the images presented to the two eyes separately were perceived as a single, fused image. To achieve this, we presented displays of either "+"s or dots to the two eyes simultaneously and asked two participants how many "+"s or dots they saw. We also asked participants to report on the sharpness of the images. If participants reported an incorrect numbers of "+"s or dots, or endorsed double vision, we modified the angle of the mirrors by a degree or two to ensure fusion.

Experiment 1 included 576 trials, over the course of six blocks. Each trial started with a 500-ms fixation on both monitors, then a 200-ms stimulus presentation of a single display on one monitor followed by a 500-ms interstimulus fixation on both monitors, and then the final stimulus appeared for 200 ms (Fig. 2*A*) on a single monitor. Participants were instructed to maintain fixation on the fused cross throughout the experiment. On each trial, two stimuli were presented sequentially: on one-half of the trials, both stimuli were presented to a single eye (equiprobably left or right) or to one eye and then the other (equal first display to right or left eye). Trials with different stimuli always differed with respect to number (of dots, or Arabic numeral, or scrambled number form). During the task, the participants evaluated whether the first stimulus was the same or different in identity as the second stimulus using a binary button response with their dominant hand. Participants completed 15 practice trials to get used to the button responses. Feedback, in the form of three small central red Xs, was given for incorrect trials only. The data for each subject were manually inspected and, for each condition, any correct trial with a RT greater or less than 2 SDs from the subject mean for that cell was removed from the analysis along with incorrect trials (average = 7.8% trials; SD = 2.6 trials).

Experiment 2.

Participants. A new group of participants (*n* = 21; female, 10; left-handed, 1; age: mean = 20.3, SD = 2.0) with normal or corrected-to-normal vision consented to participate using the same procedure as in experiment 1.

Stimuli. Stimuli were dot displays containing 8, 11, 16, 22, or 32 dots. As in experiment 1, the numerical and nonnumerical properties of these dot arrays were sampled from a 3D parameter space spanning number, size, and spacing. The size of individual dots ranged between 0.11° and 0.21° in diameter across arrays, and the dots were randomly drawn within an implicit, invisible circle that ranged between 1.28° and 2.56° in diameter. This design

allowed comparable variations in numerical and nonnumerical dimensions of the dot arrays. In creating pairs of stimuli for trials, each number was followed by each other number equally often (8v11, 8v16, 8v23, 8v32, 11v16, 11v23, 11v32, 16v23, 16v32, 23v32, vice versa). Within a trial, for each stimulus, the size of individual dots, and the field area containing the dots were randomly and independently generated, independent of the number of dots in either stimulus. Trial ratios were created by dividing the larger number by the smaller number. Trials with similar ratios were grouped together for analysis.

Procedure. The stereoscope apparatus was calibrated for each participant individually to ensure perceptual fusion for images presented on two screens. In the experiment, participants saw two stimuli presented sequentially, either monocularly to the same eye, or dichoptically to one eye followed by the other (Fig. 3*A*). The trial sequence was identical to that in experiment 1. Stimulus duration was 150 ms, and interstimulus interval was 400 ms. Stimulus duration was 50 ms shorter than in experiment 1 to make the task more difficult and to prevent preverbal counting, as has been done in other numerical tasks (80, 81). Importantly, unlike in experiment 1, a numerosity judgment task was used: participants explicitly evaluated whether the number of dots in the first stimulus or second stimulus was larger and indicated their response with a binary button press using their dominant hand. Participants completed 15 practice trials to get used to the button responses. Feedback, in the form of three small central red Xs, was given for incorrect trials only. Participants completed 576 trials, counterbalanced for number, ocularity, and screen order. Trials were randomized and divided into three blocks of 192 trials. Outliers were removed (average = 3.9%; SD = 0.4%) from the data using the same method adopted in the previous experiment.

Experiment 3.

Participants. A new group of participants (*n* = 19; female, 11; left-handed, 3; age: mean = 20.4; SD = 2.6) were recruited in the same manner as experiments 1 and 2, met the same criteria, and consented in the same way.

Stimuli. Stimuli in experiment 3 were identical to the dot stimuli used in the first experiment, with dot sets containing one, two, three, or four dots. Dot stimuli were constructed identically to experiment 1, except the dots were drawn within a slightly smaller invisible circle that ranged between 1.28° and 2.56° in diameter. In creating pairs of stimuli for trials, each number was followed by each other number equally often (1v2, 1v3, 1v4, 2v3, 2v4, 2v4, vice versa). Within a trial, for each stimulus, the size of individual dots, and the field area containing the dots were randomly and independently generated, independent of the number of dots in either stimulus. Trial ratios were created by dividing the larger number by the smaller number. Trials with similar ratios were grouped together for analysis.

Procedure. As in both previous experiments, the stereoscope apparatus was calibrated for each participant individually to ensure perceptual fusion for images presented on two screens. The trial sequence and structure were identical to that in experiment 2. Participants completed 576 trials for numbers 1–4, counterbalanced for number, ocularity, and screen order.

Because the numbers used in this experiment were within the subitizing range, participants completing the task could deduce the answer (more or less) based on the first stimulus if it contained one (can guess "more" for second stimulus) or four (can guess "less" for second stimulus) dots. To prevent this boundary strategy, the experiment included an extra 80 trials interspersed in the experiment in which the first and second stimuli both contained one or four dots. A similar approach has been taken previously (54). This required that the participant incorporate the second stimulus in a three-way decision (first display more/second display more/displays are equal) on each trial. Participants completed 15 practice trials to get used to the button responses. Feedback, in the form of three small central red Xs, was given for incorrect trials only. RT data were inspected and outliers removed using the same procedure as in previous experiments and, on average, 3.9% (SD = 1.4%) of trials were excluded from analysis. IE was then calculated for each cell (5 ratios × monocular/dichoptic).

Experiment 4.

Participants. A new group of participants (*n* = 29; female, 15; left-handed, 2; age: mean = 23, SD = 2.5) had normal or corrected-to-normal vision and consented to participate using the same procedure as in previous experiments.

Stimuli. As the goal of this experiment was to balance the probability of the response selection (or correct answer) at the individual trial level, participants were given a fixed "reference" numerical quantity as the first stimulus (always 20 dots) and the second "test" stimulus that was either smaller (5, 7, 10, or 15 dots) or larger (27, 40, 60, or 80 dots) than the first one. Across trials, the reference array contained 20 dots that ranged between 0.13° and 0.27° in diameter, which were randomly drawn within an invisible circle that ranged between 5.33° and 10.65° in diameter. The test arrays were

constructed so that, on one-half of the trials, the total surface area of all of the dots matched between the reference and the test arrays, whereas on the other half of the trials, the area of individual dots matched between the two arrays. Independently of this manipulation, on one-half of the trials, the density of the array matched between the reference and the test arrays, whereas on the other half of the trials, the area of the invisible circle encompassing the dots matched between the two arrays. Trials were balanced such that each test number (i.e., other than 20 dots) occurred equiprobably in the second stimulus of the trial.

Procedure. As in the previous experiments, the stereoscope apparatus was calibrated for each participant to ensure perceptual fusion for images presented on two screens. Trial structure and timing were identical to previous experiments. There were 720 randomized trials split into four blocks. Participants were instructed to evaluate the relative number of dots in the first and second stimuli, and report which stimuli contained more dots using a binary button response with their dominant hand. Participants completed 15 practice trials to get used to the button responses. Feedback, in the form of three small central red Xs, was given for incorrect trials only. Outliers (mean = 5.16%; SD = 1.65%) and RTs from incorrect trials were removed from the data using the method adopted in the previous experiments, and, again, IE served as the dependent measure.

Choice analysis. The regression of three orthogonal stimulus properties (number, size, and spacing) onto participant choice (described above) yielded β values for each subject. There was one outlier ($z > 5.0$) participant whose β values were replaced with the mean values for each cell. We conducted one-sample t tests on the β values for each stimulus property in monocular, dichoptic, and all trials. The analysis done on all trials yielded the following: number [$t_{(28)} = 18.07$; $P < 0.00001$; d = 3.35], size [$t_{(28)} = 1.76$; $P = 0.08$; d = 0.32], and spacing [$t_{(28)} = 2.71$; $P = 0.01$; d = 0.50]. The analysis done on monocular trials yielded the following: number [$t_{(28)} = 17.02$; $P < 0.00001$; d = 3.16], size [$t_{(28)} = 0.67$; $P = 0.50$; d = 0.12], and spacing [$t_{(28)} = 3.58$; $P < 0.01$; d = 0.66]. The analysis done on dichoptic trials yielded the following: number [$t_{(28)} = 15.88$; $P < 0.00001$; d = 2.95], size [$t_{(28)} = 2.06$; $P = 0.04$; d = 0.38], and spacing [$t_{(28)} = 0.87$; $P = 0.39$; d = 0.16]. The effect sizes from the above number contrasts show a large contribution of number to participant choice, and that this contribution is about an order of magnitude larger than those from stimulus size and spacing. In summary, the stimulus parameter that best explains participant choice during the experiment is number.

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