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Evolutionary foundations of number: spontaneous representation of numerical magnitudes by cotton-top tamarins

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Although animals of many species have been shown to discriminate between visual–spatial arrays or auditory–temporal sequences based on numerosity, most of the evidence for numerosity discrimination derives from experiments involving extensive laboratory training. Under these conditions, animals' discrimination of two numerosities depends on their ratio and is independent of their absolute value. It is an open question whether any untrained non-human animal spontaneously represents number in this way, as do human children and adults. We present the results of familiarization–discrimination experiments on cotton-top tamarin monkeys (*Saguinus oedipus*) that provide evidence for numerosity discrimination in the absence of training. Presented with auditory stimuli (speech syllables) controlled for the continuous variables of sequence duration, item duration, inter-stimulus interval and overall energy, tamarins readily discriminated sequences of 4 versus 8, 4 versus 6, and 8 versus 12 syllables. By contrast, tamarins failed to discriminate sequences of 4 versus 5 and 8 versus 10 syllables, providing evidence that their numerosity discrimination is approximate and shows the ratio signature of numerosity discrimination in humans and trained non-human animals. These results provide strong support for the hypothesis that representations of large, approximate numerosity are evolutionarily ancient and spontaneously available to non-human animals.

Keywords: number representations; primates; evolution; comparative evidence

1. INTRODUCTION

Research shows that human adults, children and infants form spontaneous representations of numerosity in both visual–spatial and auditory–temporal arrays, and that these representations are an important foundation for symbolic number and mathematics (Gallistel 1990; Dehaene 1997; Gallistel & Gelman 2000). For example, adults who are presented with arrays of dots or sequences of sounds under conditions that prevent or discourage verbal counting can reliably compare the arrays based on numerosity when continuous variables are controlled (Barth *et al.* 2003). Moreover, infants who are repeatedly presented with an array of dots or sequence of sounds of constant numerosity, but variable size or duration, show a decrease in their looking at that array or sequence and then recover their looking when numerosity changes (Xu & Spelke 2000; Lipton & Spelke 2003). Finally, when children and adults perform operations such as numerical comparison and addition on symbolically presented numerosities (Arabic symbols or words), they form representations of approximate numerical magnitudes that influence their performance (Dehaene 1997; Dehaene *et al.* 1999). In all these cases, numerosity representations are approximate and accord with Weber's Law: discriminability of two numerosities depends on their ratio and is independent of their absolute value.

Research with non-human primates suggests that the capacity for recursive, symbolic number representations is unique to humans; even though chimpanzees and parrots can learn symbols for small numerosities (Matsuzawa 1985; Pepperberg 1987; Boysen & Bernston 1989; Washburn & Rumbaugh 1991). However, they require extensive training to learn these symbols, and they fail to use the symbols productively, as humans do, to represent and operate on large numerosities. What is less clear, however, is whether non-symbolic numerical abilities are unique to humans or shared with other animals. Many non-human animals including pigeons, rats and monkeys have been shown to discriminate between visual arrays or motor sequences that differ in numerosity (Gallistel 1990; Dehaene 1997; Roberts 1997; Shettleworth 1998; Hauser 2000; Brannon & Terrace 2001). In almost every study in which animals have shown spontaneous discrimination in the absence of training, however, number was confounded with continuous variables such as total area or volume, and the continuous variables were, most plausibly, the basis of animals' responses (Hauser *et al.* 1996, 2000; Call 2000; Beran 2001; Beran & Rumbaugh 2001; Uller *et al.* 2001; Hauser & Carey 2003). For example, chimpanzees given the choice between two bowls of equal-sized chocolate chips will choose the bowl with more chips (Rumbaugh & Washburn 1993), but their choice probably results from a maximization of continuous quantities rather than number. Further, in studies that have controlled for continuous variables, and require animals to respond to number, extensive training is required, at least in the initial phase of the experiment (Olthof *et al.* 1997; Brannon & Terrace 1998; Roberts *et al.* 2000; Nieder *et al.* 2002). These findings have led some investigators to propose that non-human animals represent numerosity

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only as a last resort, and that such representations play little or no part in their normal behaviour (Davis & Perusse 1988).

It is possible, however, that animals represent both number and continuous quantities spontaneously, and that training serves only to indicate which quantitative variable is relevant to a particular task (Gallistel 1990; Hauser & Carey 1998; Gallistel & Gelman 2000; Hauser 2000). To distinguish between these accounts, it is crucial to devise situations in which a non-human animal's spontaneous number representations might be revealed. The only relevant study involving no training showed that cotton-top tamarins discriminate two-item from three-item sequences using speech syllables as habituating stimuli and pure tones as test stimuli (Hauser *et al.* 2002*a*). Although the stimuli used in these experiments were reasonably well controlled, it is difficult to be certain that responses to continuous variables were eliminated, because the change in auditory format (speech to tones) causes some problems in equating all the appropriate dimensions. Furthermore, these results do not illuminate the format of the tamarins' representations or its limits.

We report an experiment that satisfies both the methodological and theoretical requirements for assessing the nature and limits of spontaneous number representation. The experiment, on laboratory-reared cotton-top tamarins, uses a habituation–discrimination method similar to one that has been used extensively with human infants (Eimas *et al.* 1971) and that has served in past research on the tamarins' capacities for speech discrimination (Ramus *et al.* 2000; Hauser *et al.* 2001, 2002*b*). Using head orienting as a response, tamarins first were familiarized with sequences of speech syllables that varied in syllable type (e.g. 'ma' versus 'lu'), vocal pitch (e.g. high female versus low male voice), and duration, but that presented a constant number of syllables (e.g. four). Tamarins were then tested with new syllable sequences of equal duration, presenting either the familiar or a novel number of syllables. If tamarins spontaneously represented the number of syllables in the habituation sequence and discriminated between the two numerosities, they were expected to orient more frequently toward the speaker on trials presenting the novel numerosity.

To avoid the possibility of tapping mechanisms that are strictly involved in small-number quantification (Carey 2001), we focus on discrimination of quantities above four. In the first experiment, we presented numerical values where the difference ratio varied from 2.0 (four versus eight) to 1.25 (four versus five), to determine monkeys' discrimination thresholds at this range of numerical values. In the second experiment, we presented numerical values that were twice as large (eight and above), to test whether discrimination depends on the ratio difference in accord with Weber's Law.

2. MATERIAL AND METHODS

(a) *Subjects*

We tested adult cotton-top tamarins from a colony housed in the Primate Cognitive Neuroscience Laboratory, Harvard University. All animals were born in captivity and have been reared in social groups consisting of at least one breeding pair and up to two generations of offspring. The colony currently consists of 27 adults divided into seven social groups. Animals are fed once at the end of the day; the diet consists of marmoset chow, peanuts, sunflower seeds, fruit and yoghurt. Animals have *ad libitum* access to water throughout the day.

(b) *Stimuli*

We presented tamarins with Consonant–Vowel (CV) syllables obtained from three different speakers; one adult female, one adult male with an average-pitched voice and a second adult male with a low-pitched voice. We used CVs as stimuli because in our previous research (Hauser *et al.* 2001, 2002*a,b*) such stimuli elicited robust responses in the context of a habituation–discrimination procedure.

To ensure that subjects would respond to differences in number of CVs as opposed to some other continuous dimension, we followed the procedures described by Lipton & Spelke (2003) in their work on number discrimination in human infants. Table 1 provides an explicit description of the stimuli used in Condition 1 contrasting sequences of four versus eight syllables; all other conditions used the same controls and stimulus dimensions, but varied the numerical contrasts. During familiarization, we presented each subject with a total of eight different sequences of CV syllables, sampling different consonants and vowels, spoken by three speakers; the female and male with an average-pitched voice always contributed three CVs each, while the male with the low-pitched voice always contributed two CVs. The duration of CVs in the familiarization set ranged from a low of 172 ms to a high of 660 ms, while the inter-stimulus duration ranged from a low of 70 ms to a high of 150 ms. Because the durations of individual syllables and inter-stimulus intervals (ISIs) were equated for the sequences of four versus eight syllables, the latter sequences were more than twice as long (range of 1856–5962 ms) as the former (range of 895–2908 ms). For the test stimuli, we used three novel CVs, one each from the three speakers. Test sequences of four versus eight sequences were equated for total sequence duration, and so the individual syllables in the eight-item sequences were half the lengths of those in the four-item sequences (see table 1). These stimulus controls ensured that the change in number was not correlated with changes in any continuous variables such as sequence duration, item duration, item frequency or amount of acoustic energy.

(c) *Playback design*

For testing purposes, we removed subjects from their home cage, transported them to the test room and then transferred them to a test box inside an acoustic chamber. This testing setup has been used in previous work on tamarin communication (Ghazanfar *et al.* 2001; Weiss *et al.* 2001) and speech processing (Ramus *et al.* 2000; Hauser *et al.* 2001, 2002*b*). In brief, subjects sat in a test box with wire mesh in front and Plexiglas on all other sides. All stimuli were presented from a speaker placed up and to the left of the box, out of sight. Sessions were viewed from a monitor located outside the test chamber. Responses were scored online, video-recorded, and then later coded offline by new observers blind to condition. Inter-observer reliabilities across all conditions ranged from 0.86 to 0.95 based on coding by two or more trained observers of 20–30 different trials. In cases of disagreement between two observers, a third was called in to score the trial. If this third observer agreed with one of the other two, then the paired score was kept, otherwise the trial was excluded from the analyses.

As in our previous studies, we scored a response if subjects

Table 1. Stimulus dimensions for Condition 1: four versus eight.

(File names list the sex of the speaker followed by CV syllable. All temporal measures are in milliseconds; ISI, inter-stimulus interval.)

familiarization stimuli	duration	ISI
female-go	344	70
female-lu	489	140
female-ji	172	70
lowmale-di	554	110
lowmale-du	660	80
male-yo	616	150
male-ra	596	110
male-tu	255	80
test stimuli for four		
male-ba	616	—
female-mi	510	—
lowmale-ko	344	—
test stimuli for eight		
male-ba	308	—
female-mi	255	—
lowmale-ko	172	—

test file	energy duration	ISI	total ISI duration	total sign length
four-male-ba	2464	150	450	2914
eight-male-ba	2464	64	448	2912
four-female-mi	2040	150	450	2490
eight-female-mi	2040	64	448	2488
four-lowmale-ko	1376	150	450	1826
eight-lowmale-ko	1376	64	448	1824

Figure 1. Tamarin response to playback. Prior to playback, all subjects were stationary, looking down and away from the speaker located out of view, up, back and to the subject's left. A response was scored if the subject turned and looked back in the direction of the speaker. The numbers in the upper left-hand corner of each image correspond to frames in the sequence, with a frame rate of 30 frames sec^{-1}.

turned back and oriented toward the hidden speaker (figure 1). In less than 5% of all trials, the experimenter scored the trial as 'bad'. Such trials included cases where a subject was oriented toward the speaker at the time of playback or was jumping around when the playback was initiated. In an additional 5% of trials, the experimenter scored the response as 'ambiguous', meaning that it was not possible to provide an unambiguous 'yes' or 'no' response score; this typically occurred when a subject's face was occluded by part of the test apparatus or its orientation to the speaker was unclear.

Familiarizations were conducted by playing back 80 exemplars of the target number while the subject sat in the test box and an experimenter provided small pieces of a sweetened cereal. The familiarization set for a given session consisted of a randomized ordering of the eight unique CV exemplars played 10 times in a different order. The number of exemplars played was determined based on prior studies using speech, and it approximated the modal number of trials that tamarins require to reach habituation (Hauser *et al.* 2001, 2002*b*; Ramus *et al.* 2000).

Following familiarization, the experimenter left the chamber, closed the door and started the test trial sequence. Each subject was presented with six test trials, three consisting of the same target number presented during familiarization and three consisting of a different number; same and different test stimuli alternated. We divided the colony into four groups. Two groups
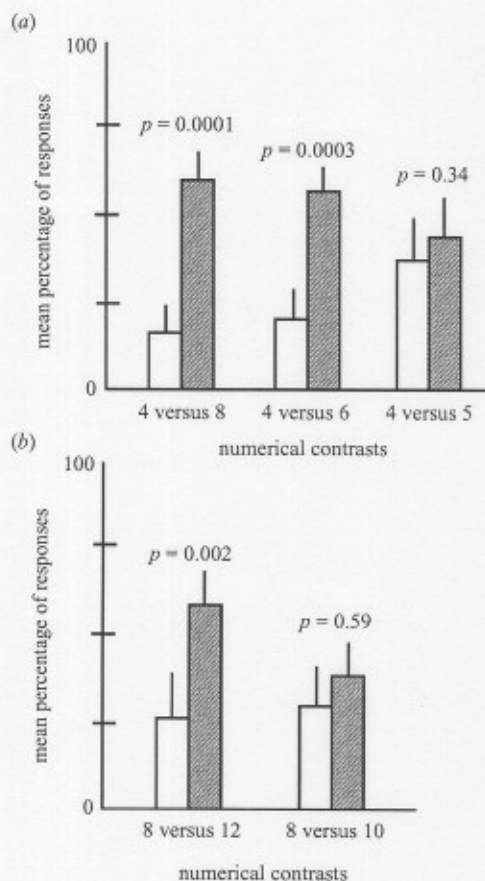
(a)

(b)

Figure 2. (a) Experiment 1 results. (b) Experiment 2 results. Mean (+ s.e.) proportion of responses to test trials presenting the same or different number as in the familiarization period. *p*-levels are two-tailed and refer to values from Wilcoxon signed ranks test.

were familiarized to one number class while the other two groups were familiarized to the second number class. Within these two subgroups, one started the test sequence with a presentation of the same number class presented during familiarization while the other group started with a different number class. Thus, across groups, we counterbalanced for familiarization number as well as whether the first test trial constituted the same or a different number.

3. RESULTS

(a) *Experiment 1*

Condition 1 involved a contrast between four and eight. After familiarization, subjects responded significantly more often to the different number than to the same, independent of whether they were familiarized to four or eight (Wilcoxon signed rank: $z = 3.97$, $p = 0.0001$; figure 2a). Further, 20 out of 22 subjects showed this pattern ($p < 0.0001$). Condition 2 involved a contrast between four and six. Again, subjects showed a significantly higher level of response to the different number than to the same number (Wilcoxon signed rank: $z = 3.65$, $p = 0.0003$), with 18 out of 21 subjects showing this response pattern ($p < 0.002$). Condition 3 involved a contrast between four
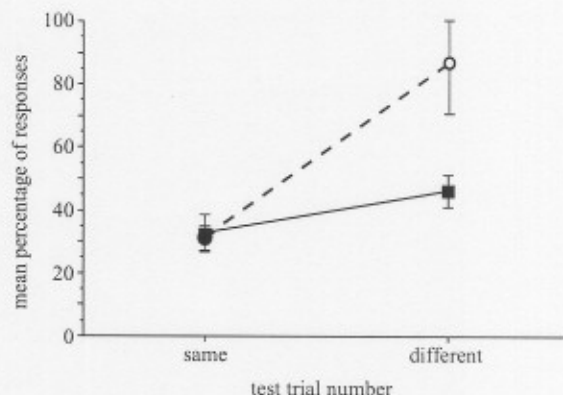

Figure 3. Combining data from experiments 1 and 2, this figure plots the tamarins' performance as a function of ratios. The *y*-axis plots the mean (± s.e.) proportion of responses on test trials presenting the same or different number (*x*-axis) as a function of ratios; open circles and dashed line (1.5 ratio for both the 4 versus 6 condition and the 8 versus 12 condition); filled circles and solid line (1.25 ratio for both the 4 versus 5 condition and the 8 versus 10 condition).

and five. In contrast with the previous two conditions, tamarins failed to show a significant discrimination between the same and different number after familiarization (Wilcoxon signed rank: $z = 0.96$, $p = 0.34$; figure 1). Only 10 out of 21 subjects showed a higher level of response to the different number ($p > 0.05$). Based on these findings, it appears that tamarins have the capacity to discriminate sequences of four syllables from sequences of eight or six but not five syllables.

(b) *Experiment 2*

Is the tamarins' discrimination threshold determined by the ratio of the two numerosities or their absolute values? Condition 1 involved a contrast between 8 and 12. Tamarins showed a significantly greater level of response to the different number than to the same number (Wilcoxon signed rank: $z = 3.12$, $p = 0.002$; figure 2b), with 17 out of 21 subjects showing this pattern of response ($p < 0.008$). Condition 2 involved a contrast between 8 and 10. Tamarins failed to show a statistically significant difference in the proportion of responses to the same versus a different number (Wilcoxon signed rank: $z = 0.53$, $p = 0.59$), with only 13 out of 24 subjects responding more to the different number after familiarization ($p > 0.05$). Tamarins discriminated between the numerosities at the 1.5 but not the 1.25 ratio.

To explore overall effects, as well as consistency within subjects across conditions, we ran a repeated-measures ANOVA with ratios collapsed as a factor; given that not all subjects participated in every condition, we analysed only the data for 17 subjects completing conditions 2 and 3 of experiment 1, and conditions 1 and 2 of experiment 2. Analyses (figure 3) revealed a significant interaction between ratios and the mean proportion of responses on same and different test trials ($F = 5.20$, $p = 0.03$). By contrast, there were no statistically significant ($p > 0.05$) main effects or interactions involving set size. Thus, subjects responded significantly more often in the different-

number test trials when the ratio was 1.5 than when it was 1.25. In accord with Weber's law, tamarins' discrimination depended on the ratio difference between the set sizes and was independent of the absolute magnitudes of the set sizes.

4. DISCUSSION

The present experiments provide the first evidence, to our knowledge, for spontaneous representations of large numerosities by a non-human animal. Cotton-top tamarins discriminated reliably between sequences of speech syllables based on numerosity, when continuous variables were strictly controlled and when testing involved no training and no efforts to focus attention on numerosity. We conclude that humans are not the only species that is spontaneously attentive to number, and that at least part of our non-symbolic system derives from an evolutionarily ancient computational mechanism (Gallistel 1990; Dehaene 1997; Hauser 2000).

The present experiments also reveal that in this non-human primate, as in human adults and infants, large number representations show a signature Weber limit on performance: discriminability depends on the ratio of the two numerosities rather than their absolute values. Human adults who are instructed to focus on numerosity show a ratio discrimination threshold of *ca.* 1.15 (Van Oeffelen & Vos 1982; Barth *et al.* 2003). Human infants, tested with a habituation–discrimination procedure and no instruction, show a ratio threshold between 2.0 and 1.5 at six months, and between 1.5 and 1.25 at nine months (Lipton & Spelke 2003). Thus, adult tamarins show comparable discrimination abilities to nine-month-old human infants. It is not clear whether subsequent improvements in human numerical discrimination result from further maturation, experience with counting and arithmetic, or task instruction.

Also of interest, both evolutionarily and ontogenetically, is the extent to which tamarins may or may not apply the same system of number representation to smaller numbers. In studies of human infants, for example, when the same methods are applied to presentations of one versus two and two versus three—ratios that are readily processed with higher numbers—subjects fail to discriminate (Clearfield & Mix 1999; Xu & Spelke 2000; Feigenson *et al.* 2002*a*; Lipton & Spelke 2003). This finding suggests that for humans, the approximate number system may not apply to small numbers, and that some other system—such as the object file mechanism that is involved in object tracking (Kahneman *et al.* 1992; Pylyshyn & Storm 1998; Scholl & Leslie 1999)—is tapped for such computations (Wynn 1998; Uller *et al.* 1999; Carey 2001; Feigenson *et al.* 2002*a,b*). In studies of animals, the situation is more complicated. Like human infants, rhesus monkeys and tamarins appear to tap the small-number object-tracking system when monitoring objects that are occluded one by one, as evidenced by successes with discriminations less than three and failures with numbers above three but with the same favourable ratios (Hauser *et al.* 1996, 2000; Sulkowski & Hauser 2000; Uller *et al.* 2001; Hauser & Carey 2003). Thus, Hauser *et al.* (2000) showed that in a two-box choice task involving the presentation of different quantities of food into each box, rhesus monkeys success-

fully discriminated one versus two, two versus three, and three versus four, but failed at four versus five, and even four versus eight and three versus eight. These data illustrate the set size signature of the small exact number system. In studies using extensive training, by contrast, rhesus monkeys show no break in their processing of small versus larger numbers (Brannon & Terrace 1998; Nieder *et al.* 2002). It remains to be determined whether this difference stems from the effects of training or differences in species or age.

Although humans have unique cognitive skills, these skills often build upon cognitive systems that are shared by other animals. Our findings suggest that number provides such a case (Dehaene 1997; Gallistel & Gelman 2000; Hauser 2000). The uniquely human capacity for symbolic arithmetic depends, in part, on a system for representing large, approximate numerical magnitudes—the 'number sense'. The present experiments provide evidence that the number sense is shared by other animals and expresses itself spontaneously when the animals confront sequences with large numbers of elements. This building block of human intelligence therefore has a long evolutionary history and may be amenable to systematic study at multiple levels, including comparative studies of the underlying neural mechanisms.

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