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Monkeys match and tally quantities across senses

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ABSTRACT

We report here that monkeys can actively match the number of sounds they hear to the number of shapes they see and present the first evidence that monkeys sum over sounds and sights. In Experiment 1, two monkeys were trained to choose a simultaneous array of 1–9 squares that numerically matched a sample sequence of shapes or sounds. Monkeys numerically matched across (audio–visual) and within (visual–visual) modalities with equal accuracy and transferred to novel numerical values. In Experiment 2, monkeys presented with sample sequences of randomly ordered shapes or tones were able to choose an array of 2–9 squares that was the numerical sum of the shapes and sounds in the sample sequence. In both experiments, accuracy and reaction time depended on the ratio between the correct numerical match and incorrect choice. These findings suggest monkeys and humans share an abstract numerical code that can be divorced from the modality in which stimuli are first experienced.

1. Introduction

Number representation and calculation are not the unique province of humans. Various non-human species can represent and compare number independently of non-numerical stimulus features such as density or surface area, and their accuracy and reaction time in making these numerical judgments are modulated by the ratio between compared values (e.g., Cantlon & Brannon, 2006). Similarly, when adult humans are prevented from verbally counting, their number judgments are also ratio-dependent, and performance is often indistinguishable from that of nonhuman animals tested on the same tasks (e.g., Cantlon & Brannon, 2006, 2007; Cordes, Gelman, & Gallistel, 2001; Pica, Lemer, Izard, & Dehaene, 2004; Whalen, Gallistel, & Gelman, 1999).

A language-independent, analog magnitude system has been proposed to underlie many of these nonverbal numerical abilities (e.g., Dehaene, 1997; Gallistel & Gelman, 1992). This is a separate system from that underlying verbal numerical knowledge. The signature property of the analog magnitude system is that it is ratio-dependent and obeys Weber's Law, which states that $\Delta I/I = C$, where ΔI is the increase or decrease in stimulus intensity that is required to produce a detectable change in a standard stimulus and C is a constant. Therefore, if a student requires a gain or loss of 2 pounds to detect a change in a 10-pound backpack, the same student would need a 20-pound increment or decrement to detect a change in a 100-pound backpack.

Data showing that numerical discriminations adhere to Weber's Law have been obtained using a wide variety of different species and paradigms (e.g., Beran, 2004; Cantlon & Brannon, 2006; Emmerton & Renner, 2006; Fetterman, 2003; Jordan & Brannon, 2006; Judge, Evans, & Vyas, 2005; Nieder, Freedman, & Miller, 2002; Platt & Johnson, 1971; Roberts, 2005; Smith, Piel, & Candland, 2003). These discriminations are not limited to the visual modality, as there is evidence that non-human animals can represent number in the auditory modality and that these representations are also limited by ratio. For instance, Hauser, Tsao, Garcia, & Spelke, 2003 found that cotton-top tamarin monkeys familiarized to sequences with a constant number of sounds orient longer to sequences that contain a novel number of sounds, and that their ability to detect numerically novel

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sequences is dependent on the ratio between the novel and familiar numerosity. Similarly, Meck and Church (1983) found that rats' numerical discriminations in an operant task using auditory stimuli conformed to expectations of Weber's Law. Thus, number discrimination is ratio-dependent in both the visual and auditory domain.

Animals are also capable of matching numerosities within either of these sensory modalities across presentation formats. For example, Hauser, Dahaene, Dahaene-Lambertz, & Patalano, 2002 found that cotton-top tamarin monkeys spontaneously recognized the numerical equivalence between small numbers of speech syllables and tones. Similarly, in the visual modality, Nieder, Diester, & Tudusciuc, 2006 found that rhesus monkeys could select a visual array that numerically matched a sample of visual elements that was presented sequentially for the small values 1–5.

Number is an amodal property of a set of discrete elements, and adult humans easily count over sounds, sights, touches, smells, or even concepts. While language clearly allows humans to represent the number of events abstractly independent of the sensory modality in which an event is experienced, a recent study indicates that even when adults are representing number without language, their representations traverse sensory modalities. Barth, Kanwisher, and Spelke (2003) presented adults with two sequences of tones or circles too rapid to verbally count and asked subjects to indicate whether there were the same or a different number of events in the sequences. They found that humans show virtually no cost in accuracy for comparing numerosities across the visual and auditory modalities compared to within a single modality, suggesting that they possess nonverbal number representations independent of stimulus modality. If non-human animals and humans share a nonverbal system for representing number as analog magnitudes, is it thus possible that even the number representations held by nonhuman animals are sufficiently abstract to transcend sensory modality?

A recent study found that rhesus monkeys looked longer at a video containing images of the number of monkeys matching the number of monkeys they simultaneously heard vocalizing (Jordan, Brannon, Logothetis, & Ghazanfar, 2005). In that study, monkeys heard choruses of 2 or 3 monkeys vocalizing, and regardless of which number they heard, they looked longer at the numerically matching video. Field studies also suggest that non-human animals predict the number of intruders they expect to see based on the number of vocalizing intruders they hear (e.g., Kitchen, 2006; McComb, Packer, & Pusey, 1994); the probability that a group of chimpanzees, for example, will approach a speaker emitting vocalizations from an unfamiliar conspecific depends on the number of chimpanzees present in the group (Wilson, Hauser, & Wrangham, 2001). An important question that remains unresolved, however, is whether the ability to cross-modally match based on number is context-specific and isolated to social judgments or instead is sufficiently abstract to extend to arbitrarily related, non-ecologically relevant stimuli. A second related question is whether animals can actively match across sensory modalities such that they can choose a numerically matching array that is presented in a different sensory modality. In other words, are the numerical cross-modal matching abilities suggested by social contexts accessible to the monkey, or do they reflect more implicit knowledge that might be used only in specific contexts?

A third vital question is whether non-human animals, like humans, rely on a ratio-dependent, analog magnitude system for representing and comparing a large range of numerosities across senses. Previous studies have used only small numerical values and are therefore unable to determine whether animals' cross-modal numerical capacities generalize to larger values or show the ratio-dependent hallmark of human nonverbal number judgments. For example, a pair of prior studies that tested the ability of rats to make numerical discriminations with light flashes and tones limited the numerosities tested to a few small values (Church & Meck, 1984; Davis & Albert, 1987). Church and Meck (1984) trained rats to press one lever after hearing 2 tones or seeing 2 lights and a second lever after hearing 4 tones or seeing 4 lights. The rats were then presented with a compound stimulus of 2 tones and 2 lights. Rats reliably chose the lever associated with 4 tones or 4 lights when presented with these compound stimuli, suggesting they had summed across lights and sounds. In contrast, however, Davis and Albert (1987) trained rats to discriminate 3 sequentially presented sounds from 2 or 4 sounds and found no evidence that rats transferred their auditory numerical discrimination to the visual modality when presented with sequences of 2, 3, and 4 lights. The results from Davis and Albert (1987) raise the possibility that the rats in the Church & Meck, 1984 made dichotomous, intensity-based judgments (i.e., they equated the less intense sound with the less intense light), leaving open the question of whether the calculations made by the animals were in fact based on the representation of numerical equivalence.

A final question we seek to answer is whether animals can *sum* across sensory modalities. Only one prior study has attempted to address whether nonhuman animals can go beyond basic cross-modal numerical comparisons and perform other arithmetic operations, such as summation, across sensory modalities. In this study by Church and Meck (1984) which was described above, rats behaved as if they summed 2 sounds and 2 sights by classifying the compound stimulus as 4. However, it is possible that they merely categorized the 4-compound stimulus as more intense than the alternative stimuli. Furthermore, the representational system that might enable non-linguistic organisms to sum items across sensory modalities has never been investigated. No current data inform whether non-human animals use a ratio-dependent system to nonverbally sum a large range of numerical values across senses. Given that Barth et al., 2006 found that adult humans can nonverbally add visual and auditory items and that accuracy is modulated by ratio, it seems likely that if non-human animals and humans share a system for representing number as analog magnitudes, animals can also integrate items across different senses to extract the total numerical value.

Experiment 1 tests whether non-human primates can actively match arbitrarily related stimuli based on numer-