Common Representations of Abstract Quantities

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ABSTRACT—***Representations of abstract quantities such as time and number are essential for survival. A number of studies have revealed that both humans and nonhuman animals are able to nonverbally estimate time and number; striking similarities in the behavioral data suggest a common magnitude-representation system shared across species. It is unclear, however, whether these representations provide animals with a true concept of time and number, as posited by Gallistel and Gelman (2000). In this article, we review the prominent cognitive and neurobiological models of timing and counting and explore the current evidence suggesting that nonhuman animals represent these quantities in a modality-independent (i.e., abstract) and ordered manner. Avenues for future research in the area of temporal and mathematical cognition are also discussed.***

KEYWORDS—***analog magnitudes; interval timing; number representation; abstract quantities***

Interactions with the environment—from balancing a checkbook to coordinating motor movements—consistently rely upon an understanding of time and number. These quantities are everywhere and, by virtue of their abstract nature, are not tied to any particular domain or modality. Five Shih Tzus, five bell chimes, five taps on your shoulder, five scents, and five ideas are all instances of the number five, regardless of whether they were seen, heard, felt, smelled, or thought. In both animals and humans, skills as diverse as language acquisition, visual perception, and foraging are dependent upon representations of quantities (Gallistel, 1990; Gallistel, Gelman, & Cordes, 2005), but whether this means animals have a true concept of time and number is unclear. In addition, quantity representations are selectively impaired in persons affected by Parkinson's disease, schizophrenia, and dyscalculia (developmental disability in mathematics comprehension; Buhusi & Meck, 2005). An increased understanding of both the behavioral and neurobiological mechanisms responsible for time and number representations will not only further our understanding of learning in general but may also lead to improvements in the diagnosis and treatment of these debilitating disorders.

The ability to represent abstract quantities is not dependent upon language; demonstrations in nonhuman animals confirm that this ability is shared across species. Meck and Church (1983) trained rats to discriminate two signals in which time and number were confounded. Lever presses on the left side were rewarded following a 2-second signal consisting of two noise bursts, and presses on the right were rewarded following eight bursts lasting a total of 8 seconds (0.5 seconds on, 0.5 seconds off; Fig. 1a). Following training, unrewarded probe trials were presented. On number-relevant probe trials, rats experienced anywhere from two to eight bursts, with total stimulus duration set at 4 seconds. On duration-relevant trials, the rats heard four bursts, but total stimulus duration varied from 2 to 8 seconds. Data revealed that the probability of a right lever response was clearly a function of the relevant stimulus value (Fig. 1b), suggesting the rats attended to both temporal and numerical stimulus cues. That is, on number-relevant trials, they responded based on the number of bursts they heard, and on duration-relevant trials, they timed the bursts and responded accordingly. Representations of abstract quantities served as the basis for responding in this task, as they have in many other studies involving a variety of species (Gallistel, 1990).

The results obtained from such counting and timing tasks ubiquitously obey Weber's law: The speed and accuracy with which two values are discriminated is dependent upon their ratio (2 vs. 8 is just as easy as 20 vs. 80, despite a 10-fold discrepancy in the absolute difference between magnitudes). In the behavioral data, this is evidenced by scalar variability—response variability (the standard deviation in the distribution of responses, or more simply, the magnitude of estimation errors) increases in direct proportion to the magnitude of the quantity (Cordes, Gelman, Gallistel, & Whalen, 2001; Gallistel, 1990).

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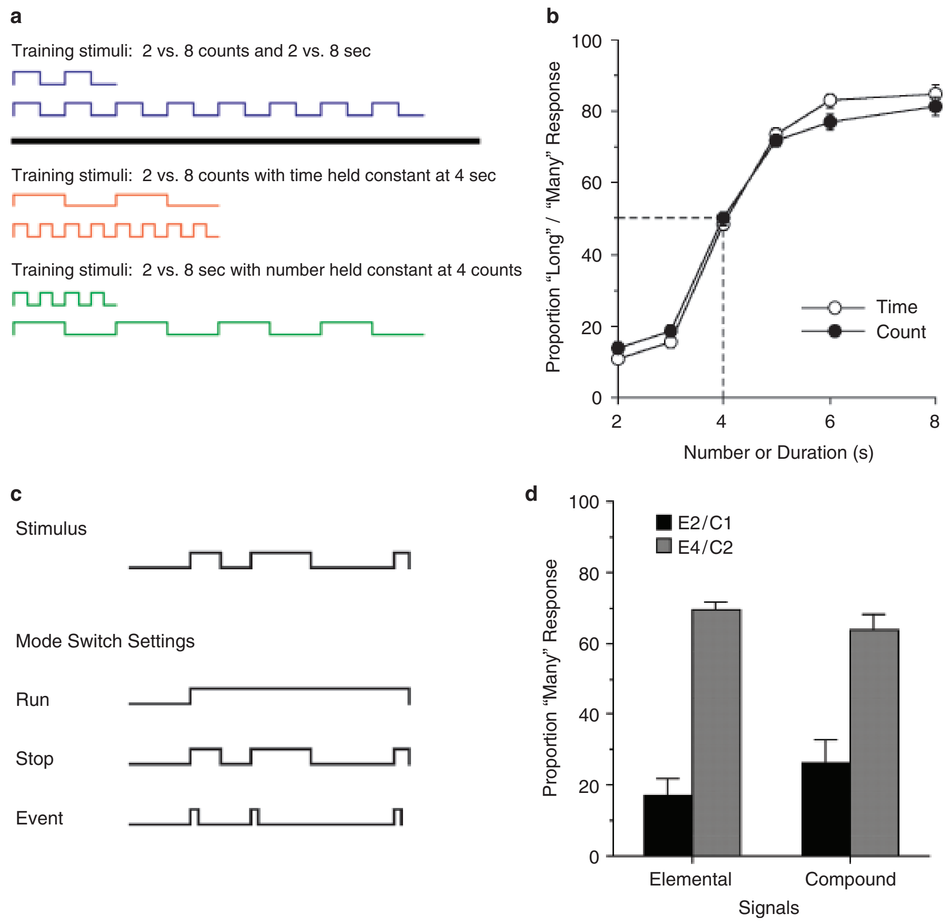

Fig. 1. Testing animals' representation of time and number. Panel a illustrates the type of training and test stimuli used in Meck and Church (1983). Each elevation corresponds to a stimulus presentation for a given duration. Animals were trained to discriminate two sounds in 2 seconds from eight sounds in 8 seconds, and then were tested with intermediate values in which one quantity (time or number) was held constant at four. Data from this task are shown in panel b: The animals' probability of choosing the "8" lever varied as a function of the stimulus value for both time and number test trials. Open circles represent variation in signal duration (time) and closed circles represent variation in the number of cycles (count; adapted from Meck and Church, 1983). Panel c illustrates the three modes (Run, Stop, and Event) in which the switch to the mental accumulator can operate during the presentation of an intermittent stimulus, according to Meck & Church's (1983) mode control model. The Run mode keeps track of the duration of the entire stimulus presentation (including time between stimuli); the Stop mode times only when the stimulus is present; and the Event mode keeps track of the number of stimuli presented. Panel d shows the results of a task in which animals were trained to distinguish two elemental signals (two sounds or two lights) from four elemental signals and then were presented with sounds and lights simultaneously in the test phase. Animals responded as if counting each of the individual components independently (e.g., they pressed the "4" lever—the "many" response—when presented with two lights and two sounds simultaneously). The graph shows the mean proportion of "many" responses as a function of the number of elemental (E) light or sound signals or compound (C) light + sound signals presented on each trial (the darker bars, E2/C1 correspond to trials in which the animals experienced two elemental signals, as in training, or one light and one sound; E4/C2 corresponds to trials in which four elemental signals or two compound signals—two lights and two sounds—were presented). Adapted from Church and Meck (1984).

Obviously, humans also represent abstract quantities. By looking at a clock, we can tell exactly what time it is. By counting students in a class, we know precisely how many copies of an exam to make. What may be less obvious is that humans share the same primitive representational capacities as nonhuman animals, independent of language. We know this, in part, because human timing also reveals scalar variability (Buhusi and Meck, 2005). Essentially, this means that when you head into the kitchen for a snack during a 3-minute TV commercial break, you may misestimate the amount of time you have to return by, say, 30 seconds, but when judging how much longer before the 30-minute show is over, you may be off by as much as 5 minutes.

But what about number? Humans have an exact representation of "ten," right? Cordes et al. (2001) had adult humans rapidly press a button as many times as indicated by a numeral while repeating the word "the" with each press, which prevented verbal counting. Participants' mean number of presses increased as a function of the numeral, indicating they were able to estimate number nonverbally. This finding was also echoed in the discovery of scalar variability in the nonverbal counting data, which contrasted with the non-scalar variability pattern found when participants explicitly counted their presses, indicating different counting processes in the two conditions (i.e., nonverbal and verbal). Results were analogous to those of the animal counting studies and they were inconsistent with verbal counting, supporting the idea that humans share with animals a system for representing number approximately, without language.

TIMING AND COUNTING MODELS

What sort of cognitive system is responsible for representing quantities? Meck and Church (1983) proposed a mode-control model to account for the animal counting and timing data, and it has since been adopted to explain the human data as well. According to this model, when an interval is timed, a neural pacemaker continuously generates pulses into a mental accumulator ("run mode," like water running from a hose into a bucket) until the interval is over ("stop mode," like the hose being turned off). The magnitude in the accumulator (water in the bucket) at the end of the interval represents the duration of that interval; thus subjective quantity is a linear function of objective quantity (a gallon of water represents an interval four times longer than a quart). In the case of number, instead of a continuous flow of pulses into the accumulator, a switch closes and opens for a set duration for each enumerated item ("event mode," like a cupful of water being poured into a bucket for each item). Both time and number, in this model, are represented by the same analog magnitudes; the only difference between the two is the accumulation process (Fig. 1c; Meck, 1997).

Once the set of items has been counted or the interval has been timed, the final magnitude in the accumulator is transferred to memory. These magnitudes are inherently noisy (they have error), such that scalar variability in the underlying representation begets scalar variability in the behavioral data. That is, when you misestimate the amount of time you have for a 3-minute commercial break, it is due to imprecision in your representation of 3 minutes.

How is this model instantiated neurobiologically? Studies pinpoint the basal ganglia (a brain area implicated in movement disorders such as Parkinson's), notably a part of it called the striatum, as a focal point for interval timing (Buhusi and Meck, 2005). In one recent model, called the striatal beat-frequency model (Fig. 2; Buhusi & Meck; Matell & Meck, 2004), the basal ganglia is central to monitoring and regulating the firing patterns of oscillating neurons in frontal cortex. Spiny neurons in the basal ganglia monitor the sequence of beats from thousands of cortical neurons, detecting unique firing patterns for every timed interval—a temporal code. Once firing patterns match those of a previous timing experience from memory, the animal or human thinks that the interval has elapsed. This model is both neurobiologically plausible and predictive of interval timing, as simulations mimic the scalar property of actual behavioral data.

A TRUE CONCEPT OF QUANTITY?

In summary, animals both human and nonhuman share a primitive, imprecise system for representing abstract quantities nonverbally. Does this mean that animals have a true concept of time and number? In distinguishing between numerical categories and concepts, principles of a true counting process have been outlined (Gallistel & Gelman, 2000). Although initially applied specifically to the domain of number, these principles have been adopted to describe the accumulation of mental magnitudes representing both numerosity and duration. True quantity concepts require an appreciation of basic arithmetic principles, including, among others, the stable order and abstraction principles. That is, a true concept of quantity involves an understanding that time and number are both ordered systems and that they are independent of stimulus modality. The first refers to the fact that while animals distinguish 2 from 8, they should also have an appreciation that 2 is *less than* 8 (ordinality). The second refers to the abstract nature of these quantities—two dots, two beeps, and two pats are all sets of two. The question is: Do nonhuman animals recognize this?

Ordinal Abilities

Very little is known about the ordinal abilities of animals. There have been few direct investigations into whether animals can use the ordering of magnitudes algebraically—that is, respond based on which magnitude is larger. Although mental magnitudes are themselves an ordered system, the question is whether animals appreciate the inherent relationship between quantity representations. While tasks like the one used by Meck & Church (1983) appear to tap into ordinal competence, these tasks are in fact by their very nature categorical. Meck (1997) trained rats to discriminate 4 from 8 (time and number confounded). When presented novel intermediate test values (5, 6), the rats responded in an orderly fashion—with the probability of an "8" lever press increasing as a function of the value. When presented with novel values outside of the training range (2, 15), however, the animals responded at chance. The rats were not more likely to press the "4" lever when presented with a 2-stimulus, indicating that the discrimination was not based on a more/less distinction but instead on a similarity judgment of the probe value to the trained values.

Despite the lack of direct tests of ordinal judgments in rodents, there have been a few studies investigating these abilities in

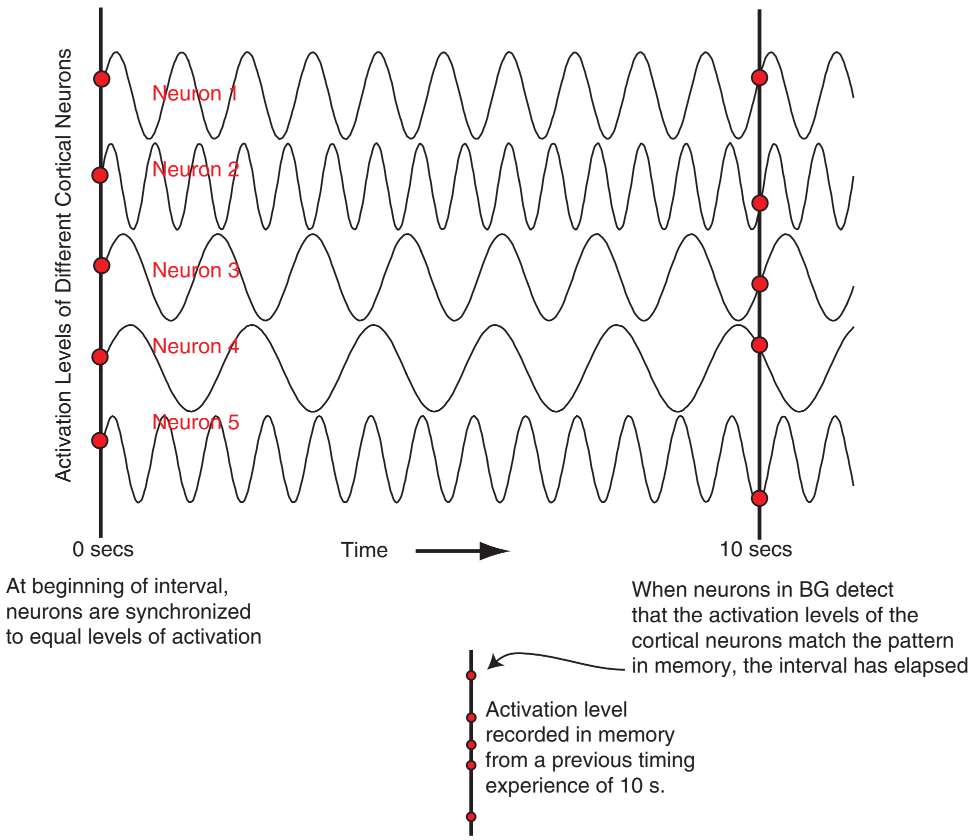

Fig. 2. The striatal beat frequency model of interval timing. In this model, intervals are timed via neurons in the basal ganglia (BG) that monitor activation patterns of neurons in the cortex; these cortical neurons have patterns of activation that oscillate with varying frequencies, as shown. At the beginning of an interval (0 secs), these oscillating cortical neurons are synchronized to the same level of activation; once the interval has elapsed (e.g., 10 secs), the distinct pattern of activation of these neurons at that point in time is recorded in memory as a way of identifying that interval. Later, when that same interval is timed again, neurons in the BG compare the current pattern of activation of these neurons with the pattern recorded in memory to determine when the interval has elapsed (i.e., when to expect a reward). When the patterns match, the interval has elapsed. Adapted from Buhusi and Meck (2005).

nonhuman primates. Primates will pick the larger of two quantities of food, although it is unclear whether number, size, or the simple hedonic value of the food is driving the discriminations (see Brannon & Roitman, 2003). Brannon and Terrace (2000) trained rhesus macaques to order stimuli based on the numerousness of the display. The animals were trained to order heterogeneous displays of one to four items. Interestingly, attempts to train one of the monkeys on an arbitrary sequence (3–1–2–4) failed despite extensive training, suggesting that the ordinal nature of the stimuli was salient to the animals. The monkeys spontaneously generalized the ordinal rule to novel values (5–9) in which they had no prior experience. These data provide the first concrete evidence of ordinal competence in nonhuman animals.

Abstraction Abilities

The ability to abstract quantitative information from a stimulus, independent of stimulus modality, is also a prerequisite for conceptual competence. That is, do animals recognize that six flashes and six sounds are both instances of the same numerosity? There have been a handful of studies investigating these cross-modal abilities. Meck and Church (1982) tested rats on the ability to generalize responding based on stimuli from one modality (vision) to another (audition). In four different tasks, rats were trained to respond according to the duration either of sounds or of periods of darkness. Following training, the modality of the discriminative stimulus was switched. Although there was a slight compromise in accuracy and/or response rates, the rats spontaneously generalized response rules to the novel modality, suggesting they abstracted the temporal information of both stimuli alike.

In a study of cross-modal transfer of number, Church and Meck (1984) trained rats to press one lever following two light flashes or two sounds, and the other lever following four light flashes or four sounds. When presented with compound stimuli in the test (e.g., two light flashes *and* two sounds), rats responded as if counting stimuli across modalities (pressing the "4" lever), suggesting auditory and visual stimuli were equally considered (Fig. 1d). In addition, Meck (1997) found that prior experience with a value influenced future performance across distinct tasks. Rats were trained to discriminate either two from six sounds (numerical discrimination) or a red from a green light (visual discrimination). Both groups were subsequently placed in a 12-arm radial maze, where they retrieved food pellets from the end of 4, 6, or 8 arms before entering the "exit" arm, indicating completion of the task. Maze performance revealed positive transfer in the numerical-discrimination group, such that rats trained on the 2-versus-6 discrimination performed significantly better (entered the exit arm more often after completion of the maze) when the number of baited arms was 6 but not when it was 4 or 12. In contrast, performance of the visual-discrimination group did not vary as a function of the number of baited arms. Prior experience with one absolute value (6) led to more accurate responding with that same value across tasks.

The ability to match numerical and temporal values across modalities is also evident in other nonhuman species. In a recent study, Jordan, Brannon, Logothetis, and Ghazanfar (2005) presented rhesus monkeys with two displays simultaneously—one with two monkey faces and the other with three. When they heard two monkey calls, the monkeys preferentially looked to the display with two faces, and they looked to the other when they heard three calls, again suggesting that nonhuman animals appreciate that quantity information is independent of the stimulus conveying it.

FUTURE DIRECTIONS

While the field of temporal and numerical cognition has made great advances in recent years, there are still a number of questions to address. There has been only one line of investigation into the ordinal abilities of nonhuman animals, involving numerical ordering in primates. Whether an appreciation of ordinality is specific to primates or is shared by all animal species is unclear. Whether these abilities apply to other abstract quantities, such as time, should also be investigated.

Studies into the neurobiological mechanisms involved in timing and counting are also warranted. The striatal beat-frequency model accounts for the interval-timing data but has yet to be applied to numerical representations. If it is the case that temporal and numerical values are represented by the same system, then this neural network should also be responsible for tracking numerosity. Future directions should also lead to investigations of the potential influence of neuroendocrine (hormonal) mechanisms. Previous work has revealed that sex hormones modulate spatial abilities (Williams, Barnett, & Meck, 1990), a domain closely connected to time and number. It is likely that exposure to these hormones around the time of birth similarly affects adult timing and counting abilities by producing organizational changes in specific brain regions (e.g, the hippocampus, the striatum).

It has been argued that learning about the world involves computing statistics about the regularity of events (e.g., the frequency of feedings, the probability that two syllables heard paired together form a word) and that quantity representations serve as inputs to these online statistical computations (Gallistel, 1990; Gallistel et al., 2005). This is possible, as temporal and numerical representations can be arithmetically manipulated. Recently, Meck and Williams (2006) found that rats spontaneously subtracted the number of times a tone was turned off from the number of sounds experienced, without prior training. Examinations of the variability associated with magnitude arithmetic may provide a window onto learning and lead to an understanding of the neurobiological mechanisms involved, much as it has in the case of interval timing.

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