Numerical Subtraction in the Pigeon: Evidence for a Linear Subjective Number Scale

Elizabeth M. Brannon*, Courtney J. Wusthoff#, C.R. Gallistel^, and John Gibbon@

- * Center for Cognitive Neuroscience and Department of Psychology: Experimental, Duke University
- # Department of Psychology, Columbia University
- ^ Department of Psychology, UCLA
- @ Department of Psychology, Columbia University and Department of Psychobiology Biopsychology, New York State Psychiatric Institute

Please address Correspondences to:
Elizabeth M. Brannon
Center for Cognitive Neuroscience
Box 90999
Duke University
Durham, North Carolina 27708-0999
brannon@duke.edu
919-668-6201

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Abstract

To explain why it takes longer to judge which of two numbers is bigger the smaller the percent difference between them, it is often assumed that the subjective number continuum is logarithmically compressed (e.g., Dehaene, 1997; Moyer and Landaeuer, 1967). An alternative hypothesis is that the subjective number continuum is linear but positions farther along it are proportionately fuzzier, that is, less precisely located (Meck and Church, 1983; Gallistel and Gelman, 1991, 1992). These two hypotheses have been treated as functionally equivalent because of their similar empirical predictions (magnitude and distance effects; Dehaene, 1992). The current experiment sought to resolve this issue with a paradigm originally developed by Gibbon and Church (1981) to address the subjective representation of time (“time-left”). In our adaptation, pigeons were required to compare a constant number to the number remaining after a numerical subtraction. Our results indicate that subjective number is linearly not logarithmically related to objective number.

Converging evidence from many different laboratories and paradigms demonstrates that animals represent number (see Davis and Perusse, 1988; Gallistel and Gelman, 1992, 2000 ; Dehaene 1997 for reviews). For example, animals can produce a certain number of responses (e.g., Mechner 1958), discriminate the numerosity of visual or auditory stimuli (e.g., Hicks, 1956; Meck and Church, 1983), represent the ordinal relations between numerosities (Brannon and Terrace, 1998, 2000), and even learn the relationship between arbitrary symbols and numerosities (e.g., Matsuzawa, 1985).

A growing body of data supports the conclusion that non-human animals and humans represent number in a similar way (Dehaene, 1998; Gallistel and Gelman, 2000). For example, when human or animal subjects are required to determine which of two numerical values is larger (or smaller), their accuracy and reaction-time are systematically influenced by both the numerical distance between the two values (the distance effect) and their magnitude (the magnitude effect, Moyer and Landaeur, 1967; Brannon and Terrace, 1998, 2000). Reaction-time is longer and accuracy is lower for values that are similar in magnitude (e.g., 2 and 3) compared to values that are disparate in magnitude (e.g., 2 and 6). When distance is held constant, accuracy decreases and latency increases as the magnitudes of the values being compared increase.

One explanation for the effect of magnitude on numerical ordering is that the internal representation of number is logarithmically compressed (e.g., Dehaene & Mehler, 1992; Rule, 1969; Moyer and Landaeuer, 1967), so that the representatives of 12 and 13 lie closer together on a mental continuum than do the representatives of 2 and 3. If there is noise or fuzziness in the positioning of these representatives on the continuum, then the closer together they lie, the harder it will be to determine their ordering. Alternatively, the subjective number scale may be a linear reflection of objective number, but the uncertainty about where exactly a given quantity falls on the mental continuum may increase in proportion to the size of that quantity. Thus, the ordering of two big numbers will be harder to distinguish than the ordering of two small numbers the same distance apart, because the positions of the big numbers on the mental number continuum are more fuzzily defined (Fetterman, 1993; Gibbon, 1977; Gallistel and Gelman, 1992; Whalen, Gelman, and Gallistel, 1999). Both hypotheses predict the observed effect of numerical magnitude on ordering (e.g., more difficulty in judging the order of 12 and 13 than 2 and 3).

Recent research suggests that animals represent both time and number in a similar way (Meck and Church, 1983; Meck, Church and Gibbon, 1985; Roberts and Boisvert, 1998). For example, Meck and Church (1983) used a psychophysical choice procedure to train rats to discriminate signals that differed in both duration and number. Although duration and number were confounded in training, test sessions revealed that the rats had encoded both duration and number. Furthermore, the Meck and Church data suggest that a scaling factor of about 200 ms per count relates the subjective number continuum to the subjective time continuum (Meck and Church, 1983; Meck, Church, and Gibbon, 1985).

Gibbon and Church (1981) showed that one could distinguish between linear and logarithmically compressed continua with a task that requires the subject to base its behavior on the difference between two points on the continuum rather than on their ordering. Any two points that have the same ratio are the same distance apart on a logarithmically compressed continuum. If the subjective number continuum is logarithmically compressed, then two pairs of numbers with the same ratio--for example, the pairs {2,3} and {20,30}--have the same subjective separation, that is, the pairs of subjective representatives of these numbers will lie the same distance apart on the subjective number continuum. Thus, when numerical behavior is based on the subjective difference between two numbers, the behavior will be the same whenever the objective ratio of the two numbers is the same, no matter how far apart those two numbers are objectively. Gibbon and Church used this fact to show that the subjective representation of time was linearly related to objective time. Here we adapt their paradigm to show that subjective number is linearly related to objective number.

Our task requires subjects to compare a numerical difference that varies from trial to trial to a constant value. They choose whichever seems smaller, the difference or the constant value. If the number scale is logarithmically compressed, then whether the difference is bigger than the constant will depend not on the objective difference between the two numbers but rather on their objective ratio. Thus, the number that is subjectively equal to a given subjective difference will not increase when we make the two numbers being differenced objectively bigger but keep the same ratio between them. Of course, when we scale up two numbers in this way, we make the objective difference between them bigger, so this outcome would be decidedly non-normative.

The constant number to which differences are to be compared is called the *standard* or *S* number. The first of the two numbers whose difference is to be compared to *S* is called the *initially required* or *I* number. The second is called the *tallied* or *T* number. At the moment of choice, the subject must judge whether $I - T < S$, that is, whether the initially required number of pecks minus the tallied number is less than the standard number. If so, it chooses one key, called the *number-left key*; if not, it chooses the other key, called the *standard key.*

The task works like this: first the middle key among three keys is illuminated, signalling its activation. Pecking it then produces brief flashes of the light in a food hopper on a variable ratio schedule, a schedule in which the number of pecks required to produce a flash varies unpredictably about a mean value. With a variable ratio schedule, the amount of time required to generate a given number of hopper flashes varies considerably. We make use of this fact to deconfound time and number in our data analysis. After the pigeon's pecking of the middle key has produced a variable number, *T*, of hopper flashes, the light on the middle key goes out, and the keys on either side are illuminated, confronting the pigeon with a choice: which side key should it peck? Whichever side key it pecks first, it must then continue to peck in order to collect a food reward, because pecking one side key inactivates the other side key. Continued pecking of a side key generates hopper flashes, and the pigeon gets to eat from the hopper after it has produced the requisite number of flashes for the side key it has chosen. The requisite number is always the same on the standard side key. The requisite number on the number-left side key, however, is $I - T$, where T is the number of flashes the pigeon has already tallied by pecking on the middle key. The standard key is the better choice when $I - T > S$; the number-left key is the better choice when $I - T < S$.

The value of T at which the subject is equally likely to choose the number-left key and the standard key is called the subjective indifference point. The critical question in this experiment is whether T increases when we increase the values of I and S by the same factor, thereby maintaining their ratio. The indifference point in this experiment depends on how far apart I and S are on the subjective continuum, because the subjective magnitude of T at the indifference point must be equal to the subjective difference (or separation) between I and S. The indifference point indicates the difference (the number left) that seems to the subject to be equal to the standard number. If the mental continuum is logarithmically compressed, then this subjective difference will depend on the ratio of the two numbers, not their difference. So long as we keep their ratio the same, we should keep the value of T at the indifference point the same.

Method

Subjects

Subjects were four White Carneaux pigeons maintained at approximately 80% ad-lib body weight. Subjects were exposed to a regular 12:12 hour light/dark cycle and were tested 5 days a week.

Apparatus

Experimental sessions were conducted in a BRS/LVE Small Environment Cubicle (SEC-002), with minimal external light and noise. Normal illumination was provided by an overhead house light, except during reinforcement presentation. Stimuli were presented through the BRS/LVE Pigeon Intelligence Panel (PIP-010 through PIP-016), equipped with three illuminated pecking keys. Using an IEE one-plane readout projector (# 00010-01-XXXX-1820), each key was illuminated a specific color; the central key was white in each case, while the colors of the left and right keys were yellow and green, counterbalanced for color and position across subjects. A Macintosh computer controlled the experiments and recorded the data.

Procedure

Training. Subjects were first trained to peck two keys on a continuous reinforcement schedule. On each trial, one of two keys was illuminated and pecking at the illuminated key resulted in 3.5 seconds of access to the illuminated hopper. One key was green and the other yellow, and the left and right position of the two keys was counterbalanced across subjects. Subjects were then shifted to a VR8 reinforcement schedule.

The next phase of training required the pigeons to keep track of the number of hopper flashes (100 – 300 ms each), rather than the number of pecks or the time spent pecking. Subjects were reinforced on the second hopper illumination and each hopper illumination was produced on a VR8 (4 - 12) schedule. Thus the birds were required to peck anywhere from 8 to 24 times for each reinforcement. Subsequently the number of flashes to reinforcement was increased to 4, requiring anywhere from 16 to 48 pecks per reinforcement. In the next phase of training the number of flashes to reinforcement was again increased, but only for the number-left key, which now required 8 flashes to reinforcement; the standard key still required 4 flashes. Each flash was provided on a VR8 schedule.

A central white middle key was then introduced. On each trial subjects were required to respond to the middle key to produce a number, T, of hopper flashes between 1 and 7. Flashes were again provided on a VR8 schedule. After *T* flashes, the middle key was extinguished, and either the standard or number-left key became available. If the standard key was illuminated, the subject was required to produce 4 additional flashes for reinforcement regardless of the number of the flash tally from the middle key. However, if the number-left key was illuminated, the subject was required to produce 8 - *T* additional flashes before reinforcement. There were 42 trials per session; each of the 7 possible *T* values was tested 6 times in a random order.

In the final phase of training subjects were given a choice between the standard and number-left keys on a subset of trials. After pecking produced *T* flashes on the middle key, both the standard and the number-left keys were illuminated. The first response to one key eliminated the availability of the other key. As in Phase 6 of training, the standard key required 4 additional flashes to reinforcement and the number-left key required 8 - *T* flashes to reinforcement. The remaining trials were *forced* in that only the standard or number-left key was illuminated as in the previous phase (no choice). In each session, choice trials were presented on two out of every six trials for each of the 7 middle key values (14 trials per session). The ITI was 10 seconds throughout training and testing.

Training continued until the choices the animals made varied systematically as a function of the flashes obtained on the middle key. Training required 25 –30 days for each subject.

<u>Testing</u>. Phase 1 of testing was essentially identical to the final training phase in that the standard key required 4 flashes to reinforcement and the number-left key 8 – *T* flashes to reinforcement (S - 4, I = 8). The only change was that subjects were given a choice between the standard and number-left keys on 4 of the 6 trials at each of the middle key values (28 trials). The remaining trials were forced (i.e., either the standard or number-left key was illuminated at the *T*th middle key flash). This test phase continued for 40 sessions.

In Phase 2 of testing the required number of flashes to reinforcement was increased by a factor of .5 for both the standard and number-left keys. Thus the standard key required 6 flashes to reinforcement and the number-left key required 12 – *T* flashes to reinforcement ($S = 6, I = 12$). The middle key required 1, 2, 3, 4, 6, 8, or 10 flashes. There were 28 choice trials per session and 14 forced choice trials per session. Birds were tested on these values for 25 days.

In Phase 3 of testing the standard and number-left key values were returned to the Phase 1 testing values ($S = 4, I = 8$). Ten sessions were conducted.

Finally in Phase 4 of testing the standard and number-left key values were reduced to 3 and 6 – *T* respectively ($S = 3, I = 6$). The middle key required 1, 2, 3, 4, or 5 flashes. There were 28 choice trials per session and 14 forced choice trials per session. Ten sessions were conducted.

Results

The central findings were that the pigeons' choice between the two side keys was controlled by the number of flashes it had generated by pecking the middle key and that increasing the *I* and *S* values by varying amounts had a linear effect on the indifference point; the bigger the objective difference between *I* and *S*, the higher the indifference point, contrary to the predictions of the logarithmic compression hypothesis.

Figure 1: *Psychometric functions relating probability of choosing the number-left key to the tallied number of flashes on the middle key for each of the four birds for the last 5 days of Condition 1. The fitted line is the best-fit model by a cumulative normal distribution.*

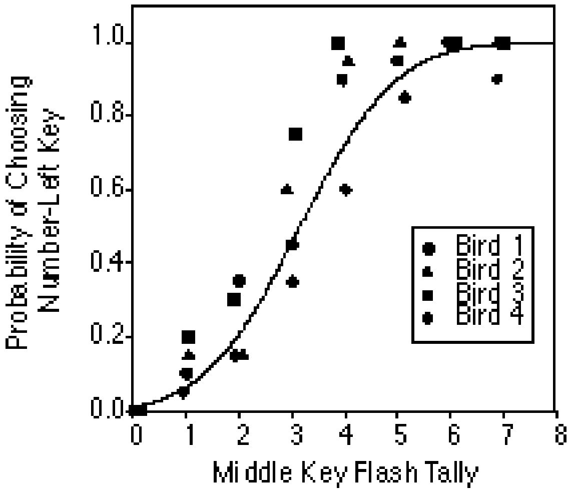

Figure 1 shows the probability of choosing the number-left key as a function of the number of flashes on the middle key in the first condition, where *I* = 8 and *S* = 4. When the tally of flashes generated by pecking on the middle key was low, the pigeons chose the standard key; when it was high, they chose the number-left key. A cumulative normal ogive fit to these data accounted for 99% of the variance. The indifference point is the tally (number of middle key flashes) at which this ogive crosses the 0.5 level. When the tally was less than the indifference point, the bird preferred the standard key; when it was greater than the indifference point, the bird preferred the number-left key.

Figure 2: *A: Psychometric functions relating the probability of choosing the number-left key to the tallied number of flashes on the middle key. B: Psychometric functions relating the probability of choosing the number-left key to the proportion of tallied flashes on the middle key.*

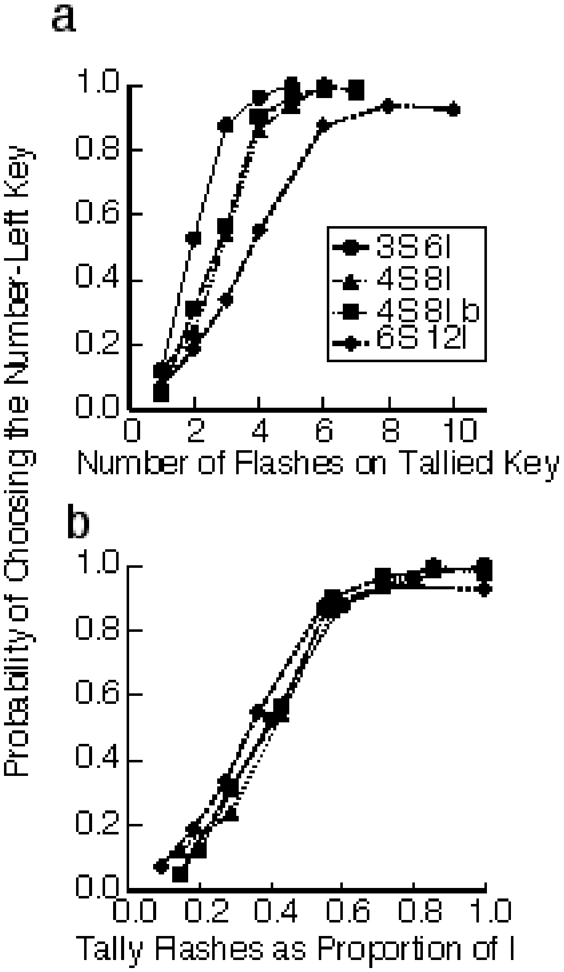

Figure 2a shows the same functions (probability of choosing the number-left key as a function of the middle key flash tally) for each of the four conditions. Each function reflects average values for the four birds for the last 5 sessions of the condition[1]. The indifference point shifted to the right, toward higher tallies, when the *S* and *I* values were doubled and to the left, toward lower tallies, when they were reduced by 25%. Figure 2b shows that the functions for the four conditions superpose when the probability of choosing the number-left key is plotted as a function of the proportion of middle key flashes. Thus the probability of choosing the number-left key was determined by the proportion of the initial number that had been produced by pecking the middle key in the period leading up to the choice.

Cumulative normal functions fit to the data in Figure 2 accounted for 99% of the variance in each case, so these curves accurately represent the data. The tallies at which these curves cross the 0.5 level gave us the indifference points for each condition. Figure 3 plots those indifference points for each of the four birds, as a function of the value of the standard, hence also as a function of the value of *I*, which was twice the standard in each condition. In each case, the indifference point appears to be a linearly increasing function of *S*, and thus of the $S - I$ difference for a condition. Regression analyses for each bird revealed that the slopes of the functions in Figure 3 were significantly different from zero for each bird ($p < .05$), while their intercepts were not significantly different from zero ($p > .1$). Thus increasing or decreasing the *S* and *I* values by the some factor produced a proportional increase or decrease in the indifference point.

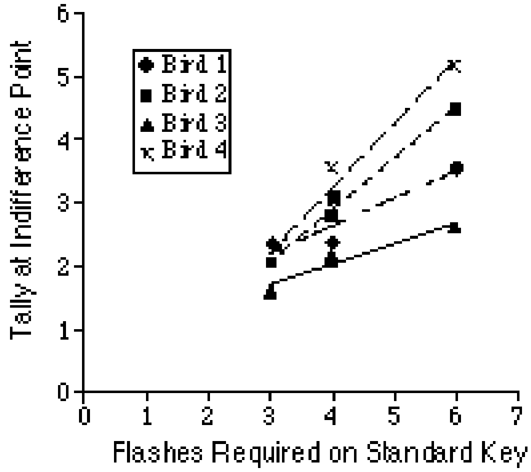

Figure 3: *The indifference point for each of the four conditions for each bird. Lines fit by least squares regression.*

Deconfounding Number and Time. It is already known that subjective time increases as a linear function of objective time (Gibbon and Church, 1981) our goal in this paper was to test whether this is also the case for number. Since pigeons peck at an approximately constant rate, the time spent pecking a key tends to covary with the number of flashes thereby generated. Furthermore, it has been demonstrated that timing sometimes contributes to numerosity discrimination in pigeons (Fetterman, 1993). It was therefore essential to show that the pigeons' choices were controlled by the number of hopper flashes that they generated, and not by the time spent generating them. That was the justification for delivering flashes on a variable ratio schedule. Such a schedule produces considerable variation in the number of pecks, hence the amount of pecking time, required to generate any given number of hopper flashes. Figure 4a shows the cumulative distribution functions for the time spent pecking on the middle key when *T* ranged from 1-7 flashes. The point where the cumulative function begins to rise gives the minimum amounts of time spent generating the requisite number of flashes; the point where it attains asymptote gives the maximum amounts of time so spent. Clearly, these minimum and maximum amounts of time were well separated for each flash tally. Most importantly, there was a great deal of overlap in these time distributions for different numbers of flashes (different tallies). Thus, we can determine whether the pigeons' behavior was controlled by time or by the number of flashes generated by plotting the probability of choosing the number-left key after a given tally of hopper flashes, as a function of the time spent generating that tally (Figure 4b). If time influenced pigeons' choice, these functions should rise, but in fact they are more or less flat, so variation in time did not affect choice. By contrast, for each increase in the middle-key flash tally, there is a marked increase in the probability of choosing the number-left key. Thus, choices were controlled by the flash tally, not by the time spent generating that tally.

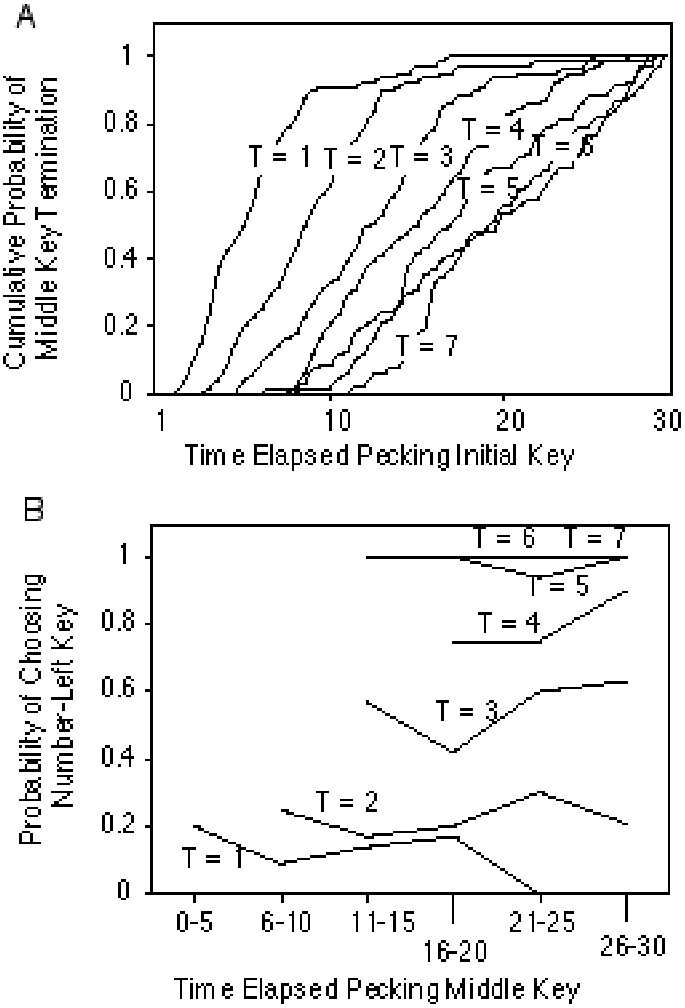

Figure 4: A *Cumulative probability distributions for the time spent pecking the middle key for each tallied number.* B *The conditional probability of choosing the number-left key as a function of the amount of time spent pecking the middle key. The amount of time spent pecking the middle key was a continuous variable but was averaged in discrete time bins for simplification. The probability of choosing the number-left does not vary systematically across time for any tallied number. The data in panels* A *and* B *are average values for the 4 birds and reflect the last 5 days of the first condition (4S: 8C).*

Discussion

In this experiment pigeons were required to estimate the numerical difference between two values (I - T) and compare that difference to a constant number, S. If, as has commonly been assumed, the subjective representation of numerosity were logarithmically compressed, then the tally number T, at which they judged the difference between I and T (the number left) to equal S should be constant for a constant ratio between I and S, even though the objective difference between I and S is made bigger by increasing both numbers by a common factor. This prediction of the logarithmic compression hypothesis is clearly false.

The alternative model, based on Gibbon's (1977) scalar expectancy theory, is that the subjective continuum is linearly (indeed, almost proportionately) related to the objective continuum but that the variability of the magnitudes read from memory increases in proportion to their mean value. The magnitudes representing the fixed numerosities I and S must live in memory, and be read from memory on every trial.

In scalar expectancy theory, the variability in the values read from memory accounts for the trial-to-trial variability in which key the subject chooses after a given flash tally. For any given intermediate tally, the subject sometimes chooses the standard key and sometimes chooses the number-left key. However, the greater the tally, the more likely the subject is to choose the number-left key. In scalar expectancy, this is explained by assuming that on each trial, the subject reads from numerical memory subjective magnitudes for S and I. Because, memory is noisy, the magnitudes read vary from trial to trial. On a trial when the magnitude read for S happens to be unusually low and the magnitude for I unusually high, the tally required in order for the subject to choose the number-left key will be unusually high. On trials, where the opposite variations occur, it will be unusually low. That is why, for a given intermediate tally, the subject sometimes chooses the number-left key and sometimes the standard key. Gibbon and Fairhurst (1994) have shown that in order to predict the superposability of the cumulative distributions shown in Figure 2b, it is necessary to assume: 1) that the variability in the magnitudes read from memory is proportional to the target magnitudes; and 2) the subjective variable that determines which choice the subject makes is the ratio of the two quantities being compared, in this case the ratio of $I - T$ and S.

An alternative explanation. As in the time-left paradigm, the number-left paradigm used here assumes that subjects subtract their count of the flash tally (their subjective tally) from their memory for the initial value, I. Subjects must then compare the result of this subtraction to their subjective reference value for the standard (also from memory). An alternative explanation, also considered by Gibbon and Church (1981), involves a kind of paired associate learning. High tallies on the middle key are associated with short delays of reinforcement on the number-left key, while low tallies are associated with long delays. Perhaps the birds learn simply to avoid the number-left key after low tallies and choose it after high tallies. While we cannot entirely rule out that possibility, our data suggest that it is unlikely, because the indifference point shifted immediately when the birds were shifted from the $S = 4, I= 8$ condition (indifference point for days 36-40 = 2.8) to the $S = 6, I = 12$ condition (indifference point for day 1 = 3.593). This change of condition reverses the signal values of intermediate tallies. Several tallies that used to signal the choice of the number-left key now signal the choice of the standard key. On the paired-associate hypothesis, this should require discrimination reversal learning, and, hence, the shift should not be seen immediately.

Can there also be logarithmically compressed representations of numerosity elsewhere in the brain? The logarithmic compression hypothesis is an hypothesis about how numbers are represented at the point in the brain at which the operation of determining their order is performed. Elsewhere, and for other purposes, numerosity might be represented on a continuum with different properties. What we have shown is that at the point in the brain where the separation between two representatives of numerosity is determined--for the purpose of comparing that numerical separation to another numerical quantity--the subjective continuum is not logarithmically compressed. It seems to us odd--and certainly not parsimonious--to suppose that the continuum used for the determination of the order of two numerosities is different from the continuum used for the determination of their separation, but there is no question that this could be the case. More generally, the fact that some property is represented in one way at one point in the brain and for one set of purposes is no guarantee that it is represented in the same way at other points in the brain and for other purposes. There is no reason to believe that there is only one representation of numerosity in the brain.

In summary, our findings support the conclusion that at least one subjective number scale is not logarithmic, namely, the scale used when a subject must compare differences in numerosity. Assuming that the subjective scale that mediates judgments of numerical order and the subjective scale that mediates judgments of numerical separation are one and the same, this implies that the magnitude and distance effects, which have inspired the logarithmic compression hypothesis, are rather to be attributed to the fact that the variability in the signals read from numerical memory is proportional to their mean value. This property is commonly called scalar variability (Gibbon, 1977). We believe our experiment also demonstrates, almost incidentally, that pigeons can do numerical subtraction.

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[1] Although data throughout this paper reflects the last 5 sessions of each condition, there is one exception. Data for Bird 4 in the 6S: 12C condition was taken from days 16-20 (rather than 21-25) because his indifference point decreased in the last block and was not representative of his previous performance.