

The neural basis of the Weber–Fechner law: a logarithmic mental number line

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The recent discovery of number neurons allows for a dissection of the neuronal implementation of number representation. In a recent article, Nieder and Miller demonstrate a neural correlate of Weber’s law, and thus resolve a classical debate in psychophysics: the mental number line seems to be logarithmic rather than linear.

Some twenty years ago, it was fashionable for many scientists to separate psychology from the study of the brain. Functionalist philosophers such as Jerry Fodor convinced a generation of psychologists that the comprehension of the mind called for the development of purely computational theories, without concern for their biological implementation. The computer metaphor promoted a logical separation of the software from the hardware, and led inevitably to the conclusion that the details of the neural machinery were irrelevant to the psychological enterprise.

Today, however, we know that this view was unnecessarily narrow. The new cognitive neuroscience routinely mixes psychological and neural observations in the same experiments. Psychological concepts are not ruthlessly eliminated, as was initially foreseen by the most opinionated anti-functionalist philosophers [1]. Rather, they are enriched, constrained and transformed by the accruing neural data. In a recent article, Andreas Nieder and Earl Miller [2] provide a beautiful illustration of this by showing how the study of the neural coding of number can resolve a classical problem in psychophysics: what is the mental scale for number?

Mental scaling: linear, logarithmic, or power function?

The ‘scaling problem’ was integral to the birth of psychology as a scientific discipline. Founding fathers of experimental psychology, including Weber and Fechner considered as one of their central goals the mathematical description of how a continuum of sensation, such as loudness or duration, is represented in the mind. By careful psychophysical experiments, often requiring thousands of discrimination trials on pairs of stimuli, they identified basic regularities of our psychological apparatus. Ernst Weber discovered what we now know as Weber’s Law: over a large dynamic range, and for many parameters, the threshold of discrimination between two stimuli increases linearly with stimulus intensity. Later, Gustav Fechner showed

how Weber’s law could be accounted for by postulating that the external stimulus is scaled into a logarithmic internal representation of sensation. More recently, Stevens discussed the possibility that the internal scale is a power function rather than a logarithm, and Shepard introduced the multidimensional scaling method as a means of estimating, without a priori assumptions, the geometrical organization of an internal continuum. Although Weber and Fechner concentrated on perceptual continua such as loudness, Stevens and Shepard showed that more abstract parameters, including our sense of number [3], also followed Weber’s law.

In spite of these brilliant analyses, often based on solid mathematical foundations, the Fechner–Weber–Stevens debate was never fully resolved [4]. One of the reasons is that there are basic mathematical ambiguities in the modeling of behavioral data. In particular, given suitable assumptions, both logarithmic and linear models of the internal scale are tenable. Fechner’s logarithmic scale easily accounts for Weber’s finding: if the scale has a fixed internal variability, then doubling the value of the compared quantities leads to a corresponding halving of discrimination power. However, the same discrimination function can also be accounted for by postulating a linear internal scale with a corresponding linear increase in the standard deviation of the internal noise. Here too, doubling the comparanda leads to a doubling of the variability and therefore to a halving of the discriminability.

In the case of the mental representation of number, Gallistel has argued that the linear model should be preferred because it allows for a simpler calculation of sums and differences [5]. Contrary to that, Changeux and I have proposed a simple neural network of numerosity detection that assumes a logarithmic encoding of number, thus avoiding an explosion in the number of neurons needed as the range of internally represented numbers increases [6]. I have also argued, however, that the psychological predictions of the linear and logarithmic models are essentially equivalent [7]. With the possible exception of a novel psychophysical paradigm [8], it is hard to see how behavioral observations alone could ever disentangle the linear and logarithmic hypotheses.

The neuronal code for number

The ability to record from neurons that are assumed to constitute the neural basis of the psychological number

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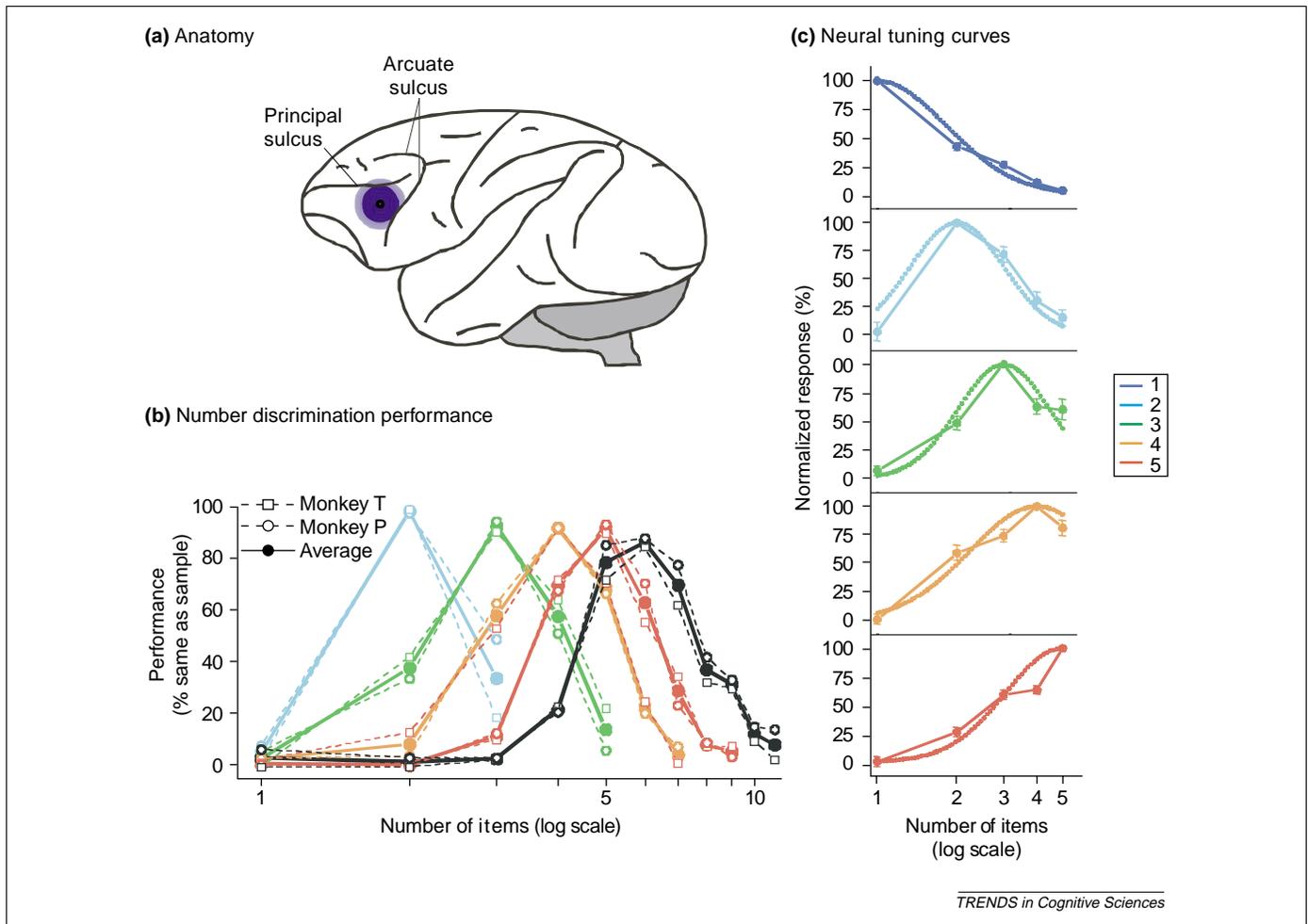


Fig. 1. Evidence for logarithmic coding of number in the monkey brain. (a) The anatomical location in monkey prefrontal cortex where Nieder and Miller recorded number neurons. In their experiments, monkeys were presented with a first set of dots, which they were then asked to discriminate from a second set of dots. (b) The percentage of trials on which they responded 'same' is plotted as a function of the second number (abscissa) for different values of the first number, which ranged from 2–6 during behavioral testing (color of plot). Performance decreased smoothly with the distance between the two numbers (i.e. the peak occurs when the two numbers are the same). This distance effect assumed a Gaussian shape when plotted on a logarithmic scale. (c) So did the tuning curves of individual number neurons (shown for 1–5).

scale now brings direct physiological evidence to bear on this issue. In the early days of neurophysiology, a few neurons that encoded number were reported in the association cortex of the cat [9], although this initial discovery was quickly forgotten. In 2002, however, two papers, one recording in parietal cortex and the other in prefrontal cortex, reported the observation of neurons whose firing rate was tuned to a specific numerosity [10,11]. A given neuron, for instance, might respond optimally to three visual objects, a little less to displays of two or four objects, and not at all to displays of one or five objects. This offered a unique opportunity to examine the neural code for an abstract psychological continuum.

As noted by Nieder and Miller, it was particularly interesting to investigate the neural basis of Weber's law with an abstract dimension such as number. For parameters that are more closely dependent on sensory physiology, such as loudness, weight or brightness, there is often evidence that the stimulus compression occurs at a peripheral sensory level. In the case of number, however, there are no obvious limitations in our ability to perceive multiple objects or sounds. Furthermore, in human subjects, Weber's law is even observed with symbolic

stimuli such as Arabic digits [3,12]. Thus, it is likely that Weber's law for numbers is determined solely by the internal organization of cortical representations.

In their paper, Nieder and Miller analyzed in minute detail the behavioral and neural response curves of two monkeys, which had been engaged in a task of discriminating the numerosity of two visually presented sets [2] (Fig. 1). They found clear evidence for Weber's law. Both animals showed a linear increase in their discrimination thresholds as the numerosity increased. Furthermore, the data were sufficiently regular to allow for a detailed analysis of the exact shape of the response distributions. When plotted on a linear scale, both behavioral and neural tuning curves were asymmetrical, and assumed a different width for each number. Both sets of curves, however, became simpler when plotted on a logarithmic scale: they were fitted by a Gaussian with a fixed variance across the entire range of numbers tested (Fig. 1b,c). Thus, the neural code for number can be described in a more parsimonious way by a logarithmic than by a linear scale.

It should be stressed that this form of internal representation was not imposed by the training scheme the monkeys had. Training was based solely on the

numbers 1 to 5, which were presented with roughly equal frequency. The optimal coding scheme would therefore have been a linear code with an exact encoding of each number 1, 2, 3, 4 and 5. The fact that the monkeys could not help but encode the numerosities on an approximate compressed scale confirms that this approximation mode is the natural way that number is encoded in a brain without language [13].

Future prospects

The monkey data of Nieder and Miller are just a first stab at the problem from the neurophysiological standpoint, and do not fully resolve the Fechner–Weber–Stevens debate yet. When Nieder and Miller fitted their data with a power function, they obtained only a slightly worse fit than that with the logarithmic scale. To discriminate the power and the logarithmic functions in future experiments, it will be important to increase the range of numbers tested. We know from behavioral paradigms that, once trained with small numerosities, monkeys generalize to larger numbers up to 10 or more [14]. This is another proof that the numerical ability of animals is not merely inculcated in them by laboratory training, but is inherent in their mental toolkit [12]. It is already remarkable that one can discriminate linear and logarithmic coding schemes with a range of numbers as small as 1 to 5. By testing the neurons with a greater range of numbers, it should be easier to see if the small advantage of the logarithmic fit over the power function fit found over the range 1 to 5 will continue to hold with larger numerosities.

Overall, Nieder and Miller's recordings confirm Fechner's intuitions of 130 years ago. The neural representation of number is comparable to the slide rule that some of us learned to use before the advent of electronic calculators, which was also graduated with a logarithmic scale. The advantages of this instrument were two-fold.

First, it was compact enough to allow the processing of arbitrarily large numbers with a pocket-sized device. Second, it ensured an accuracy proportional to the size of the numbers involved, something that was pertinent for real-life engineering applications. Perhaps the very same reasons can explain why nature selected an 'internal slide rule' as its most efficient way of doing mental arithmetic.

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Structure and pragmatics in informal argument: circularity and question-begging

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Most everyday arguments are informal, as contrasted with the formal arguments of logic and mathematics. Whereas formal argument is well understood, the nature of informal argument is more elusive. A recent study by Rips (2002) provides further evidence regarding the roles of structure and pragmatics in informal argument.

An exemplar of formal argument is the syllogism: *Socrates is a man, all men are mortal, therefore we may conclude that Socrates is mortal*. Formal argument is deductive;

given that the premises are true, any conclusion made without violating any rules of logic is also necessarily true.

Formal argument plays an essential role in areas such as mathematics and logic [1,2]. Informal arguments, however, are based on induction and marked by uncertainty. All propositions about the world are inherently imperfect; we believe that the sun will rise tomorrow, but we can as easily conceive of the alternative [3]. Countless events could turn us on our head, literally and metaphorically. No theory about the world can ever be fully proven or refuted; all are built upon countless unstated assumptions [4]. When we argue about whom to vote for or the best recycling policy, the imperfections

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