

Triangular lattice neurons may implement an advanced numeral system to precisely encode rat position over large ranges

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We argue by observation of the neural data that neurons in area dMEC of rats, which fire whenever the rat is on any vertex of a regular triangular lattice that tiles 2-d space, may be using an advanced *numeral system* to reversibly encode rat position. We interpret measured dMEC properties within the framework of a residue number system (RNS), and describe how RNS encoding – which breaks the non-periodic variable of rat position into a set of narrowly distributed periodic variables – allows a small set of cells to compactly represent and efficiently update rat position with high resolution over a large range. We show that the uniquely useful properties of RNS encoding still hold when the encoded and encoding quantities are relaxed to be real numbers with built-in uncertainties, and provide a numerical and functional estimate of the range and resolution of rat positions that can be uniquely encoded in dMEC. The use of a compact, ‘arithmetic-friendly’ numeral system to encode a metric variable, as we propose is happening in dMEC, is qualitatively different from all previously identified examples of coding in the brain. We discuss the numerous neurobiological implications and predictions of our hypothesis.

Recent experiments reveal that rats, notoriously good navigators, encode information about their position in 2-dimensional spaces in a remarkable way [1, 2]. Each neuron in the dorsolateral band of the mediolateral entorhinal cortex (dMEC) fires when the rat is on any vertex of an imagined regular triangular lattice, tiling the plane. The firing pattern is independent of the enclosure size and shape, and updates correctly as the rat moves around, even in complete darkness. These observations, together with lesion studies, hint that dMEC may play a central role in rodent path integration [2–5].

Nearby dMEC neurons share the same lattice period (λ) and orientation, and differ only in their relative spatial phases [2]. Thus at any instant, the active subset of neurons only specifies current rat position as a phase: upto, or *modulo*, all possible periodic displacements of the lattice. Moving ventrally along the length of dMEC, the neural lattice period increases monotonically, but the measured range is narrow: from approximately 30 cm to 70 cm [2]. In summary, we note that dMEC neurons decompose the 2-dimensional vector of rat position into a set of phases, modulo a set of lattice periods, along two independent lattice directions.

While phases within the smallest lattice – about the size of the rat – might arguably vary at the appropriate scale for fine position discrimination during navigation, the largest lattice period (< 2 m, by extrapolation along dMEC length) puzzlingly appears to fall far short of the range over which a rat might know its position.

Can the phases of such a narrow range of lattices even theoretically contain enough information to unambiguously represent position over the behaviorally relevant range of distances covered by rats? And even if so, what is the advantage of decomposing rat position – a quantity that can in theory be represented simply by a pair of numbers – in this distributed, seemingly bizarre way?

Based on the observation that dMEC stores only mod-

ulo information about rat position, we suggest that dMEC may be encoding and enabling the reconstruction of the two-coordinate rat position vector according to a generalized version of a residue number system (RNS) [6], a scheme with uniquely useful properties in the neurobiological context. In an RNS, a number x (e.g., position in 1-d) is represented by a list ($x_i = x \bmod \lambda_i$) of its *residues*, or remainders after division by a set of fixed numbers ($\lambda_1, \lambda_2, \dots, \lambda_N$), relatively prime to each other, called *moduli*. For example, if the moduli are (13, 15, 16, 17, 19), the number 1000000 is represented by the residues (1, 10, 0, 9, 11). The Chinese Remainder Theorem (CRT) guarantees that any number smaller than the product of all the moduli is uniquely specified by (and therefore can be reconstructed from) its residues. In the example above, any number up to 1007760 has a unique representation. An RNS has striking parallels to dMEC encoding: According to our interpretation, the dMEC lattice periods are the RNS moduli (which need not be co-prime integers, as we discuss later); the lattice phases, specified by the active set of neurons at any given rat position, are the residues.

In an RNS, large numbers (e.g. position in a large space) are represented combinatorially and thus compactly; this property is shared with base numeral systems like decimal or binary. A small set of registers (N) can represent a very large range of numbers ($[0, 10^N - 1]$: decimal, $[0, 2^N - 1]$: binary, or $[0, \lambda^N - 1]$: RNS, where λ is the approximate size of the moduli, and N is the number of moduli; in the example above, $\lambda \approx 16$, $N = 5$). By contrast, in a sparse encoding scheme where each element represents one possible number (e.g. place-cell representation of position in hippocampus), N elements only cover the range $[0, N - 1]$. But besides its combinatorial capacity, two unique features of an RNS make it especially useful, compared to base numeral and other systems, for position encoding in dMEC.

First, the set of registers in an RNS that support its vast representational capacity can be very closely spaced, span-

ning a narrow range: as illustrated above, all moduli may be nearly equal. By contrast, successive registers in base numeral systems must represent information on geometrically spaced scales differing by powers of say 2 or 10. The largest register must represent a scale comparable to the largest representable number and the smallest register scale must be comparable to the finest resolvable detail. The ability of an RNS to use closely spaced registers to represent a large range of positions is critically useful for position encoding in dMEC, with its narrowly distributed lattice periods.

Second, addition, subtraction, and multiplication are completely parallelized in an RNS, because unlike base numeral systems, they require no “carrying-over” of information from one register to the next: the sum of two numbers is the modulo sum of their residues computed independently within each register. In computer science, this property has long been appreciated and is used to perform fast, parallelized computations in signal processing and RSA applications [6–8]. The moving rat, using an RNS, can update its estimate of position by independently incrementing the phases of each lattice, without carrying phase winding information from one lattice to another. Indeed, in dMEC each lattice phase is independently updated as a function of rat position, without evidence of jumps in phase when a smaller lattice completes one winding.

Some important properties of dMEC encoding differ from a standard RNS. Lattice periods in dMEC are probably not co-prime integers, but real numbers, as is rat position. Also unlike an RNS, where the number of residues (distinguishable phases or phase resolution) grows with modulus size (lattice period), the phase resolution in dMEC seems constant across lattices. Under these conditions, existing exact formulas for reconstructing numbers from their residues using the CRT no longer apply, and the representational capacity may be much smaller than possible in a standard RNS. But despite these differences, summation and multiplication are still fully parallelized, and we show without recourse to any particular decoding scheme, that the representational capacity continues to scale exponentially with the number of (non co-prime) lattices, spanning a vast range of real-valued positions with high resolution (Figure 1 and Supplementary Information). The uniqueness of this representation guarantees that an inverse map from lattice phases to position still exists. The capacity (Figure 1) under a generalized RNS encoding is far in excess of the navigational requirements of rats, and the surplus capacity could be devoted to redundancy for error correction [6, 8] and robustness.

To summarize our argument, we suggest that dMEC treats position simply as a 2-coordinate vector, and then encodes the coordinates, two real *numbers*, using a unique numeral system that can represent large numbers with a narrowly spaced set of registers. At first glance, one might have imagined that dMEC firing reflects some kind of integral transform (e.g. Fourier or Wavelet) of 2-dimensional space and the rat’s location in it. To do this, dMEC would have to treat rat position as an entire 2-*d function*, such as a blob centered at the rat’s location in

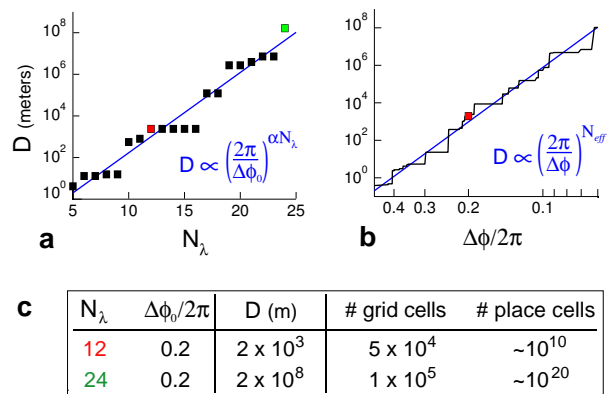


FIG. 1: Capacity of dMEC under generalized RNS encoding. The maximum uniquely representable distance, D , grows exponentially as a function of number of lattices, N_λ , **a**, and as a power of the phase uncertainty $\Delta\phi$, **b**, even when the lattice periods are not co-prime and even if the phase uncertainty is equal across lattices. [The first lattice period is 30 cm, with 4 cm increments per subsequent lattice. In **a** $\Delta\phi/2\pi = 0.2$, and in **b** $N_\lambda = 12$. The fit parameters are $\alpha \simeq 0.55$ and $N_{eff} \simeq 9.7$. See Supplementary Information for more details.] **c** 12 lattices uniformly spaced from 30 cm to 74 cm with 5 resolvable phases in each direction can unambiguously represent a $\sim 2 \text{ km} \times 2 \text{ km}$ area with 6 cm resolution. If 5000 neurons build each lattice, that would require $\sim 5 \times 10^4$ neurons. To cover the area with sparse unimodal place-cell like encoding (with 10 neurons per $(6 \text{ cm})^2$ block) would require $\sim 10^{10}$ neurons, compared to the estimated 10^5 neurons in rat dMEC [16, 17], which could sparsely represent at most $\sim 6 \text{ m} \times 6 \text{ m}$ with $(6 \text{ cm})^2$ resolution. With 24 lattices, $D \sim 2 \times 10^5 \text{ km}$ in each direction, hugely in excess of the representational requirements of rats.

space, and transform this into a set of 2-d patterns of different spatial frequency. Besides the computational unnecessary of representing two position coordinates by an entire function, the integral transform scheme is unlikely for at least two reasons: (1) It is incompatible with the data. The experiments [1, 2, 9] unequivocally show that the patterns of dMEC activity are stereotyped, and independent of enclosure size or shape; given the activity pattern of one neuron in each lattice in any one enclosure, the activities of the rest are well specified upto a spatial phase shift in all enclosures. Thus, dMEC encoding contains little additional information or flexibility to describe general functions in 2-d space, as required of integral transforms. (2) A Fourier-like transform cannot be used to represent position unambiguously over a distance greater than the largest lattice period ($\sim 2 \text{ m}$). To reconstruct a single bump of rat position over a range D with resolution D_{min} would require lattice periods ranging from smaller than D_{min} up to D .

Our focus here has been on characterizing the general theoretical properties of position *encoding* in dMEC. These insights provide the necessary foundation for understanding how information encoded in dMEC may be used by areas that receive dMEC inputs. We have illustrated, without regard to specific *decoding* schemes, how the maximal capacity

of dMEC for unambiguous position encoding scales as a function of dMEC phase resolution and lattice numbers, and have observed based on the properties of an RNS and our simulations, that these phases theoretically contain enough information to uniquely encode position over a combinatorially large range. As we discuss next, our interpretation of dMEC encoding raises several testable questions with specific implications for theory and experiment.

The most basic of these is whether the rat does actually make use of the range of information we have shown is theoretically available in dMEC under an RNS-like scheme. There are two (not mutually exclusive) ways in which rats may use this information: (1) For homing and path integration over large ranges by decoding the relative dMEC phases to compute rat displacements, or (2) For attaching unique ‘labels’, as described below, to a large number of specific locations, with landmark-independent path integration only between nearby locations. Either scenario can be probed experimentally, as we describe below, but in both cases resolving the fundamental issue requires testing in enclosures of size approaching the behaviorally relevant range for rats.

In the first case, assuming dMEC is the primary source of position representation, our proposal would be strongly supported if the rat can perform reasonably accurate landmark-free homing behaviors over ranges much larger than the largest dMEC lattice period. This scenario would require an explicit decoding of the phase encoding of position. Because position encoding by modulo residues, which we argue is happening in dMEC, is a 1-1 onto (bijective) function over the illustrated range (Figure 1) of positions, the mathematical inverse exists and is unique. However, there could be numerous possible neurobiological decoding schemes to exactly implement this inverse or approximate it. Our capacity estimate, which contains the experimentally observed phase uncertainty, bounds how much information can be extracted from dMEC and should be used as a guide for evaluating the efficiency of different decoding schemes. Experimentally, the test of the long-range position encoding hypothesis involves measuring the largest lattice period in dMEC, and quantitatively determining the range over which rats can perform accurate homing in large featureless spaces.

In the second case, the large set of unique dMEC phases as a function of rat position may be used as absolute markers for specific landmarks or positions in familiar environments. In this scenario, the rat may *not* explicitly decode position or displacements over distances larger than a lattice period, but may essentially use the vast set of distinct dMEC phases to uniquely represent a large number of distinct, spatially separated locations. The rat may locally perform path integration by updating phases, to ensure that starting from an absolute phase at landmark A, the rat can take any path to landmark B and yet obtain the correct absolute phase for B. Such a system would be useful to the rat in distinguishing a familiar landmark from a lookalike but spatially distinct location [10]. This proposal could be tested experimentally by checking at multiple familiar landmarks in large, partially occluded enclosures

whether the absolute dMEC phases for each landmark are reproducible across trials. If dMEC is reset to a set of previously assigned phases for landmark B upon reaching B from a novel occluded path and after extensive exploration in an unfamiliar landmark-rich environment, it would suggest that absolute phases are important; the RNS scheme would allow dMEC to uniquely encode a large number of landmarks.

Unlike most numeral systems, in an RNS scheme the representation of space by the different registers or dMEC lattices is not hierarchically ordered: all lattices are roughly equal in their contribution to position representation at any scale. Therefore, if hippocampal place cells are involved in reconstructing a position estimate or reading out a unique label of a landmark from dMEC, each local group of hippocampal cells must pool input from *many* different dMEC lattices; indeed, neurons in the septal (dorsal) half of the long axis of the hippocampus do appear to receive inputs from across the dMEC band [11]. In addition, position reconstruction from an RNS is susceptible to characteristic deficits following microlesions that successively destroy individual dMEC lattices. Error correction and redundancy could grant the system resilience against partial lesions, but beyond a critical point, there should be a sudden degradation in position estimation or location representation at all scales. By contrast, in any scheme where different lattices encode positions at their corresponding spatial scales, selectively lesioning the smallest (largest) lattices is likely to destroy fine (coarse), but not coarse (fine), position estimation.

When rats are trained to explore small enclosures or 1-d tracks, neurons in the hippocampus – the primary output target of dMEC, and a critical locus of spatial learning and memory – tend to form unimodal place-fields that resolve position with relatively high accuracy, and cover the space [12, 13]. Based on our analysis, we predict that the inefficiency of sparse encoding (Figure 1c) and limited neuron numbers in hippocampus ($\sim 10^5 - 10^6$ neurons) [16], rule out the possibility that hippocampus could fully remap large enclosures with high resolution using unimodal place-cells. Rather, driven by representational limitations in large areas, place cells must either generically develop multi-peaked responses as a function of rat position to cover space with reasonably high resolution, akin to dMEC neurons, or must disengage from finely representing all space with narrow place fields, instead covering only select locations based on other salient cues or associations. The latter scenario would make hippocampus a selective consumer and processor of position information from dMEC, leaving it free to perform more general associative tasks [9, 14, 15].

The possibility that dMEC may be representing position, a continuous metric variable, using a compact and parallelized *numeral system* amenable to arithmetic operations such as addition or shifts on the variable, is itself extraordinary. Such a numeral system code is qualitatively different from all other known examples of coding in the brain [18]: Proportional-rate coding (e.g., eye position and firing rate in the oculomotor system [19]), unary or sparse coding (e.g., head direction

cells [20], place cells [12]), or even other kinds of combinatorial codes which represent non-metric variables (e.g. odor [21]) and therefore lack an arithmetic aspect. This encoding scheme provides insight into the ingenuity of neural codes, and provokes questions at the intersection of neuroscience, mathematics, and computer science.

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