Spatial Navigation

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Based on the observation that dMEC stores only modulo information about rat position, we suggest that dMEC may be encoding and enabling the reconstruction of the two-coordinate rat position vector accoording to a generalized version of a residue number system (RNS), a scheme with uniquely useful properties in the neurobiological context.

The uniqueness of RNS representation, guaranteed by the Chinese Remainder Theorem (CRT) allows us to use a small set of cells to compactly represent and efficiently update rat position with high resolution over a large range.
To understand this numeral system, we need the help of some math stuff first.

Chinese remainder theorem (CRT) refers to a result about congruences in number theory.

Suppose n_1, n_2,..., n_k are integers which are pairwise coprime. Then, for any given integers a_1,a_2,..., a_k, there exists an integer x solving the system of simultaneous congruences.

$$\begin{cases} x \equiv a_1 \pmod{n_1} \\ x \equiv a_2 \pmod{n_2} \\ . \\ . \\ . \\ x \equiv a_k \pmod{n_k} \end{cases}$$

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Furthermore, all solutions x to this system are congruent modulo the product $N = n_1 n_2 ... n_k$.
Hence $x \equiv y \pmod{n_i}$ for all $1 \leq i \leq k$, if and only if $x \equiv y \pmod{N}$.
Sometimes, the simultaneous congruences can be solved even if the n_i's are not pairwise coprime. A solution x exists if and only if for all i and j:

$$a_i \equiv a_j (\bmod \gcd(n_i, n_j))$$

All solutions x are then congruent modulo the least common multiple of the n_i.

Example

Given moduli $(13, 15, 16, 17, 19)$, the number $1,000,000$ is represented by the residues $(1, 10, 0, 9, 11)$. 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 $1,007,760$ has a unique representation.

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We assume that unlike a standard RNS, the dMEC lattice spacings are not coprime integers, and the encoded position is a real number (not necessarily an integer).

There is no clear analytical statement for how the representational capacity of a generalized RNS, with limited, constant phase resolution across lattices and non-coprime lattice spacings, compares to that of a standard RNS, but we show without regard to any particular readout scheme that the capacity is large, and scales similar to a standard RNS.

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Consider a set of lattice spacings or moduli, $\{\lambda_i | i = 1, ..., N_\lambda\}$. A position x_1 is represented by the vector of its residues,

$$x_{1i} \equiv x_1 (\mod \lambda_i) \qquad\qquad i = 1, ..., N_\lambda$$

Or equivalently, phase vector ϕ_1, whose entries are

$$\phi_{1i} \equiv \frac{2\pi x_{1i}}{\lambda_i} (\mod 2\pi)$$

Assume that each phase can only be resolved up to a spread $\triangle\phi$. Then the lattice phases can be used to distinguish between x_1 and x_2 if there is a mismatch of more than $\triangle\phi$ in at least one entry of their phase vectors.

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In dMEC encoding, to speak of distances instead of integer numbers, we may associate a length scale of unity to the finest distance resolution, $D_{\text{min}} = 1$. The maximum representable range is then $D_{\text{max}} = N_{\text{max}} = \lambda_1 \lambda_2 ... \lambda_{N_\lambda}$.

To simplify things further, assume all the lattice periods λ_i are similar in size, then the maximum range scales exponentially with N_λ and as a power of the distinct number of states in each register $(\sim \lambda)$:

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In the more general case where the λ_i are real numbers with a finite resolvable phase resolution, phase is discretized into $2\pi/\triangle\phi$ bins which correspond to the approximate number of resolvable states of each lattice, and we have

$$N_{\max} = (\frac{2\pi}{\triangle\phi})^{N_\lambda}$$

The finest resolvable change in position is $D_{\min} = \lambda_1 \triangle\phi/2\pi$, where λ_1 is the smallest lattice spacing.
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As in standard RNS, the maximal combinatorial capacity may be achieved only for particular choices of λ_i. For generic choices of the lattice periods λ_i, the representable range may not reach the bound $D_{\max}$; nevertheless, we still expect the range $D_{\max}$ to scale exponentially with the number of lattices N_λ, and algebraically with the number of states in each lattice $2\pi/\triangle\phi$:

$$D_{\max} \propto \left(\frac{2\pi}{\triangle\phi}\right)^{\alpha N_\lambda}$$

Here the parameter α is expected to be of order unity.
And this relation is an ansatz.

In summary, our numerical results imply that capacity scales algebraically with phase resolution and exponentially with the number of lattices.

Interestingly, this implies that to achieve a large capacity with a fixed number of neurons, neurons should be devoted to building more lattices rather than increasing the phase resolution: a result which may help to explain the surprisingly poor phase resolution found in dMEC, where neural activity blobs cover 1/3 of the total lattice period.

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Interestingly, this implies that to achieve a large capacity with a fixed number of neurons, neurons should be devoted to building more lattices rather than increasing the phase resolution: a result which may help to explain the surprisingly poor phase resolution found in dMEC, where neural activity blobs cover $1/3$ of the total lattice period.

With the help of the above math stuff, we are ready to explain all data entries in Figure 1.

We first try to understand Figure 1 (a).

The relationship $D_{\text{max}} \propto (\frac{2\pi}{\triangle\phi})^{\alpha N_\lambda}$ has already been established.

α is tested by comparison with the numerical results for particular sets of the lattice spacings and in this case $\alpha \simeq 0.55$.

We conservatively assume a phase resolution of 1/5 of a period, or equivalently, $\triangle\phi/2\pi = 0.2$.

With all these fit parameters, the maximum range D_{max} does scale according to the ansatz.

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Next we try to understand Figure 1 (b).
We have a slightly modified relationship $D_{\text{max}} \propto (\frac{2\pi}{\triangle\phi})^{N_{\text{eff}}}$.
Still, we conservatively assume a phase resolution of 1/5 of a period, or equivalently, $\triangle\phi/2\pi = 0.2$.
Moving ventrally along the length of dMEC, the first lattice period is 30cm, with 4cm increments per subsequent lattice, and the last lattice period is 74cm. Thus, N_λ is 12. And the fit parameter $N_{\text{eff}} \simeq 9.7$.
With all these fit parameters, the maximum range D_{max} does scale according to the ansatz.

Figure 1 (c) is rather complicated. We try to understand it bit by bit.

We look at the first row of the table first.

$N_\lambda = 12$ as has already been explained in Figure 1 (b).

From Figure 1 (a), we see that D_{max} is roughly 2km. Thus in our Cartesian system, the lattices can unambiguously represent a 2km $\times$ 2km area.

If $5,000$ neurons (grid cells) build each lattice, that would require

$$5,000 \times 12 \sim 5 \times 10^4 \text{ neurons}$$

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$$5,000 \times 12 \sim 5 \times 10^4 \text{ neurons}$$

The resolution is given by D_{min}, whose formula we have derived before:

$$D_{\text{min}} = \lambda_1 \triangle\phi/2\pi$$

Here, $\lambda_1 = 30$, the smallest lattice spacing. And $\triangle\phi/2\pi = 0.2$, so we have $30 \times 0.2 = 6$cm resolution in each direction.
To cover the area with sparse unimodal place-cell like encoding (with 10 neurons per $(6\text{cm})^2$ block) would require

$$10 \times \frac{(2,000)^2}{(0.06)^2} \sim 10^{10} \text{ neurons}$$

Next we look at the second row of the table. It's completely analogous to the first row.
$N_\lambda = 24$ now, as a comparison to the first row.
From Figure 1 (a), we see that D_{max} is roughly 2×10^5km. Thus in our Cartesian system, the lattices can unambiguously represent a (2×10^5)km $\times$ (2×10^5)km area.
If $5,000$ neurons (grid cells) build each lattice, that would require

$$5,000 \times 24 \sim 1 \times 10^5 \text{ neurons}$$

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To cover the area with sparse unimodal place-cell like encoding (with 10 neurons per $(6\text{cm})^2$ block) would require

$$10 \times \frac{(2 \times 10^8)^2}{(0.06)^2} \sim 10^{20} \text{ neurons}$$

Accoding to exerimental results, in rat dMEC, the number of neurons is estimated to be approximately 10^5. And this could sparsely represent at most $\sim$ 6m $\times$6m with (6cm) resolution. As given by the following computation:

$$\frac{10^5}{10} \times (0.06)^2 \sim 6^2$$

We have understood the second row completely and found that the capacity obtained are hugely in excess of the representational requirements of rats, which could be devoted to redundancy for error correction and robustness.

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There are two (not mutually exclusive) ways in which rats may use this kind of dMEC information under an RNS-like scheme. We'll discuss them in the following.

For homing and path integration over large ranges by decoding the relative dMEC phases to compute rat displacements.

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 (< 2m, by extrapolation along dMEC length).

Experimentally, this involves measuring the largest lattice period in dMEC, and quantitatively determining the range over which rats can perform accurate homing in large featureless spaces.

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Attaching unique 'labels', to a large number of specific locations, with landmark-independent path integration, only occurs between nearby locations.

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.

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.

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In any sense, 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.