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# Temporal Neuronal Oscillations can Produce Spatial Phase Codes

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## Summary

The ability to integrate information over time is a fundamental operation of the brain, but the neuronal mechanisms underlying it are poorly understood. Here we describe how rhythmic variation in the activity of neurons—a common observation in neural recordings—could provide one such mechanism. In particular, we review a model that uses interference between neuronal oscillations to account for the spatio-temporal firing patterns of place cells in the hippocampus and grid cells in entorhinal cortex. The mechanism integrates movement information by varying the frequencies of the oscillations according to running velocity, thus mapping temporal oscillations into phase codes for *distance traveled* and, in combination with environmental information, *spatial location*. This provides a specific model of path integration and spatial orientation, but also provides an example of how, more generally, dynamic neural oscillations could be used to integrate and encode information. In this vein, we suggest how representations of sequential (or “rank”) order and numerosity could also be generated using such a system.

The idea of related processing mechanisms in the brain for spatial and temporal information enjoys increasing popularity among researchers, as reflected in some of the chapters in this volume (see also [1,2]). Here we discuss how subthreshold membrane potential oscillations (MPOs) could encode representations of the animal’s spatial location in their phase relationship with other oscillations. The oscillatory interference model of how the spatial firing patterns of grid cells in the entorhinal cortex [3] could result from motion-related

information on speed and direction of movement is reviewed. We discuss how, in principle, similar models could also account for representations of sequential order [4,5].

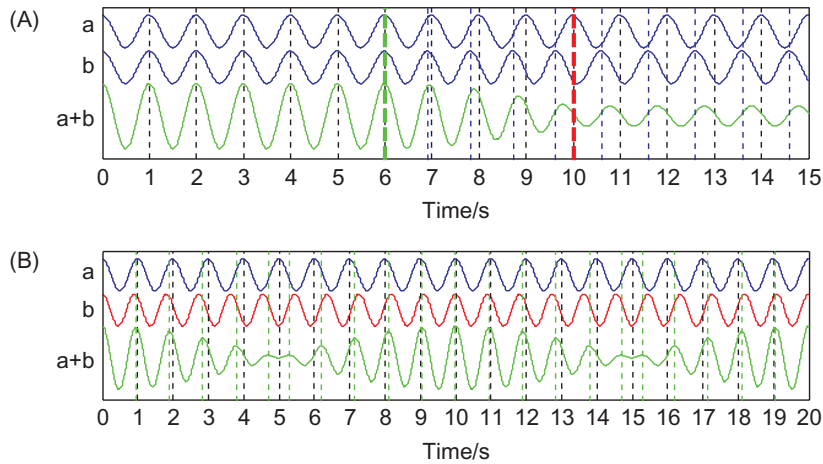
Our starting point is the observation of “theta phase precession” in the firing of “place cells” in the hippocampi of freely moving rats [6]. Place cells embody a representation of space: each cell firing whenever the animal enters a specific portion of its environment (the corresponding “place field”, see [7]). In parallel to this firing rate code for location, a temporal or phase code has also been observed relating to the theta rhythm: a large-amplitude oscillation in the local field potential of navigating rats, at 6–10 Hz in adult rats [8,9]. As the rat runs through a place field, the corresponding place cell fires bursts of spikes at systematically earlier phases of the theta rhythm such that the firing phase corresponds to the location of the rat within the place field. O’Keefe and Recce [6] suggested that this firing pattern reflected an intrinsic MPO in place cells which has a slightly higher frequency than the theta rhythm when the rat is in the place field (see also [10]). Subsequent research has confirmed the independence of the phase code from the firing rate code [11] and verified the link between firing phase and an intrinsic MPO in place cells [12].

An interesting aspect of place cell phase precession is that the phase of firing correlates with the distance traveled through the place field whether the rat runs quickly or slowly [6,11]. This suggests that the MPO frequency must increase with running speed so that the *temporal* oscillation can produce a phase code for *distance* [10]. Here we review the potential for neuronal oscillations to produce a representation of spatial location by integrating the animal’s velocity (i.e. speed and direction of running)—a process often referred to as “path integration”. Such a mechanism has been proposed to explain the spatial firing pattern of “grid cells” in the entorhinal cortex of freely moving rats [3] (see [13,14]). In addition, we examine the potential for neuronal oscillations to produce a representation of the serial order of stimuli, such as seen in recordings from primates [4,5].

## A FUNCTIONAL ROLE FOR INTERFERENCE BETWEEN NEURONAL OSCILLATIONS

Oscillatory behavior of single neurons or groups of neurons is a common finding in a variety of brain areas. On a single-cell level, this dynamic is likely linked to voltage-sensitive membrane currents (e.g., [15]). In the review below, we focus on potential functional mechanisms that utilize interference between neuronal oscillations, and leave out many of the biological details and constraints that have been discussed elsewhere [14,16,17]. The general principle of phase coding and oscillatory interference can be understood by considering a pair of oscillations, initially matched in phase and frequency, that experience a transient frequency difference (see Fig. 5.1A). Undisturbed, they will remain in phase indefinitely as long as their frequencies remain equal. However, a change in one of their frequencies will cause a drift in their phases relative to one another for the duration of the change (with a rate of drift proportional to the frequency difference). Crucially, once the oscillation frequencies become equal again, any acquired phase advance will be maintained until another frequency change should further modify it. Mathematically, the phase difference between the two oscillations,  $\phi_{ab}(t) = \phi_a(t) - \phi_b(t)$ , is the time integral of their frequency difference, i.e.

$$\phi_{ab}(t) = \phi_{ab}(0) + \int_0^t 2\pi[f_a(\tau) - f_b(\tau)]d\tau \quad (5.1)$$



**FIGURE 5.1** The amplitude of interference patterns between oscillations reveals the difference between their phase, which, in turn reflects their history of past frequency differences. (A) Oscillations a and b (blue) begin matched in frequency and phase. A transient frequency increase in oscillation a (beginning at the green vertical dashed line) causes it to drift ahead in phase relative to a. Once oscillation a returns to baseline (vertical red dashed line), the acquired phase difference is preserved. The amplitude of the interference pattern produced by their addition (green plot) reflects their phase difference. Peak times of oscillations a and b are indicated by black and blue vertical dashed lines respectively. (B) Oscillations a and b (blue and red, respectively) each have constant frequency but b is slightly faster (A: 1 Hz, B: 1.1 Hz), causing a cyclical advance in relative phase. The amplitude of their interference delineates an oscillating envelope with a wavelength of their frequency difference (i.e. 0.1 Hz). Peak times of oscillation a are indicated by black vertical dashed lines, while the peaks of the interference pattern are indicated by green vertical dashed lines.

where  $\phi_a$  and  $\phi_b$  are the phases of the two oscillations, and  $f_a(t)$  and  $f_b(t)$  are their time-varying frequencies. The relationship between oscillatory phase and frequency offers a potential mechanism for neuronal oscillations to integrate information arriving over extended periods of time. Although such protracted integration of information is a fundamental property of memory, its neuronal implementation is non-trivial. Hence one of the features of the oscillatory interference model is to offer a plausible account of how this could be achieved by neurons whose membrane potential or firing rate undergoes rhythmic variation.

If the frequency difference between two oscillations varies according to some variable  $X$ , at any given moment, the relative phase between the two oscillations will reflect the time integral of  $X$ . Since oscillatory phase is periodic, such an encoding scheme will also be cyclic; e.g., under a sustained frequency difference, two oscillations will move steadily into and out of phase with one another. When two such oscillations are combined, e.g., by addition, to generate an interference pattern, the amplitude of the resulting oscillation waxes and wanes as the two oscillations transition between constructive and destructive interference (see Fig. 5.1B). The amplitude profile is referred to as the envelope of the interference pattern, and varies with a frequency equal to the difference between the frequencies of the two oscillations. The amplitude of the envelope is proportional to the phase difference at that moment, and therefore also proportional to the time integral of  $X$ . Furthermore, the peaks of the interference pattern occur between the peaks of the two oscillations. This is an important property for phase coding discussed later since, as a consequence, the interference peaks always

advance relative to those of the slower oscillation and regress relative to the faster oscillation (see Fig. 5.1B).

In this way, oscillatory interference offers a potential mechanism to retrieve information dynamically integrated over time. First we consider how these principles have been applied to models of grid cell firing and later we describe a new potential model for the firing of rank-order cells [4].

## AN OSCILLATORY INTERFERENCE MODEL OF GRID CELL FIRING

Grid cells recorded in the medial entorhinal cortex of freely moving rats fire whenever the animal is located within one of a number of spatially defined regions or “firing fields”. The firing fields of individual cells define the vertices of a remarkably regular triangular or hexagonal array mapped onto the environment surface, providing a very specific representation of the animal’s location within the environment (see Box 5.1 and Fig. 5.2). In the

### BOX 5.1

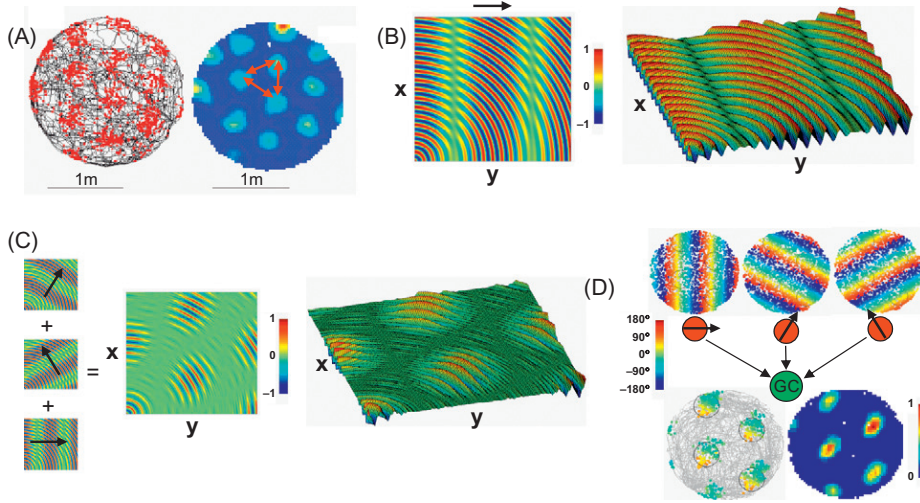
#### NEURAL BASIS OF SPATIAL NAVIGATION: ENTORHINAL GRID-CELLS

Grid cells, first discovered in the medial entorhinal cortex (MEC) of freely moving rats exhibit spatially modulated firing fields, much like the hippocampal place cells discovered before them. However, unlike place cells, a grid cell fires in multiple firing fields that are repeated across the environment, arranged in a regular triangular structure. Within individual fields, the firing rate of cells is center-peaked, diminishing with distance relative to the field center. Their spatial stability in the face of variation in the animal’s speed and direction intimate that they are performing a path integrative function, i.e. using self-movement information to continually update the animal’s estimate of its position. Furthermore, a prominent feature of the hippocampal-entorhinal brain region is the prevalence of local field potential oscillations in the theta band.

Like place cells, the majority of grid cells show a spatial organization in the phase of

firing relative to the theta oscillation; firing occurs at progressively earlier phases of subsequent theta cycles as the animal passes through the field [22]. Such phase precession can be explained if grid cell firing reflects interference between oscillations with shifting relative phases. Indeed, the oscillatory interference model was originally proposed to explain the same phenomenon in the firing of place cells [6].

The firing patterns of grid cells appear to provide a metric of space: compellingly, the grid scale of cells varies systematically along the dorsoventral axis of the MEC [35]. The activity of a few cells with different scales could unambiguously encode an animal’s location. Intriguingly, while grid cells have so far only been recorded in rats and mice, there is also evidence for grid cells in the human MEC, as well as grid-like firing in other regions putatively involved in spatial navigation and memory [25].



**FIGURE 5.2** An oscillatory interference model can explain the spatial firing patterns of grid cells. (A) Spatial firing maps of a grid cell recorded from a rat during a 30-min run in a circular environment (2m diameter; scale bars shown). Left: Spike locations (red) superimposed onto the trajectory of the animal in the enclosure (black). Note how the spikes occur within an array of distinct “firing fields”. Right: Spatial rate map showing the mean firing rate of the cell across the environment. The triangular structure of the field array is emphasized by the red arrows. Adapted, with permission, from Moser and Moser, *Hippocampus* 18: 1142–1156 (2008). (B) The spatial interference pattern between two oscillations with a velocity-modulated frequency difference, during constant velocity runs from the origin (bottom left). Amplitude modulation of the envelope occurs only along the preferred direction (arrow). Left: Flat amplitude color-coded map. Right: 3-D plot showing amplitude on the z-axis. Note the clear interference profile along the bottom edge. (C) Spatial interference patterns produced with preferred directions differing by multiples of  $60^\circ$  (left: flat patterns) can be summed to produce 2-D amplitude modulation (middle: flat spatial pattern; right: 3-D map as in B). (D) Spatial firing maps of a model grid cell (below) and its velocity-controlled oscillator inputs (VCOs, above, preferred directions shown by arrows) during a simulated 5-min run using real trajectory data in a circular environment (gray line bottom left plot). Above plots show the locations at which spikes were fired, color-coded according to their phase relative to the baseline oscillation. Bottom left: Grid cell spike phase map. Bottom right: Color-coded spatial firing rate map for the same cell. Note the equivalent baseline phase range of VCO and grid cell spikes within the field locations (circled).

oscillatory interference model of grid cell firing [13,14], the phase relationship between neuronal oscillations in the theta band encodes the animal’s current allocentric position. This is achieved in the model using so-called velocity-controlled oscillators (VCOs), which are subject to a frequency modulation from a common baseline according to the velocity of the animal. The VCOs are assumed to be direction-specific such that a VCO’s frequency varies in proportion to the component of the animal’s velocity along the VCO’s “preferred direction”. Thus, if  $f_b(t)$  is the baseline frequency,  $f_a(t)$  is the VCO’s (active) frequency,  $s(t)$  is the animal’s speed,  $\theta(t)$  is its running direction and  $\varphi_d$  is the preferred direction of the VCO then:

$$f_a(t) = f(t)_b + \beta s(t) \cos(\theta(t) - \varphi_d) \quad (5.2)$$

where  $\beta$  is a scaling constant. As described above, this produces a difference between the VCO phase  $\phi_a$  and the baseline oscillation phase  $\phi_b$  that is the time integral of the component of the animal’s velocity along the preferred direction. Thus the phase difference  $\phi_{ab}$

reflects distance traveled by the animal along the VCO's preferred direction in the time  $t$  since the phases were aligned, which we refer to as  $d(t)$ :

$$\phi_{ab}(t) - \phi_{ab}(0) = \int_0^t 2\pi[f_a(\tau) - f_b(\tau)] d\tau = \int_0^t 2\pi\beta[s(\tau)\cos(\theta(\tau) - \varphi_d)] d\tau = 2\pi\beta d(t) \quad (5.3)$$

The interference pattern formed by adding the two oscillations manifests the mapping between relative phase and environmental position with a smooth and periodic variation of its amplitude along the VCOs preferred direction (see Fig. 5.2B). Since the phase difference cycles every  $2\pi$ , the spatial period of this variation along the preferred direction is  $1/\beta$ . The amplitude modulation is one-dimensional, however, as movement perpendicular to the preferred direction elicits no frequency modulation, producing bands of equal amplitude across the environment perpendicular to the preferred direction.

A neuron's firing could be driven by such an interference pattern if both oscillations are summed at the soma (see [14,16]). In this case, the firing rate would reflect the amplitude of the interference pattern, with peak firing occurring at the locations where the phases of the contributing oscillations coincide. An extension to a two-dimensional spatial modulation of firing, as it is the case for grid cells, can be accomplished by assuming modulation from two or more VCOs with non-parallel preferred directions. Moreover, the characteristic tessellated triangle motif of grid fields can be reproduced from a cell receiving input from VCOs with preferred directions that differ by multiples of  $60^\circ$  (see Fig. 5.2C, D). This configuration produces grid nodes aligned  $30^\circ$  to the preferred directions. Since completing a VCO spatial period when traveling  $30^\circ$  (or  $150^\circ$ ) to its preferred direction requires traveling  $2/\sqrt{3}$  (i.e.  $1/\cos 30^\circ$ ) times the period, the spacing between grid nodes is  $2/\sqrt{3}\beta$ , see also [18].

The above-described VCOs are proposed to be implemented as MPOs, either occurring in dendritic subunits of the grid cell itself [13] or in individual neurons that form the driving inputs to the grid cell ([14], see also [16]). In the model, the oscillators share a common intrinsic frequency in the theta band that is modulated by velocity-dependent depolarizing inputs. Such inputs could be provided by speed-modulated head direction cells. Head direction cells [19] co-localize with grid cells in the MEC, and the pre- and parasubiculum [20,21] and only fire when the animal is facing a particular direction (regardless of their location). The firing rates of a subset of head-direction cells are further modulated by running speed ("speed-modulated head direction cells") thus offering a viable potential input to VCOs.

The implementation of VCOs in different dendritic subunits of grid cells may be ruled out by biophysical constraints. Modeling studies have suggested that multiple dendritic oscillations within the same neuron phase lock within a timescale that may rule out their use for integration ([17], but also see [36]). In the neuronal VCO implementation, however, each VCO is implemented by a distinct neuron and forms the inputs to the grid cell [14,16]. In this implementation, the VCO neurons spike periodically at the peaks of their MPO. Hence, the *phase* at which VCO spikes occur relative to the baseline oscillation shows the spatial pattern of bands perpendicular to the VCO's preferred direction (see VCO spike phase plots in Fig. 5.2D). The spikes from VCOs elicit EPSPs in the target grid cell enabling temporal integration between VCO inputs over the timescale of the decay constant of the EPSPs. Thus, the grid cell effectively operates as a coincidence detector of its VCO inputs: when the VCO

phases are sufficiently aligned, their spikes will arrive close together in time and the cell can reach threshold. The grid cell membrane potential is further modulated by the baseline oscillation to select spikes that coincide with a range of its phases. With an appropriate membrane potential spike threshold, the model produces firing patterns matching those of real grid cells (see grid cell spike phase and rate maps in Fig. 5.2D). Firing fields are arranged in a triangular structure (as expected from the interference runs in Fig. 5.2B), with spacing dependent on the scale of the velocity-modulation (i.e. the  $\beta$  parameter in Equation 5.2).

The ideas behind this model can be implemented in various ways (e.g., with different numbers of VCOs and different preferred directions). Burgess [14] proposes that the baseline oscillation frequency is actually the mean frequency of all of the VCOs, and that only those VCOs aligned with the current running direction contribute to the firing of the grid cell. This allows the input to VCOs to be solely depolarizing, rather than changing sign with running direction, as implied by Equation 5.2 (and thus not violating Dale's law). It also allows the grid cell to show theta phase precession, as seen experimentally [22]. This specific implementation of the model allows quantitative predictions to be made regarding the relationships between the frequency of the local field potential theta rhythm, the frequency of modulation of the grid cell's firing rate, the animal's running speed and the spatial scale of the grid-like firing pattern. These predictions have been broadly confirmed [23].

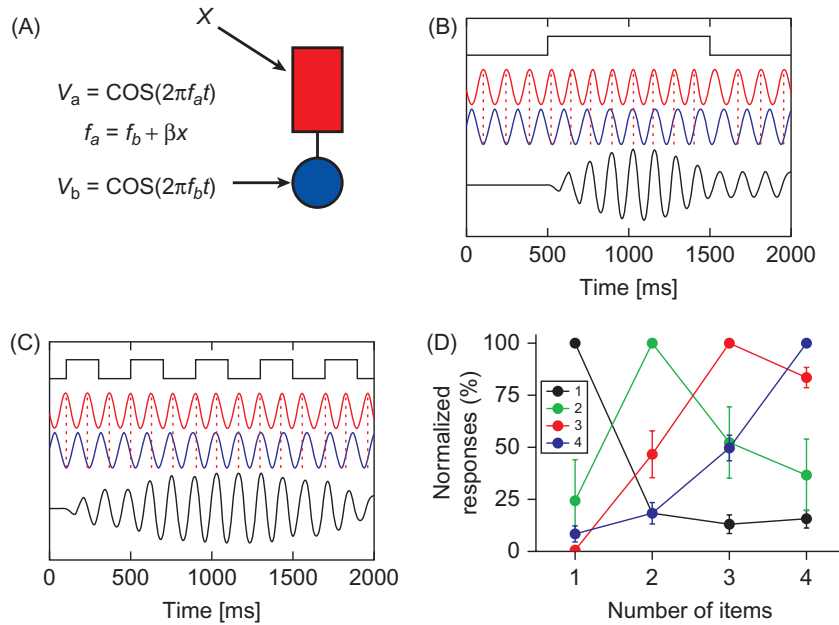
An important consideration for this model is its ability to maintain stable grids when more realistic noisy oscillators are used. In slice recordings, the variability of interspike intervals of persistent spiking cells in the entorhinal cortex is too high to produce stable grids over the timescales expected from grid cell recordings [37]. However, these slice preparations may eliminate stabilizing properties of networks *in vivo*, as intimated by their lack of the typical *in vivo* theta rhythm. Coupling the activity of populations of grid cells (or VCOs directly) could enable individually unstable oscillations to become more stable collectively [37]. Along these lines, an alternative model of grid cells firing, the continuous attractor model, utilizes recurrent connections between populations of cells to maintain a stable bump of activity [38,39]. In this model however, intricate asymmetric interactions between grid cells that are dependent on running velocity are required to allow the activity bump (and therefore the grid cell firing patterns) to track the movement of the animal. Furthermore, the model does not predict theta phase precession. However, a mechanism which combines oscillatory interference at the cellular level with recurrent connections could improve the stability of the population. The oscillatory interference mechanism would enable activity to track animal movement and provide a natural mechanism for theta phase precession.

## OSCILLATORY INTERFERENCE AND REPRESENTATIONS OF SEQUENTIAL ORDER?

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In the previous section we have shown how the oscillatory interference model of grid cell firing utilizes velocity-driven variations in frequency to produce a phase code for position that, in turn, can create a spatially modulated firing pattern. Now we consider how the same principles could be applied to findings in primate parietal cortex, specifically cells in





**FIGURE 5.3** Oscillatory interference mechanisms for temporal integration and rank order. (A) Basic architecture of an oscillatory interference model. A baseline oscillation  $v_b$  of constant frequency  $f_b$  (illustrated as a somatic input, blue) is initially out of phase with an active oscillation  $v_a$  of similar frequency  $f_a$  (illustrated as a dendritic membrane potential, red). Synaptic input  $x$  causes a proportional increase in the active frequency  $f_a$  proportional to that input. When the two oscillations are combined, an interference pattern is produced (B-C, black line). (B) Interference pattern caused by a transient input  $x$  (upper line, black). This causes a transient increase in the frequency of the active oscillation (red) relative to that of the baseline oscillation (blue), resulting in a successively increasing phase difference between the two oscillations (see vertical red dotted lines) consequent interference pattern (lower line, black). (C) If the perception of individual items each causes a similar transient input  $x$  (upper line, black), the phase difference between an active oscillation (red) and the baseline oscillation (blue) will track the number of items perceived so far. This will be reflected in an interference pattern (lower line, black) which will peak for a specific number of items, according to the initial phase difference between the oscillations, and the gain of the increase of the active oscillation with synaptic input ( $\beta$  see main text, peak after three items shown here). (D) Normalized responses from cells recorded in intra-parietal sulcus of primates are shown, adapted, with permission, from [4]. Neurons were grouped according to the rank order of the event during which they fired most and averaged separately. Different lines show firing behavior of neurons selective for different rank-order values. The neurons show graded firing rates, tuned to specific values of rank order, with substantial activity for neighboring rank order values.

the intraparietal sulcus whose firing rates show tuning to specific values of the rank order of stimuli ([4,24], see Fig. 5.3 and Chapter 8 in this volume). We note that the intraparietal sulcus has been proposed to be the locus of the interaction between number- and space-related representations [1,2]. It is perhaps of interest that fMRI data from human participants suggesting the presence of grid-like representations in entorhinal cortex also detected a similar signal in the human intraparietal sulcus [25]. This area, and its homolog in rodents, is the subject of current investigations regarding the neural mechanisms of spatial navigation, given its close connectivity to parahippocampal cortices [26,27], and the presence of representations of spatial locations relative to the body [28].

As noted above, the oscillatory interference model works as an integrator: if the perception of each item causes a transient increase in the input to the active oscillation, it will produce a phase shift relative to the baseline oscillation, see Fig. 5.3. In this way, the phase code used for distance in the model of theta phase precession in place cells, or for spatial location in the model for grid cell firing, might encode the number of items presented so far, i.e. a rank order code. Evidence for the phase coding of the sequential order of two items has been found in primate prefrontal cortex [5]. If such a phase code is read out via the interference mechanism (i.e. summing the active and baseline oscillations) it can produce neuronal responses tuned to specific values of rank order, see Fig. 5.3. In the case of sequential foveation of multiple stimuli, such a mechanism could also produce neurons tuned to specific values of numerosity. A single pair of oscillators would produce a repeating representation of number (as the oscillations go cyclically in and out of phase with each other). More generally, by analogy with Fourier analysis, one can see that populations of neurons with appropriately chosen initial phase relationships and values of  $\beta$  could be combined to approximate a single-peaked representation of number, or indeed represent any function of the temporal integration of a given input. Interestingly, the two-dimensional firing patterns of grid cells can also be seen as spatial Fourier components contributing to the single-peaked responses of place cells [40], and combinations of grids with different spatial scales could be used to encode location over extremely large areas [41,42].

Such a representation of order information, where the ordinal position of an event within a sequence is signaled, has also attracted much interest in the context of working memory for serially ordered items. There, representations of serial order information resembling rank order coding have been proposed to drive various models of working memory for serial order (e.g., [29–32]). Reasonably accurate models of human performance in working memory for serial order can be produced by associating item information with these representations of serial order during encoding, reactivating the sequence of activity across them during retrieval, and using a “competitive queuing” mechanism [33,34] for output selection.

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## SUMMARY AND CONCLUSIONS

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We have reviewed the potential for neuronal oscillations to produce phase codes for information that can be derived from simple sensory/motor inputs by a process of temporal integration. Thus it is possible that distance traveled through a place cell’s firing field is encoded by its phase of firing relative to the ongoing theta rhythm, given an input that codes for running speed [6,10]. Equally the spatial pattern of firing of grid cells may reflect temporal integration of inputs reflecting running velocity along specific directions [13,14]. More speculatively, we have suggested that representations of serial order and numerosity might be derived in a similar manner from inputs signaling the perception of each new item. Although conclusive proof has yet to be found, these models are at least capable of generating experimentally testable predictions, and have done so in the spatial domain [18,23].

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