From smooth cortical gradients to discrete modules: A biologically plausible mechanism for the self-organization of modularity in grid cells

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Abstract

The grid cell system is a paradigmatic example of the computational advantages of modular representations. Modular grid responses emerge along a strip of cortex with smooth gradients in several biophysical properties, within days of eye opening in juvenile animals. The mechanisms underlying this emergence are unknown. We show that multiple spatially and functionally discrete grid modules can spontaneously self-organize from lateral interactions that are continuously graded in scale, when combined with a fixed-scale interaction. We derive a comprehensive analytic theory to reveal that modularization through this mechanism is highly generic and robust. It predicts that each term in the sequence of grid period ratios should be distinct and furnishes values that are invariant to microscopic details about dynamics and connectivity, resulting in the most accurate match to data to date. Altogether, this work reveals novel self-organization mechanisms by which simple local interactions and smooth gradients may interact to produce macroscopic modular organization.

Modular structures are robust to localized perturbations [1, 2], faster to adapt if the world requires sparse or modular changes [3], relatively expressive because of compositionality [4, 5, 6, 7, 8, 9], and probably for these reasons empirically favored by the arrow of evolution, which drives systems toward greater modularization [10]. In this sense, modularity is the crux of biological organization.

Despite the pervasiveness of modular organization in the brain, the mechanisms driving modularization are not well understood. Most models of modular emergence in neural networks require extensive goal-directed (supervised) learning or selection, and may sometimes be construed as abstracted models of how evolution selects for modular structures based on their functional advantages [11, 12, 8, 13, 14]. Though evolutionary time-scale adaptation is likely instrumental for the existence of complex structures in the brain, such information accrues in the genetic code and must be converted into neural structure through a circuit developmental process [15, 16, 17]. We currently lack mechanistic models of how genetic information could interact with neural dynamics to lead to the emergence of circuit modularity within the developing brains of single individuals.

In the context of grid cells, modularity has key functional advantages, specifically in the creation of a high-capacity [18, 7, 19] and intrinsically error-correcting code [7], with individual modules performing path integration [20, 21, 22, 23, 24]. Grid cells emerge within a week of eye opening in juvenile animals [25, 26]. We possess biologically plausible mechanistic models of the emergence from plasticity of single grid modules [27]. However, most models of multiple module emergence depend on biologically implausible function optimization and backpropagation [28, **?**, 29], with no role for the grid scale-associated biophysical gradients along the long entorhinal axis. The closest models to our proposal in spirit begin with biophysical gradients [30, 31]; however, these models lack the functionality of velocity-to-position integration [30] or rely on hypothetical structures that are difficult to map onto medial entorhinal cortex, like a multi-sheet architecture with gradients and modularity along the stacked dimension [31].

Here we contribute a biologically plausible model of modularity emergence through a process of rapid and robust self-organization that unfolds starting from simple and smooth cortical gradients along a cortical sheet. Cortex exhibits prominent and conserved gradients along several axes, including from low-level to higher-level regions [32, 33], and specifically in entorhinal cortex from the dorsal to ventral pole [34, 35, 36, 37]. Similar

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gradients are believed to be the expression of a genetically specified, albeit low-information, organizing scaffold for the development of structures in the body and brain [**?**, **?**]. Just as simple local interactions lead to pattern formation for morphogenesis [38, 39] and to the emergence of persistent memory states in brains [40, 41, 42], we show here that local interactions can additionally lead to the formation of a second, hierarchically distinct scale of global structure in the form of functionally disjoint macroscopic modules.

This paper makes four key contributions: 1) It provides a novel and biologically plausible pathway for the self-organization of structure on two hierarchical scales – local pattern formation and global module formation – based on two types of purely local interactions. 2) The pathway depends on the well-documented presence of cortical gradients in multiple biophysical properties along the dorsolateral strip of MEC along which the grid modules are organized, thus showing how relatively low-information genetic codes may be translated into complex biological structures through emergent dynamics during circuit development in individuals. 3) It provides a complete analytical description of the dynamics, showing that the process is highly generic and robust, and independent of nearly all parametric details. 4) It yields the most detailed yet almost entirely parameter-independent predictions about grid module period ratios – including the novel prediction that successive module ratios should be distinct – that furthermore provide the best fit to data to date.

Results

Smoothly varying local interaction parameters in standard grid cell models produce graded period variations

We begin by incorporating some of the smooth biophysical gradients observed along the long axis of MEC (Fig. 1a) into continuous attractor models of grid cells [24], to examine whether gradients in the local pattern-forming interactions can produce discrete modules. In grid cell attractor models, strong local inhibitory interactions [24, 43, 42] drive a pattern formation process that generates stable activity bumps organized in a triangular lattice on the cortical sheet – as subsequently observed in MEC [44]. The periodicity of the cortical pattern in the model is set by the spread of the lateral interactions, SI Fig 9 [41]. We refer to these interactions as the pattern-forming interactions.

After the addition of a smooth gradient in the width of the pattern forming interactions of the continuous attractor model (W^g, with scale $\sigma(n_{DV})$, where n_{DV} refers to position along the long axis of MEC, Fig.1c), the network dynamics still support spontaneous local patterning, producing hexagonally arranged activity bumps across the MEC. The variation in the width of the lateral interaction along the long axis produces variations in the local periodicity of the pattern. However, the variations in pattern period are smooth, reflecting the smooth lateral width gradient: there is no emergent modularization (Fig. 1d-e).

Interplay of lateral interactions with fixed and graded scales leads to modularization

Given that we seek multi-scale structure formation, we next consider the addition of a second scale in the interaction, while retaining the local nature of the interactions. The second scale takes the form of an interaction at a fixed-scale across MEC (W^f, with scale d that is fixed but wider than $\sigma(n_{DV})$ everywhere): this scale could represent a general truncation constraint on the extent of neural arborization, independent of position, Fig. 2a (orange). With the addition of a fixed-scale interaction, the network spontaneously and robustly decomposes into discrete modules, with spatially periodic activity patterns and discontinuous jumps in period in-between, Fig. 2b-c.

The size of each module is not related in any direct way to the width of the fixed interaction: each module is generally much larger than both interaction scales $d, \sigma(n_{DV})$ (cf. modules in Fig. 2b with the width of the graded and fixed interactions shown to scale in the insets, green and orange). The same combination of a graded-width interaction and a fixed-scale interaction produces robust and spontaneous decomposition of dynamics into discrete modules across 1D and 2D network models, Fig. 2c,g. (See SI Sec. 3.8 for additional numerical results for 2D.)

Further and remarkably, the results are strikingly similar across diverse shapes of the local interactions, both for the graded and fixed scales (cf. Fig. 2a-f), and regardless of whether the fixed-range interaction is localized at a distance d (Fig. 2d) or spatially diffuse over d (Fig. 2a), suggesting that a general, robust, and relatively parameter-independent mechanism underlies module emergence (see SI Fig. 10 for simulations with variety of additional lateral interactions shapes and signs, including purely inhibitory or purely excitatory fixed-scale interactions).

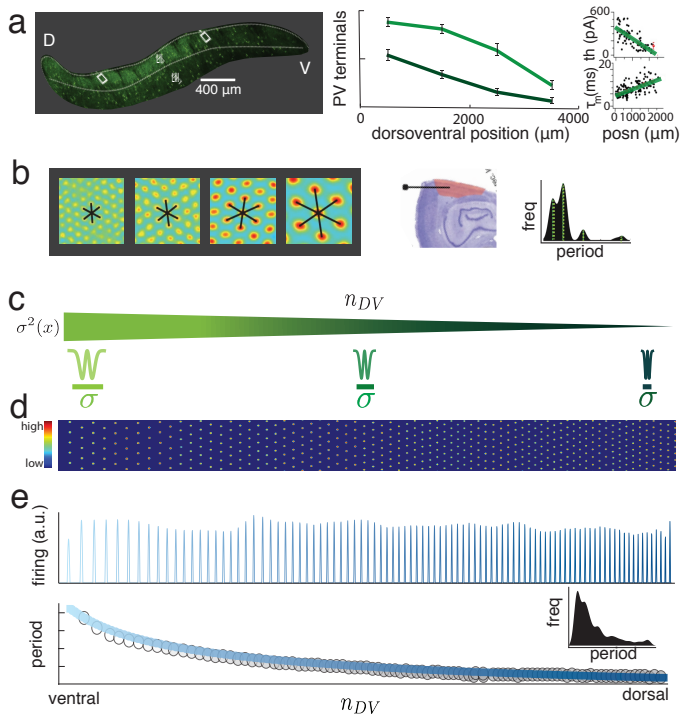


Figure 1: **Smooth gradients underlie entorhinal grid cell modules.** (a) Smooth gradient in inhibitory (PV-immunoreactive) axon terminals along the dorsoventral (DV) axis in layers II and III of the medial entorhinal cortex (MEC) [34], where grid cells are found [20]. (b) The spatial tuning curves of grid cells (left: autocorrelation of spatial responses of four cells; intensity plot as a function of two spatial dimensions) vary in spatial period along the DV axis in MEC (region and electrode penetration angle shown in middle), with period increasing ventrally. However, the variation is discrete: there are a few discrete modules with a few periods, and nearby cells have the same period (right) (adapted from [45]). (c) In a continuous attractor model of grid cells formed by pattern formation through lateral inhibition [24], we model the biophysical DV gradients in MEC by a continuous gradient in the width of lateral inhibition. (d-e) The smooth gradient of (c) results in pattern formation with smoothly varying periodicity in the population pattern, with no modularity (in (d): neural population activity pattern in a 2-dimensional neural strip; (e): top, pattern in a 1-dimensional neural strip; bottom, extracted period as a function of DV location; inset, histogram of extracted periods).

Modularity in function: Independent velocity integration per module

We next examine path integration functionality in the network: continuous attractor models of single modules respond to input velocity cues by a proportionally shifting pattern phase. Given that all network parameters and inputs are either constant or smoothly varying, and discrete modularity arises only in the emergent patterning, it is unclear whether a common velocity input to all cells can drive independent phase updating in each module, which would necessitate a sharp phase discontinuity with sliding phases between modules over time. Conversely, if the velocity integration functionality does not sharply modularize, the pattern phase of one module will influence the phase of the next, depending on the direction of pattern flow, inducing non-regular spatial tuning in all cells.

When we drive all neurons with a common velocity input, we find that the activity pattern flows across the cortical sheet but the boundaries between modules remain sharp and fixed at the same cortical locations, Fig. 3a. The preservation of a sharp boundary at a fixed location, with a sliding phase discontinuity between modules, results in veridical velocity integration within and across all modules. The result is a set of periodic spatial tuning curves per cell, Fig. 3b with discretely different spatial periods per module. Thus, the network is not only modular in the instantaneous pattern formation dynamics, but also fully and persistently modular in its velocity integration functionality.

Theory of modularizaton: genericity and robustness of mechanism with topological protection

We have seen in Fig.2 that the decomposition of a network with smoothly graded and fixed-scale lateral interactions into modules is remarkably robust, suggesting a general principal at work. We seek an analytical view of module formation that sheds light on its mechanisms and robustness.

The dynamics of the network after initialization in a uniform activity state exhibits immediate signs of modularization, beginning at the earliest time-steps (within 1-3 τ, where $\tau \approx 30$ms is the time constant of the network), Fig. 4a-b. Modularization begins before most neurons have crossed their nonlinear thresholds and unfolds con-

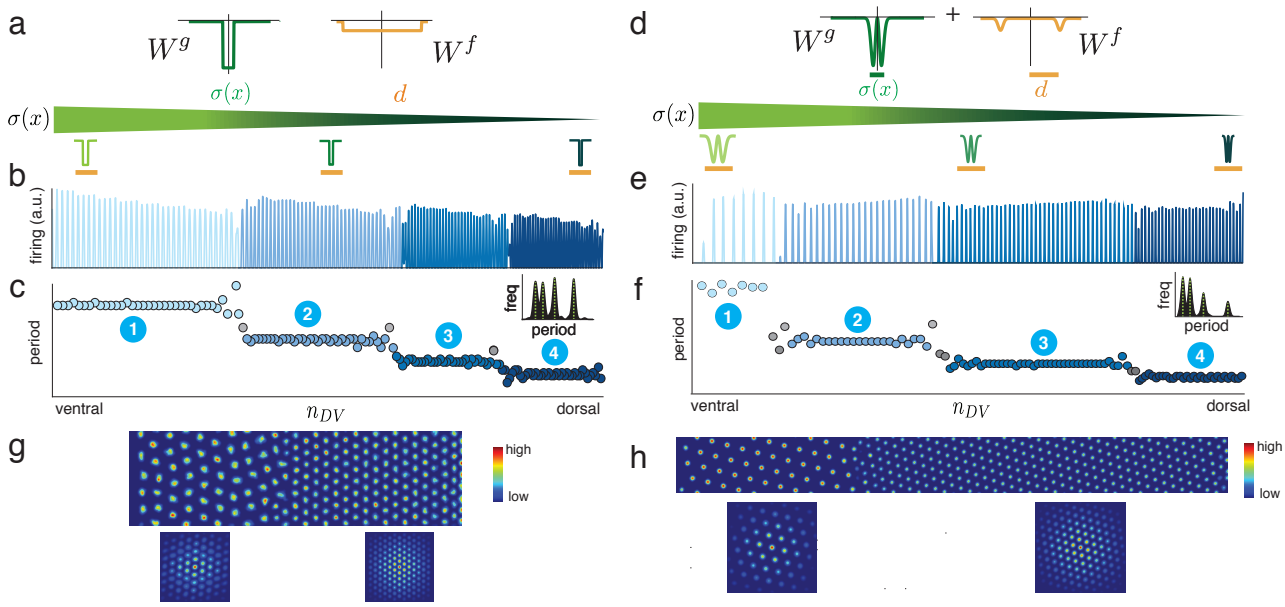


Figure 2: **A fixed connectivity range combined with smooth gradients in lateral connectivity leads to spontaneous module emergence.** (a) Two kinds of local lateral interactions: one whose width ($\sigma(n_{DV})$) varies smoothly along the DV axis (W^g, green) and one whose width (d) remains fixed along the neural strip. (b-c) The interactions from (a) lead to self-organized module formation (activity pattern in 1-dimensional neural strip with smaller periods more dorsally, (b); extracted periods, (c)). (d-f) Same as (a-c), but for a very different pair of W^g, W^f. (g-h) 2-dimensional pattern formation and module emergence: same as (b), for a 2-dimensional neural strip. (Bottom) 2d autocorrelation function of the local (single-module) patterns in the neural strip.

currently with the process of local patterning (Fig. 4a,b). This observation provided us with the critical hint that it should be possible to explain both local pattern formation and larger-scale module emergence within a unified linear instability framework.

The presence of localized eigenvectors is also consistent with the emergent modularization in the system: the eigenvector of the interaction kernel is a characteristic function that grows exponentially in a linearized approximation of the system — localization of the eigenvectors is thus another signature of the local modularization of the neural sheet (cf. SI sec 6).

Multiscale perturbation theory Accordingly, we perform an analytical derivation of the dynamics of module formation through multiscale linear instability (details in SI Sec.1). For a sufficiently slow gradation in the width of the pattern-forming interaction, the system is locally translation-invariant. Thus, we can decompose the local dynamics at each location n_{DV} in the neural strip into Fourier activity modes and examine their stability. Local pattern formation is dominated by the fastest-growing mode, which is given by where the Fourier-transformed

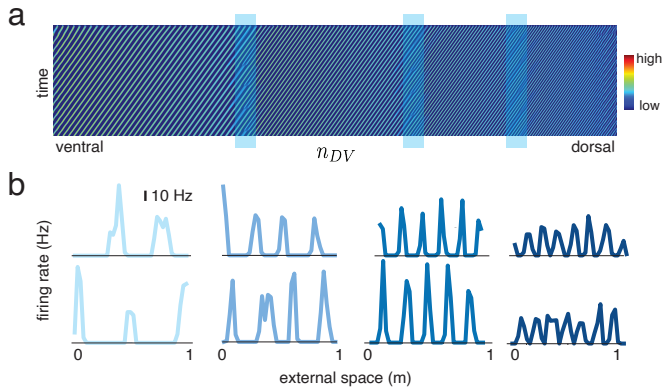


Figure 3: **The formed modules integrate velocity inputs independently and thus function as independent modules.** (a) Network response to a constant velocity signal injected globally into all cells: Within a module, bumps move coherently to maintain the pattern period in response to velocity input. Between modules, the boundary locations remain fixed (highlighted by vertical light-blue bars) while relative between-module phases change as each module's phase updates differentially relative to its neighbors. ; (b) Spatial tuning curves of 2 example cells per module (top and bottom). Tuning curves are generated by collecting spikes in response to a sinusoidally varying velocity input corresponding to multiple left-right traversals of a 1-dimensional environment and plotting the histogram of spike counts as a function of position in the environment.

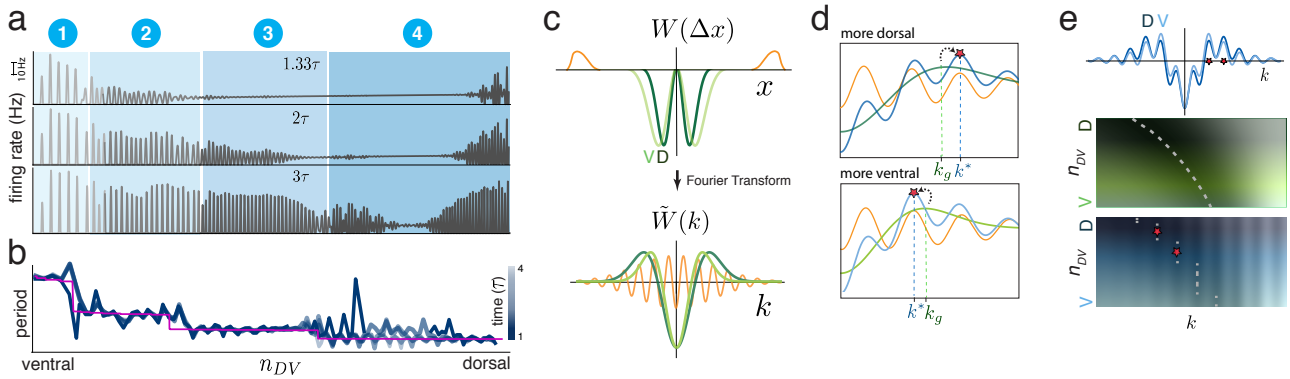


Figure 4: **Theory of module formation: multi-scale linear instability and topological peak selection.** (a) Snapshots of population activity in the neural strip within a few neural time-constants (τ) of running the dynamics. (b) Modules appear at the same time as the local pattern, and both appear before most neurons have hit their nonlinear thresholds. (c) Top: Schematic of the fixed-range (orange) and graded (green) interactions from two different DV locations on the neural strip (top), and bottom: their Fourier transforms. Fourier peaks of the fixed-range interaction remain unchanged dorsoventrally but the graded interaction peak slides smoothly inward when moving ventrally. (d) Peak selection process: the global maximum in Fourier space is based on the combination (blue) of the shallow graded-interaction peak (green) and the multiple narrow fixed-interaction peaks (orange). The smoothly shifting graded-interaction peak "selects" which of the local maxima from the fixed interaction is the global maximum. Thus, the global maximum jumps abruptly from one local maximum to the next. (e) The Fourier transform of the combined interactions, for a dorsal and a ventral location (top), and the Fourier-space location of the global maximum of just the graded interaction as a function of DV location (middle) and the combined interaction (bottom).

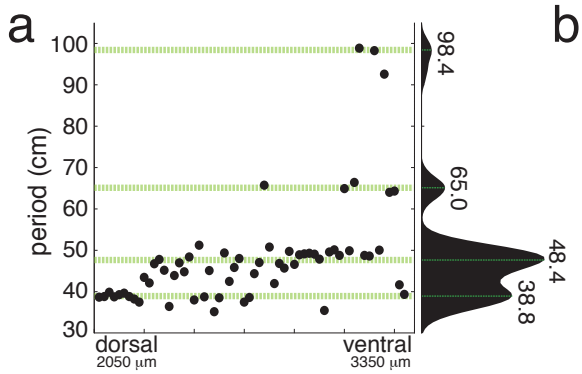
combined interaction has its peak ($k^*(n_{DV}) = \arg\max_k \tilde{W}(k; n_{DV}) = \arg\max_k \{\tilde{W}^f(k) + \tilde{W}^g(k; n_{DV})\}$ if $\tilde{W}(k^*) > 1/\tau$) [46, 47, 48, 49, 24, 50]. The result is a locally patterned state with period $\lambda^*(n_{DV}) = 2\pi/k^*(n_{DV})$.

To understand the spatial structure of these periodic solutions along the neural strip, note that $\tilde{W}^f(k)$ prominently contains a set of maxima, narrowly spaced every $1/d$, because of the dominant spatial scale d in W^f. Because W^f is fixed along the neural strip, the set of local maxima in $\tilde{W}^f(k)$ remains the same (Fig. 4c, orange). On the other hand, the narrow graded interaction $W^g(n_{DV})$ exhibits a very broad Fourier peak (of scale $\sim 1/\sigma(n_{DV}) \gg 1/d$) that smoothly contracts more ventrally (Fig. 4c, green). Though the graded interaction drives pattern formation and is ultimately responsible for any variation in spatial period along the neural sheet, its peak is too shallow to fully determine the global maximum of the combined interaction. Rather, the narrow peaks from $\tilde{W}^f(k)$ determine the set of potential locations of the global maximum, while the smoothly moving peak from $\tilde{W}^g(k)$ performs "peak selection" (cf. SI Movie 1) on these possibilities through a "stepping mechanism": for positions along the neural strip, one of the narrowly spaced fixed-interaction peaks will be the global maximum; moving ventrally causes the peak of $\tilde{W}^g(k)$ to move smoothly leftward while the global optimum remains fixed, until the leftward shift has progressed far enough that the next peak of $\tilde{W}^f$ on the left becomes the global maximum, Fig. 4d-e. Thus, moving smoothly along the neural strip results in a constant-period intervals, with discrete and rapid steps through discrete peak selection. The theoretical derivation of all module periods accurately matches those from numerical simulation, Fig. 4b (see SI Fig. 10 for a comparison of theoretical predictions and numerical simulation for a variety of lateral interactions shapes).

Topological robustness of peak selection Is it possible to determine what properties of the network and interaction kernels determine the periods of the formed modules, their sizes, and how many modules will form? Our results reveal that these quantities emerge through a topological process, and thus that they are topologically protected — robust to nearly all parametric variations.

In particular, the periods of different modules are given by different peaks in $\tilde{W}^f$, the Fourier-transformed fixed-scale interaction, and if this interaction has a dominant scale $d \gg \sigma(n_{DV})$, these peaks will occur at multiples of $1/d$. Thus, the module formation process and module periods are independent of details of the shape of the W^f and W^g, and very large variations in the shape still result similar outcomes as seen in Fig. 2 and the additional profiles in SI (SI Fig.10).

The number of formed modules is independent of the shape of the lateral interactions, of the length of the neural sheet, and of the shape of the function describing how the lateral interaction scale $\sigma(n_{DV})$ varies across the neural sheet. The number of modules is given by how many integer multiples of $1/d$ fit into the interval $[1/\min(\sigma), 1/\max(\sigma)]$ (SI Sec. 3.7). If the extremal widths are fixed, the modularization process generates the same number of modules regardless of neural sheet size (cf. SI Fig.15) and the details of the boundary conditions (periodic or aperiodic [41]). Thus, the number of modules depends on the graded interaction parameters only through the extremal widths $\min(\sigma), \max(\sigma)$, and not on any details of how the interaction scale varies between the extremal values (SI Sec. 3.7 and SI Fig.14). As a corollary, because the number of modules depends only on



b

observation	$r_m(0)$ prediction	deviation
1.514	3/2	0.93%
1.343	4/3	0.75%
1.247	5/4	0.24%

Figure 5: **Detailed match between prediction and measurement of the sequence of module period ratios.** (a) Observed periods of grid cells from multiple modules [45] (b) Successive period ratios computed from the observation (left column), and predicted period ratios for $\phi = 0$ (middle column). Ratios match predicted values with $R^2 = 0.999$ (right column).

the extremal values of the gradient but not the network size, it follows that the average module size grows linearly with network size (if the extremal values are held fixed). This explains why the formed modules in Fig. 2b,e are much larger than and unrelated to the length-scales of both the lateral interactions. Thus, module formation exhibits self-scaling with the size of the neural sheet, producing the same relative module sizes and same module periods regardless of the size of the physical substrate. Furthermore, small changes in the extremal values also have no effect on the number of modules, until a critical point at which another module would be added; thus, the number of modules is a topological invariant [51].

In sum, the module formation mechanism is at its essence a topological process with each module arising — through a combination of interactions with a smoothly varying scale and a fixed larger scale — as a topologically protected phase[51] that is independent of most details and parametric variations (SI Sec.3.7).

Energy landscape view Finally, the peak-selection process can be reformulated as minimization on an energy landscape (SI Sec. 4). In other words, whenever two functions together define an optimum that governs the local dynamics, one with a fixed set of narrowly spaced minima and another with a broader but shallower minimum that moves smoothly as a function of some spatial gradient, the dynamical system will form a step-like solution as a function of the spatial gradient, SI Sec. 5. This analytical formulation provides a novel and simple mathematical perspective on how smooth gradients lead to discrete patterning and modular specialization [52, 53, 54].

Detailed prediction of pairwise module period ratios

Returning to grid cells, the theory generates a quantitative and topologically robust prediction about how the entire sequence of grid module period ratios. We assume that the interaction kernel W^f is *simple*, i.e., it is primarily characterized by the length-scale $d \gg \sigma(n_{DV})$, without other prominent features, and any other length-scales in W^f are much smaller than d. Then, except for a set of measure zero in the space of functions W^f (SI Sec. 3.5.1 for details), its Fourier transform has an approximate form ($\sim \cos(kd - \phi)$) with relatively evenly spaced peaks occurring every m/d for integer m (Fig. 6a) together with a single phase ϕ; as we discuss next, this phase depends only on gross properties of the shape of the fixed-range interaction. Since module periods correspond to successive peaks of this function, it follows that the period ratio is given by (SI Sec. 3.6):

$$r_m = r_m(\phi) = (m + 1 + \phi/2\pi)/(m + \phi/2\pi). \tag{1}$$

The predicted average period ratio from this formula for the first three period ratios is 1.37 (averaging also over all ϕ), in good agreement with known results [45]. But further, and unlike existing experimental fits in which the period ratios $r_m = \lambda_{m+1}/\lambda_m$ for all m are described by a single parameter $\alpha \sim 1.4$, the prediction of the present model gives further detail on the sequence of successive period ratios as a function of m. We compare our more fine-grained successive period ratio prediction with experimental results, Fig.5b. The prediction with $\phi = 0$ matches the sequence of observed period ratios strikingly well for these data and others for which multiple grid periods are available from the same individual (SI Sec. 3.10).

Period ratios depend only slightly and predictably on lateral interaction shapes We derive analytically that a small number of characteristics of the fixed-width interaction W^f determine the value of ϕ in the prediction of

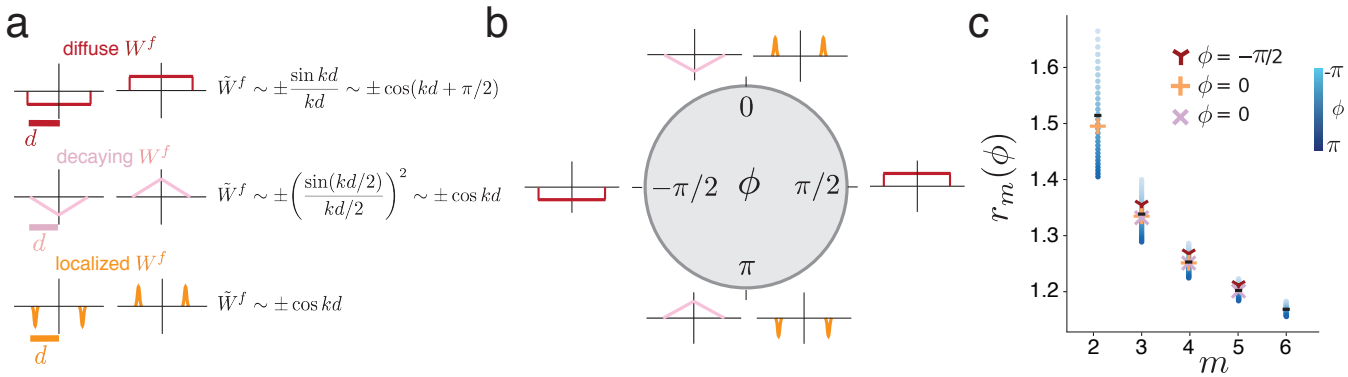


Figure 6: **Module period ratios depend weakly and predictably on the fixed-scale interaction shape.** (a) Left: examples of diverse fixed-scale interaction profiles that produce modularization: the profiles can be described as diffuse, decaying, or localized; right: the dominant terms in their Fourier transforms $\tilde{W}^f$. (b) The phases of the Fourier transforms for the diverse simple interactions in (a), all of which follow the same formula, Eq. 1, for period ratios. (c) The theoretically predicted sequence of period ratios for all values of ϕ (blue) for module numbers 2-6, together with numerical simulation of neural circuit models with three of the interaction profiles shown in (b). The variation in period ratio as a function of ϕ (and hence the sensitivity to the shape of the fixed-scale interaction) is smaller for higher module numbers (smaller module periods).

period ratios, as illustrated in Fig. 6. A diffuse W^f out to scale d leads to $\phi \approx \pm\pi/2$ for inhibitory or excitatory interactions respectively; a localized W^f lead to a value of ϕ close to 0 or π for excitatory or inhibitory interactions respectively; a decaying W^f also leads to ϕ close to 0 or π for inhibitory or excitatory interactions, respectively. Intermediate values of ϕ can be obtained by interpolating between these described forms of fixed-scale lateral interactions (See Fig. 10 for examples of numerical simulations for several cases).

Different values of ϕ inferred from experimental period ratio observations might therefore be used to constrain an inferred shape of the fixed-scale lateral interaction kernel (under the assumption that W^f has a single dominant scale; in the case of multiple dominant scales, more-complex kernels can also be consistent with $\phi = 0$, SI Fig.12).

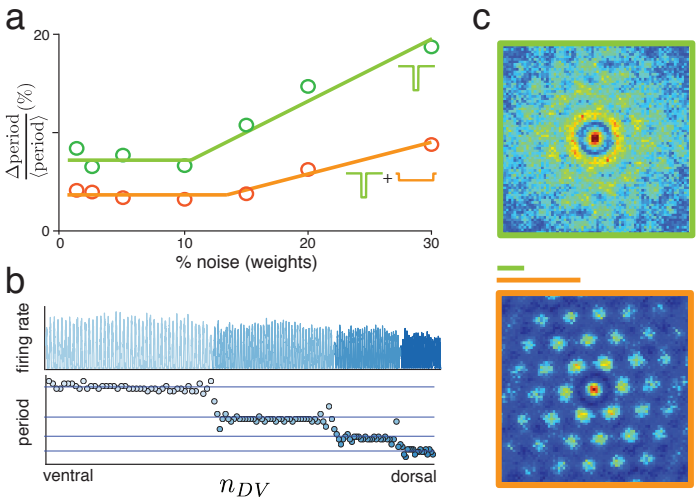


Figure 7: **The fixed-scale lateral interaction confers within-module robustness to weight noise and heterogeneity.** (a) The addition of independent random noise to all pairwise weights between neurons in a 1-dimensional grid cell model (single module, with only the pattern-forming lateral interaction W_g, as in standard continuous attractor models [41]) results in local variations in the formed pattern. Pattern variation is measured as the ratio of the standard deviation to the mean of the pattern period (green). The addition of the second (fixed-scale) lateral interaction suppresses the effects of noise in the pattern forming weights (orange). (b) Module formation in a 1-dimensional network with noise in W_g: the within-module periods remain flat and the between-module transitions remain sharp. (c) Top: Spatial patterning that is destroyed by heterogeneity in W_g (shown is the pattern autocorrelation) is rescued by the addition of a secondary interaction W_f, even with noise in both W_f and W_g (bottom). Simulation performed on a 100x100 neuron network. The pattern forming kernel W_g in a-c is from Fig. 2d-f.

Robustness to inhomogeneities and local perturbations

Peak selection-based modularization is invariant to global variations in parameters, function shapes, and parameter gradients, as seen above. We now show that it is also robust to several forms of local heterogeneity and perturbation.

Robustness to spatial heterogeneity in lateral interactions Since emergent modules are determined by the set of maxima of $\tilde{W}^f(k)$ with selection by $\tilde{W}^g(k; n_{DV})$, our theoretical expectation is that spatial heterogeneities in W^g should not affect module periods. To test this, we construct noisy pattern-forming interaction weights, independently per neuron, that break radial symmetry and introduce spatial heterogeneities in scale (See SI Sec. 3.9 for more details)

In accord with the theoretical expectation, the peak selection mechanism strongly suppresses the effects of this noise, Fig. 7a, and the periods across comodular cells remain constant and continue to correspond well to analytical predictions, Fig. 7b. Robustness in the module-formation setting with the interaction of a fixed and graded-scale interaction greatly exceeds that seen in the corresponding conventional (single-module, single-scale interaction) network, Fig. 7a-b.

Additional heterogeneities in the fixed-scale interaction can result in deviations from periodicity in $\tilde{W}^f(k)$, and thus lead to variations in the emergent grid period. However, as we show in SI 3.9, the variation in the mth grid module is suppressed by the factor $\sim 1/m$, resulting in additional robustness to grid modules corresponding to larger m (smaller periods). This results in robust pattern formation even in the presence of spatial heterogeneities in all lateral interactions, Fig. 7c.

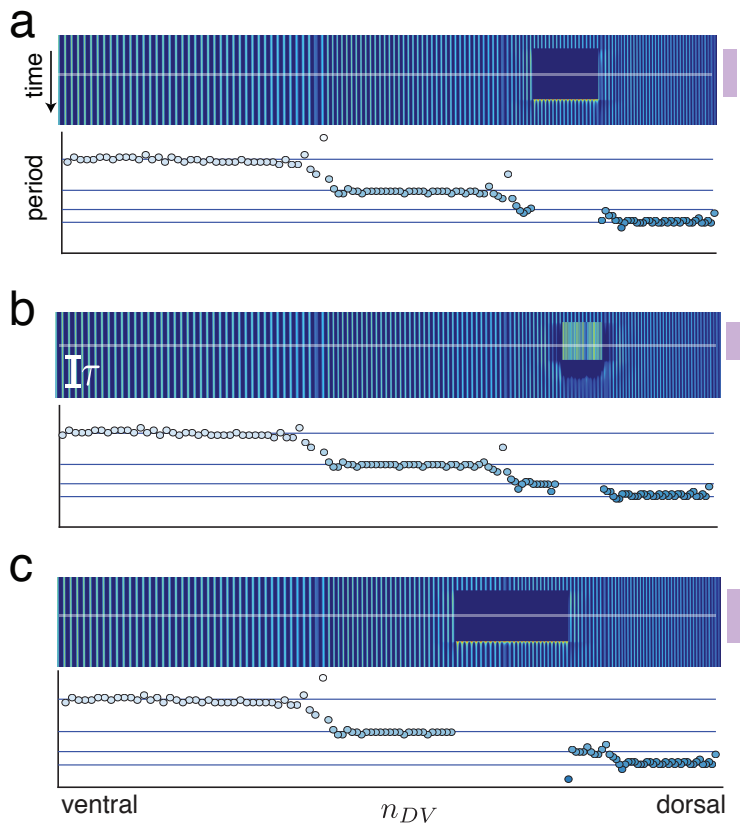


Figure 8: **Robustness of modularization and patterning to large activity perturbations.**(a) All neurons within one module are transiently silenced for 50 ms (duration of perturbation shown by purple bar at right). The existence of other modules, their locations and boundaries in the overall network, and their dynamics and periods remain unchanged despite this large perturbation. (b) Similar to a, but with large-amplitude fixed and independent random perturbations to a subset of cells in one module. This perturbation results in a surrounding local zone of suppressed activity, but other modules remain unchanged and the perturbed module recovers within the cellular biophysical time-constant of $\approx \tau$. (c) A silencing perturbation that spans two modules. Dynamics in the remaining portions of each module remain unaffected, with preserved periods and period changes across the silenced boundary. After the perturbation is lifted, the module boundary reapppears at approximately the same location.

Robustness to large localized perturbations in activity Since the formed modules emerge locally and are functionally independent (cf. Fig. 3), we expect that localized perturbations to even large fractions of a module will not affect the periodicity and function of the rest of the modules. Indeed, upon silencing activity in one module (mimicking optogenetic inactivation) the other modules, module periods, and module boundaries remain stable, Fig.8a. When a subset of cells in one module are driven to maintain randomly chosen values between 0 and 20Hz, patterned activity is disrupted in adjacent regions of the module, Fig.8b; when the perturbation is lifted, the module period is restored at the site of perturbation as well. If a region that spans the boundary between two modules is silenced, the dynamics and periods in spared parts of the two modules remain unchanged and the

boundary re-emerges at its pre-perturbation position after removal of the suppressive input, Fig.8c. In all cases, the pre-perturbation periodicities are restored within $\approx \tau$ timesteps. These findings are in contrast to existing models of module formation with graded interactions in which the architecture consists of stacked cortical sheets [31]: these models exhibit cascading dependencies between modules, so that perturbation of one module has propagating effects across all downstream modules. In sum, our model predicts that localized perturbations of grid cells should leave both nearby grid cells and other grid modules unaffected.

Discussion

Summary. We have found that the combination of two types of local interaction, one with a fixed range and a second with a spatially graded extent, leads to the spontaneous self-organization of structure on two scales: local patterning and global modularity. The process involves the selection of a global peak in Fourier space from a set of fixed local maxima; the spatially graded interaction defines a smoothly shifting shallow optimum that causes the global maximum to jump from one local maximum to the next. This mechanism of "peak selection" is a novel recipe for bottom-up modularization in neural circuits, which leads to functionally independent modules.

The number of formed modules is independent of the shape of the spatial gradient and the size of the network, if the extremal values of the lateral interaction are kept fixed. Complementary mechanisms to maintain the extremal value difference could therefore lead to total invariance to system size [55, 56]. The topological roots of module emergence also endow the network with other invariances and robustness in various forms, including in the overall shape of the lateral interactions, heterogeneity and noise in the interactions, and random activity perturbation in submodular regions or entire modules – testable predictions for future experiments. Independent of the problem of multiple module formation, the addition of a fixed-scale lateral interaction renders individual grid modules substantially more robust to inhomogeneities in the weights, paralleling recent findings in morphogenesis [57]. Thus, it substantially reduces the tuning requirements for the network weights.

Co-existence of graded and fixed-scale lateral interactions. The sound match of our model with experimental data suggests that MEC may contain a fixed-width lateral interaction across its dorsolateral extent, complementing the observed gradients in cellular and network properties along that axis. The co-existence of spatially graded properties with spatially non-graded properties is consistent in general with experimental findings that several cellular properties like intrinsic subthreshold oscillation frequency [58, 59, 36], the immunofluorescence labeling proportion of parvalbumin (PV)+ putative axon terminals, the strength of PV basket cell-mediated inhibition onto principal cells [37], gamma oscillation power[34], membrane conductance gradient mediated by HCN, and leak potassium channels and the time window for synaptic integration [35] vary in a gradient along the dorso-ventral axis, but other properties like the concentration of vesicular GABA transporter (V-GAT), a marker of GABAergic terminals [34], the input resistance and firing threshold of vasoactive intestinal peptide (VIP) expressing interneurons [60] and the time constant of hyperpolarization activated currents [35] do not. Small cytochrome oxidase patches in MEC have at most either slight variation or no gradation in their size along the dorso-ventral length of the medial entorhinal cortex [61].

One interpretation of our posited fixed-scale interaction is as a fixed physical arbor size, with the graded scale interaction given by a dorsoventral variation in synaptic densities on the arbor. In support of the potential plausibility of such a mechanism, there is evidence that MEC neurons exhibit structured and precisely controlled synaptic density profiles along their arbors [62]. Another interpretation is that two distinct cell types [63], one with a graded interaction scale along the dorsoventral axis and another with a fixed scale, mediate the lateral interactions that produce grid cell activity. The microcircuitry of entorhinal cortex along the dorsoventral axis and its relationship to multi-module formation remains experimentally under-characterized. Regardless of one specific mapping to cellular properties, our work makes the theoretical prediction for future microcircuit tracing studies that the coexistence of a graded and fixed scale of interaction may be a key ingredient of multi-module emergence. Since the secondary (fixed-scale) interaction can theoretically be much weaker than the primary (graded) pattern forming interaction, SI Fig.10, it could be harder to detect with few-cell reconstructions or small-scale microcircuit studies. However, the predictions might be ideal for testing with connectomic reconstructions of the network [64, 65, 66, 62]. The fact that $\phi = 0$ provides the best description of the data further suggests possible forms of the fixed-width lateral interaction.

Related work. Our work contrasts with supervised learning approaches to module emergence [67, 28, 68, 14, 11, 12, 8, 13, 11, 69, 70, 71, 72] in a number of ways: Selection and supervised learning require top-down in-

structive or selective feedback that requires global information propagation– they are not local processes, while module formation through peak selection proceeds entirely from local interactions. Second, supervised learning approaches employ biologically implausible learning rules while the peak selection process is the result of activity dynamics with no learning. Third, while supervised learning proceeds slowly and through extensive training, module formation through peak selection is spontaneous and rapid. Slow supervised learning is sometimes interpreted as evolutionary time-scale learning in biological systems, to explain away the problem of extensive training on individual lifetimes, but in that case the evolutionary learning should pass through intermediate genetic codes rather than acting directly on neural weights. In our model, the initial smooth gradients may be viewed as arising through simple genetically encoded instructions, while modularization in the presence of the smooth gradient is a nearly instantaneous emergent dynamics.

Two interesting recent works address the question of rapid module emergence based on biophysical gradients: In the first, grid tuning derives from pattern formation on place cell inputs with a continuum of adaptation timescales [30]. The resulting grid-like cells do not perform path integration, posited to be a central function of grid cells [20, 24], and lack their demonstrated low-dimensional structure in which cell-cell relationships are preserved across environments [73, 74, 75, 76, 77]. In the second, grid module formation proceeds from a stacked multi-sheet architecture in which each sheet has lateral grid pattern-forming connectivity with a scale that increases vertically, and the sheets are also coupled vertically through connections between matching locations on each sheet [31]. The resulting grid cells path integrate, but deletion of part or all of a module strongly and globally affects pattern formation and module formation across all subsequent modules, in contrast to our model where local module deletion does not affect other modules. Our model makes detailed period ratio predictions for each term in the sequence of adjacent grid modules, in contrast with all the other models described above, which produce a general constant ratio across modules. These predictions of period ratios vary nearly not at all with parameters, while they can vary substantially depending on parameters in all the works above. Finally, our work provides a theoretical analysis of the dynamics of module emergence.

Our results provide a dynamical and mechanistic interpretation for the observed ratios of grid periods, an alternative though not exclusive perspective to coding-theoretic [6, 7, **?**] and function optimization approaches [**?**, 29]. In addition, our period ratio predictions are unique relative to existing work, both in suggesting that the ratios form a sequence of distinct values and in the precision of their fit to the data.

Potential generality of modularity mechanism. Although we primarily focused on the peak selection process in Fourier space for multi-periodic patterning in grid cells, we also showed that it has a general formulation in terms of dynamics on an energy landscape: One (spatially invariant) interaction sets up an optimization problem with multiple local minima, while a second (spatially graded) interaction defines a locally shallow single-optimum landscape, with a smoothly shifting optimum as a function of space. Thus, we hypothesize that the peak-selection principle for module emergence may apply to a range of dynamical systems without periodic pattern-formation.

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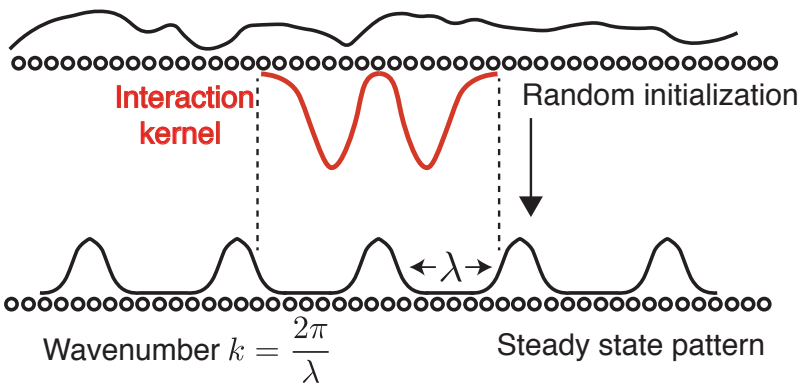


Figure 9: Local pattern formation in continuous attractor models of grid cells: Through local amplification of random fluctuations, the lateral interaction forms periodic patterns.

Supplementary materials

Materials and Methods

We use a continuous attractor network (CAN) model [78, 79, 80] for grid cells [24, 81, 44, 74], with neural dynamics obeying

$$\frac{\partial s(i,t)}{\partial t} + \frac{s(i,t)}{\tau} = \phi\left[\sum_j W_0(i,j)s(j,t) + B(i,t)\right], \tag{2}$$

where $s(i,t)$ represents the synaptic activation of neuron i at time t, $W_0(i,j)$ represents the synaptic strength of the coupling from neuron j to neuron i, $B(i,t)$ represents the feed-forward bias to neuron i, and ϕ is a non-decreasing nonlinearity, for which we use the rectification function ($\phi(z) = [z]_+ = z$ for $z > 0$ and 0 otherwise). Each neuron i has a preferred direction θ_i that is used to perform velocity integration. In the one-dimensional version of our setup, each spatial location $\mathbf{x}$ on the neural sheet has two neurons, with preferred directions $\theta = 0$ and $\theta = \pi$. Correspondingly, in the two-dimensional version of our setup, each location on the neural sheet has four neurons, with preferred directions $\theta = n\pi/4$ for $n \in \{0,1,2,3\}$. The synaptic weights $W_0(i,j)$ are defined via an interaction kernel $W(\Delta x)$ such that

$$W_0(i,j) = W(|\mathbf{x}_i - \mathbf{x}_j - \mathbf{l}(\theta_j)|), \tag{3}$$

where $\mathbf{x}_i$ represents the spatial location of neuron i, and $\mathbf{l}(\theta)$ is a vector with length l oriented parallel to the angle θ. The feed-forward bias $B(i,t;\theta)$ is given by

$$B(i,t) = b + b_{vel}|\mathbf{v}|\cos(\theta_\mathbf{i} - \psi), \tag{4}$$

where ψ is the direction of the input velocity signal and $|\mathbf{v}|$ is the speed. This results in neurons with direction preference θ driving activity in the network towards the direction of their outgoing weight shifts $\mathbf{l}(\theta)$. This mechanism is responsible for velocity integration by the network [24].

As noted in the main text, the interaction weight kernel W is given by the sum of two components $W = W^g_\mathbf{x} + W^f$. The first, $W^g_\mathbf{x}$ drives local pattern formation, and has a spatial scale $\sigma(\mathbf{x})$, which varies smoothly in a gradient along the dorso-ventral axis, and the second, W^f has a fixed spatial scale d everywhere on the neural sheet. A variety of functions $W^g_\mathbf{x}$ can drive local pattern formation. For concreteness, we use two specific examples: the Mexican-hat profile[24] (used in Figs. 2a-c, 3, 1 and SI Fig. 10)

$$W^g_{\text{mexican-hat}}(\Delta x) = \alpha_E \exp\left[-\gamma\frac{(\Delta x)^2}{2\sigma_{mh}(\mathbf{x})^2}\right] - \alpha_I \exp\left[-\frac{(\Delta x)^2}{2\sigma_{mh}(\mathbf{x})^2}\right], \tag{5}$$

and the box-function profile[43] (used in Fig. 2 and SI Fig. 10)

$$W^g_{\text{box}}(\Delta x) = \alpha_0 \times \mathbb{1}_{|\Delta x| < \sigma_b(\mathbf{x})} = \begin{cases} \alpha_0 & \text{if } |\Delta x| < \sigma_b(\mathbf{x}), \\ 0 & \text{if } |\Delta x| \geq \sigma_b(\mathbf{x}). \end{cases} \tag{6}$$

Parameter	Value
τ	30
dt	0.05
b	$\begin{cases} 70 & \text{in 1D} \\ 1 & \text{in 2D} \end{cases}$
b_{vel}	$\begin{cases} 105 & \text{in 1D} \\ 1 & \text{in 2D} \end{cases}$
l	2

Table 1: Parameters held constant across all numerical simulations

For the fixed-width interaction $W^f(\Delta x)$, we implement 3 main types — localized (used in Figs. 2,3 and SI Fig. 10), diffuse (used in Fig. 2 and SI Fig. 10) and decaying (used in SI Fig. 10).

$$W^f_{\text{localized}}(\Delta x) = \alpha_S \exp\left[-\frac{(|\Delta x| - d_{loc})^2}{2\epsilon_S^2}\right],$$
$$W^f_{\text{diffuse}}(\Delta x) = \alpha_1 \times \mathbb{1}_{|\Delta x| < d_{dif}},$$
$$W^f_{\text{decaying}}(\Delta x) = \alpha_T \times [d_{dec} - |\Delta x|]_+.$$

In particular,

- In Figs. 1d-e we use only a smoothly varying Mexican-hat pattern forming kernel $W = W^g_{\text{mexican-hat}}$
- In Figs. 2a-c,g and 3 we use $W = W^g_{\text{mexican-hat}} + W^f_{\text{localized}}$
- In Figs. 2d-f,h we use a 'Lincoln hat' profile $W = W^g_{\text{box}} + W^f_{\text{diffuse}}$
- and, in SI Fig. 10 we present numerical simulations of other combinations of pattern forming and fixed-scale kernels.

To construct spatially heterogeneous kernels for analyzing the robustness to inhomogeneity in Fig. 7 we use the box function to construct

$$W^g_\xi[\mathbf{x}, \mathbf{x}'] = \alpha_0 \times \mathbb{1}_{|\mathbf{x}-\mathbf{x}'| \times (1+\xi^g_1(\mathbf{x}')) < \sigma^0_b (1+\xi^g_2(\mathbf{x}'))},$$
$$W^f_\xi[\mathbf{x}, \mathbf{x}'] = \alpha_1 \times \mathbb{1}_{|\mathbf{x}-\mathbf{x}'| \times (1+\xi^f_1(\mathbf{x}')) < d_{dif} (1+\xi^f_2(\mathbf{x}'))},$$

where $\xi^{g,f}_{1,2}(\mathbf{x}')$ are independent random numbers chosen uniformly from $\epsilon^{g,f}_{1,2} \times [-1, 1]$. For the particulars of Fig. 7b, $\epsilon^g_2 = 0.1$ and other noise terms are set to zero (In the one-dimensional case ϵ_1 and ϵ_2 have the same effect); for Fig. 7c, $\epsilon^g_1 = 0.2$, $\epsilon^g_2 = 0.3$, $\epsilon^f_1 = 0.05$ and $\epsilon^f_2 = 0$ (See SI Sec. 3.9 for more details).

In Table 1 we present a list of common parameters used across all numerical simulations. Then, in Tables 2,3 we present the parameter values used for the kernels used in our numerical simulations

Supplementary Text

The supplemental information is structured as follows: We will first present the mathematical analysis for pattern formation, and demonstrate in SI Sec. 1 that simply introducing a gradient in the pattern forming kernel of the continuous attractor model is *not* sufficient to result in modularization, as demonstrated in Fig. 1 of the main text. Then, in Sec. 1.1 we show how the addition of a Gaussian localized kernel results in self-organized modularization. We then generalize this result in SI Sec. 2, to show that arbitrary fixed-scale kernels will almost always result in module formation as demonstrated in Fig. 3. Among arbitrary kernels, we will show in Sec. 3 that kernels with a simple features result in a simple equation describing the detailed period ratios of the formed grid modules as shown in Fig. 4. This will lead to simple estimates for the number of modules and their sizes in terms of other system parameters, which we derive in SI Sec. 3.7. After having described our results primarily for the case of one-dimensional grid cells, we then demonstrate in Sec. 3.8 that our arguments extend naturally to two dimensions,

$W^g_{\text{mexican-hat}}$ parameters	Value
α_E	1000
α_I	1000
γ	1.05
N^{1D}	3000
N_y^{2D}	100
N_x^{2D}	1000
$\sigma_{mh}(x)$	$1/\sqrt{2\beta(x)}$
$\beta(x)$	$\beta_0 + (\beta_1 - \beta_0)x/N'$
N'	$\begin{cases} N^{1D} & \text{in 1D} \\ N_x^{2D} & \text{in 2D} \end{cases}$
β_0	$\begin{cases} 2.5 \times 10^{-2} & \text{in 1D} \\ 3/676 & \text{in 2D} \end{cases}$
β_1	$\begin{cases} 2.5 \times 10^{-1} & \text{in 1D} \\ 9/338 & \text{in 2D} \end{cases}$
W^g_{box} parameters	Value
N^{1D}	5000
α_0	-40
$\sigma_b(x)$	$15 + 30x/N$

Table 2: Pattern forming kernel parameters used for numerical simulations

$W^f_{\text{localized}}$ parameters	Value
α_S	4
d_{loc}	$\begin{cases} 84 & \text{in 1D} \\ 50 & \text{in 2D} \end{cases}$
ϵ_S	$\begin{cases} 4.77 & \text{in 1D} \\ 1.6 & \text{in 2D} \end{cases}$
W^f_{diffuse} parameters	Value
α_{dif}	-0.25
d_{dif}	135
W^f_{decaying} parameters	Value
α_T	25
d_{dec}	150

Table 3: Fixed-scale kernel parameters used for numerical simulations

and we present numerical results demonstrating the same. In SI Sec. 3.10 we then demonstrate that our results and predictions of grid period ratios are consistent with available data sources to a large extent. We then end with some brief remarks relating our result to the context of energy minimization in neural networks (SI Sec. 4), and providing broader perspectives of our results in the contexts of general loss optimization (Sec. 5) and eigenvector localization (SI Sec. 6).

We will largely restrict our analysis to the continuum limit of a large number of neurons (a neural field model) for mathematical convenience. However, as shown in the main text, the results hold for and accurately predict the dynamics of networks of discrete neurons. We will use a continuous index to represent position along the neural sheet. In this limit, the dynamics of rate-based neurons is given by:

$$\frac{\partial s(\mathbf{x},t)}{\partial t} + \frac{s(\mathbf{x},t)}{\tau} = \phi\left[\int_{-\infty}^{+\infty} W(\mathbf{x},\mathbf{x}')s(\mathbf{x}',t)d\mathbf{x}' + B(\mathbf{x})\right], \tag{7}$$

where $s(\mathbf{x})$ is the synaptic activation of the neuron at the vector position $\mathbf{x}$ on the neural sheet, τ is the biophysical time-constant of individual neurons, ϕ is a monotonic non-decreasing nonlinearity, and $B(\mathbf{x})$ is the feedforward input to the neuron. For simplicity, we will use the the rectification function ($\phi(z) = [z]_+ = z$ for $z > 0$ and 0 otherwise) as the nonlinearity in all of our results.

In nonlinear continuous attractor models the interaction weights $W(\mathbf{x},\mathbf{x}')$ are chosen to have a continuous symmetry, usually a translation-invariant symmetry such that $W(\mathbf{x},\mathbf{x}') = K(|\mathbf{x}-\mathbf{x}'|)$, where the weight between neurons at locations $\mathbf{x}$ and $\mathbf{x}'$ depends only on their separation, and not on their absolute locations. One example of such a weight K is the so-called Mexican-hat function described by a difference-of-Gaussians, in which neurons excite their immediate neighbors and inhibit those slightly further away; there is no interaction between faraway neurons:

$$W(\mathbf{x},\mathbf{x}') = W(\mathbf{\Delta x}) = \alpha_E \exp\left(-\frac{\mathbf{\Delta x}^2}{2\sigma_E}\right) - \alpha_I \exp\left(-\frac{\mathbf{\Delta x}^2}{2\sigma_I}\right). \tag{8}$$

Continuous attractor grid cell models of individual modules rely principally on a local inhibitory interaction (the excitatory center interaction is dispensable) [24, 43].

Motivated by the experimental observations described in the main text, we modify the Mexican-hat function to introduce a smooth gradient in the characteristic interaction widths σ_E, σ_I.

$$W^g_{\mathbf{x}}(\mathbf{\Delta x}) = \alpha_E \exp\left(-\frac{\mathbf{\Delta x}^2}{2\sigma_E(\mathbf{x})}\right) - \alpha_I \exp\left(-\frac{\mathbf{\Delta x}^2}{2\sigma_I(\mathbf{x})}\right), \tag{9}$$

where $\sigma_E(\mathbf{x})$ and $\sigma_I(\mathbf{x})$ are now functions that depend on position in the neural sheet, and encode the smoothly varying characteristic scale of the Mexican-hat interaction, say

$$\sigma_{E/I}(\mathbf{x}) = \sigma_{E/I} + \sigma'_{E/I}(0)\cdot\mathbf{x}. \tag{10}$$

For such graded kernels, we will use $W(\mathbf{x},\mathbf{x}')$ and $W_{\mathbf{x}}(\mathbf{x}-\mathbf{x}') = W_{\mathbf{x}}(\mathbf{\Delta x})$ interchangeably.

1 Pattern formation with graded kernels

In the limit of very slow changes in the length-scale of the interaction kernel $W_{\mathbf{x}}(\mathbf{\Delta x})$ along the dorso-ventral axis of the MEC, we can analyze the pattern formation process at position $\mathbf{x}$ by assuming that $W_{\mathbf{x}}(\mathbf{\Delta x})$ is locally constant.

Under this approximation, we perform a linear stability analysis of the neural dynamics, to identify the the growing periodic modes locally at the position on the neural sheet $\mathbf{x}$.

We first identify an unstable steady-state solution to Eq. (7), which we denote as $s_0(\mathbf{x})$. This solution satisfies

$$\frac{s(\mathbf{x})}{\tau} = \phi\left[\int_{-\infty}^{+\infty} W_{\mathbf{x}}(\mathbf{x}-\mathbf{x}')s_0(\mathbf{x}')d\mathbf{x}' + B(\mathbf{x})\right]. \tag{11}$$

In the limit of very slowly varying changes in $W_{\mathbf{x}}(\mathbf{\Delta x})$ as a function of $\mathbf{x}$, the unstable steady state solution will be

$$s_0(\mathbf{x}) = \frac{\tau\bar{B}}{1-\tau\bar{W}}, \tag{12}$$

where $\bar{B} = \int B(\mathbf{x})d\mathbf{x}$ and $\bar{W} = \int W_{\mathbf{x}}(\mathbf{x}-\mathbf{x}')d\mathbf{x}'$.

We then consider a perturbative analysis, by examining the evolution of $s(\mathbf{x},t) = s_0(\mathbf{x}) + \epsilon(\mathbf{x},t)$. We apply our analysis to the early time evolution of this initial condition, such that $\epsilon(\mathbf{x},t) \ll s_0(\mathbf{x})$. Inserting our form of $s(\mathbf{x},t)$ in Eq. (7), we obtain

$$\frac{\partial \epsilon(\mathbf{x},t)}{\partial t} + \frac{\epsilon(\mathbf{x},t)}{\tau} = \phi'(\gamma \bar{W} s_0(\mathbf{x}) + B) \int_{-\infty}^{\infty} W_{\mathbf{x}}(\mathbf{x}-\mathbf{x}')\epsilon(\mathbf{x}',t)d\mathbf{x}' \tag{13}$$

Since $W_{\mathbf{x}}(\mathbf{x}-\mathbf{x}')$ is a local kernel, we approximate the above integral with one evaluated over the region $\{\mathbf{x}' : |\mathbf{x}-\mathbf{x}'| < L\}$, with L much larger than the length-scale of the kernel $W_{\mathbf{x}}$ at all $\mathbf{x}$. Over this interval, we posit that $\epsilon(\mathbf{x}',t) = \epsilon e^{i\mathbf{k}\cdot\mathbf{x}' + \alpha(\mathbf{k})t}$, where $\alpha(\mathbf{k})$ denotes the growth rate of this ϵ perturbation. Inserting this form into Eq. (13) yields,

$$\alpha(\mathbf{k}) + 1/\tau = \phi'(\bar{W} s_0(\mathbf{x}) + B) \int_{\infty}^{\infty} W_{\mathbf{x}}(\mathbf{x}-\mathbf{x}')e^{-i\mathbf{k}\cdot(\mathbf{x}-\mathbf{x}')}d\mathbf{x}', \tag{14}$$

$$= \phi'[\bar{W} s_0(\mathbf{x}) + B]\mathscr{F}[W_{\mathbf{x}}(\mathbf{x}-\mathbf{x}')], \tag{15}$$

$$= \phi'[\bar{W} s_0(\mathbf{x}) + B]\mathscr{F}W_{\mathbf{x}}(\mathbf{k}) \tag{16}$$

where $\mathscr{F}[W_{\mathbf{x}}(\mathbf{x}-\mathbf{x}')] = \mathscr{F}W_{\mathbf{x}}(\mathbf{k})$ is the Fourier transform of the interaction kernel corresponding to position $\mathbf{x}$ on the neural sheet.

Note that since $W_{\mathbf{x}}(\mathbf{\Delta x})$ is a kernel, it is a radially-symmetric real function, and hence the Fourier transform $\mathscr{F}W_{\mathbf{x}}(\mathbf{k})$ will also be real function that is radially-symmetric in k. Thus, for simplicity, we will only focus on the magnitude of $\mathbf{k}$, which we denote as $k = |\mathbf{k}| \geq 0$ (In this context, for the two-dimensional case, one may re-interpret the radial component of the Fourier transform of $W_{\mathbf{x}}(\mathbf{\Delta x})$ as the Hankel transform of $W_{\mathbf{x}}(|\mathbf{\Delta x}|)$).

By definition, the magnitude of the wave vector k^* that corresponds to the fastest growing mode locally around position $\mathbf{x}$ on the neural sheet will be the $\mathbf{k}$ that maximizes $\alpha(\mathbf{k})$. Under the approximation of slow changes in the length-scale of the interaction kernel $W_{\mathbf{x}}(\mathbf{\Delta x})$, we see from Eq. (16) that

$$k^*(\mathbf{x}) = \arg\max_k \mathscr{F}W_{\mathbf{x}}(k), \tag{17}$$

since $W_x(\mathbf{\Delta x})$ (and hence $s_0(\mathbf{x})$) has been assumed to have a negligible dependence on $\mathbf{x}$.

For $W_{\mathbf{x}}(\mathbf{\Delta x})$ given by Eq. (9), i.e., without any additional fixed-scale interaction, we obtain from Eq. (17)

$$[k^*(\mathbf{x})]^2 = \frac{2}{\sigma_E(\mathbf{x})^2 - \sigma_I(\mathbf{x})^2} \log\left(\frac{\alpha_E \sigma_E(\mathbf{x})^3}{\alpha_I \sigma_I(\mathbf{x})^3}\right). \tag{18}$$

If we assume that $\sigma_{E/I}(\mathbf{x}) = \eta_{E/I}\sigma(\mathbf{x})$, where η_E and η_I are $\mathbf{x}$-independent constants, then we obtain

$$k^*(\mathbf{x}) \propto 1/\sigma(\mathbf{x}), \tag{19}$$

and hence

$$\lambda^*(\mathbf{x}) \propto \sigma(\mathbf{x}), \tag{20}$$

where $\lambda*(\mathbf{x})$ is the periodicity of the grid pattern formed locally around position $\mathbf{x}$. This results in a smooth change of grid period, corresponding to the observation in Fig. 1g of the main text.

Note that this result is generally true for any pattern forming kernel $W^g_{\mathbf{x}}(\mathbf{\Delta x})$ that has a Fourier transform with at least one local maximum, and *does not* rely on the specific form of a Mexican-hat interaction. Indeed, Eq. (20) holds for any kernel $W^g_x(\Delta x)$ that depends on a length-scale $\sigma(x)$. As an example, we present the corresponding analysis for the box-shaped kernel employed for pattern formation in Ref. [43]. In this case

$$W^g_{\mathbf{x}}(\mathbf{\Delta x}) = -W_0 \mathbb{1}_{\mathbf{\Delta x} \leq \sigma(\mathbf{x})}. \tag{21}$$

As discussed above, the quantity of interest is $\mathscr{F}W^g_{\mathbf{x}}(\mathbf{k})$

$$\mathscr{F}W^g_{\mathbf{x}}(\mathbf{k}) = \int_{-\infty}^{\infty} -W_0 \mathbb{1}_{|\mathbf{x}| \leq \sigma(\mathbf{x})} e^{i\mathbf{k}\cdot\mathbf{x}} d\mathbf{x} \tag{22}$$

$$= -W_0 \int_{|\mathbf{x}| \leq \sigma(\mathbf{x})} e^{i\mathbf{k}\cdot\mathbf{x}} d\mathbf{x}. \tag{23}$$

The above integral can be calculated in a one-dimensional setup to obtain

$$\mathscr{F}W_x^g(k) = -2W_0 \frac{\sin(k\sigma(x))}{k} \tag{24}$$

and can be calculated in a two-dimensional setup to obtain

$$\mathscr{F}W_{\mathbf{x}}^g(k) = -2\pi W_0 \sigma(\mathbf{x}) \frac{J_1(k\sigma(\mathbf{x}))}{k}. \tag{25}$$

In both of the above cases, note that $k^* \propto 1/\sigma(\mathbf{x})$ since $\sigma(\mathbf{x})$ is the only length-scale characterizing the kernel $W_{\mathbf{x}}^g$. In particular, numerical maximization yields

$$k^* \approx \begin{cases} 4.493/\sigma(x) & \text{if } x \text{ is one-dimensional, and} \\ 5.136/\sigma(\mathbf{x}) & \text{if } \mathbf{x} \text{ is two-dimensional.} \end{cases} \tag{26}$$

1.1 Fixed-scale interactions and modularization

We now claim that the addition of a fixed-scale kernel, $W^f(\mathbf{\Delta x})$ is sufficient to result in modularization of grid periods, with discrete changes in grid period as a function of spatial position along the dorso-ventral axis. This set of interactions can effectively be implemented by two populations of interneurons - one with fixed arborization and weaker synaptic connections and one with varying arborization length and stronger synaptic connections.

For simplicity, we shall present the specific Fourier transform computations for the one-dimensional problem, although we note that all of the qualitative results hold in two dimensions as well, with the Fourier transforms of the relevant functions replaced with their Hankel transforms (as shown in Sec. 3.8).

We include an additional weak interaction term W^f that critically does *not* depend on the neural sheet position x. For reasons that will become apparent soon, we choose kernels $W^f(\Delta x)$ such that the Fourier transform changes sign a sufficiently large number of times. We hypothesize that this requirement is not particularly restrictive, and will demonstrate that this holds for most kernels W^f.

The entire interaction profile is then given by

$$W_x(\Delta x) = W_x^g(\Delta x) + W^f(\Delta x). \tag{27}$$

We first demonstrate our result with an example of a simple kernel, to justify how Eq. (17) leads to the emergence of discrete grid modules. Consider the localized excitatory interaction

$$W^f(\Delta x) = \alpha_S \exp\left(-\frac{(\Delta x - d)^2}{2\sigma_S^2}\right) + \alpha_S \exp\left(-\frac{(\Delta x + d)^2}{2\epsilon_S^2}\right). \tag{28}$$

Corresponding to our interpretation of $W^f(\Delta x)$ above being a localized kernel, we choose $\epsilon_S \ll d$.

This choice of $W_x(\Delta x) = W_x^g(\Delta x) + W^f(\Delta x)$ leads to the the Fourier transform,

$$\mathscr{F}W_x(k) = \mathscr{F}W_x^g(k) + \mathscr{F}W^f(k), \tag{29}$$

$$= \sqrt{2\pi}\left[\alpha_E \sigma_E(x) \exp\left(-\frac{\sigma_E(x)^2 k^2}{2}\right) - \alpha_I \sigma_I(x) \exp\left(-\frac{\sigma_I(x)^2 k^2}{2}\right) + 2\alpha_S \epsilon_S \cos(kd) \exp\left(-\frac{\epsilon_S^2 k^2}{2}\right)\right]. \tag{30}$$

In our model, the magnitude of the $W^f(\Delta x)$, i.e., α_S, is chosen to be smaller than the magnitude of the Mexican-hat interaction. Thus we interpret $\mathscr{F}W^f(k)$ in Eq. (30) as being a small perturbation to the Fourier transform of the standard Mexican-hat interaction, $\mathscr{F}W_x^g(k)$. Further, since d is assumed to be much larger than the scale of the Mexican-hat, $\sigma_{E/I}$, then the term $\cos(kd)$ in $\mathscr{F}W^f(k)$ oscillates at a k-scale much smaller than the relevant scales of $\mathscr{F}W_x^g(k)$ (see Fig. 3b-c of the main text). Additionally, since $\epsilon_S \ll d$, the gaussian envelope multiplying the rapidly oscillating term has a scale $1/\epsilon$, which is much larger than the periodicity $1/d$.

Thus, in k-space, the rapidly oscillating term, $\mathscr{F}W^f(k)$ can be thought of as predefining a set $S = \{k_1, k_2, \ldots\}$ of local maxima. Under the approximations made above, the addition of the smoother function $\mathscr{F}W_x^g(k)$, will not change the position of the local maxima. This results in the *local* maxima of $\mathscr{F}W_x(k)$ also being the same set S. Importantly, we note that since S was predefined purely via $\mathscr{F}W^f(k)$, *there is no x dependence on the set S.*

Following Eq. (17), the wave-vector corresponding to the pattern formation at point x on the neural sheet corresponds to the *global* maxima of $\mathscr{F}W_x(k)$. Thus, at all points, the pattern formation corresponds to one of the discrete set of choices of wave vectors, $S = \{k_1, k_2 \ldots\}$. As can be seen from Fig. 3c, the smoothly varying gradient in the Mexican-hat term, $\mathscr{F}W_x^g$ as a function of x picks different choices of k_i depending on the position x — the $k \in S$ that is nearest to the maxima of $\mathscr{F}W_x^g(k)$ will be chosen as the global maxima, and will be the wave vector corresponding to the pattern at x. We refer to this mechanism as "peak selection".

For our particular choice of $W^f(x)$ made in Eq. (28), we obtained

$$\mathscr{F}W^f(k) = 2\alpha_S \epsilon_S \cos(kd) \exp\left(-\frac{\epsilon_S^2 k^2}{2}\right). \tag{31}$$

We can then approximate the local maxima of $\mathscr{F}W^f(k)$ as occurring at

$$S = \left\{ \frac{2m\pi}{d} \middle| m \in \mathbb{Z}^+ \right\}. \tag{32}$$

This immediately indicates that the ratios of periods of successive grid modules will be given by

$$\frac{\lambda_{m+1}}{\lambda_m} = \frac{m+1}{m}. \tag{33}$$

Thus, the addition of a fixed-scale interaction, W^f such as Eq. (28) results in discrete grid modules. We now show that this peak-selection mechanism, and hence modularization, occurs for arbitrary choices of the fixed-scale interaction kernel $W^f(\Delta x)$.

2 Kernels that lead to modularization

The peak-selection modularization mechanism described above arises naturally from the presence of the rapidly oscillating term in $\mathscr{F}W^f(k)$. In fact, for discrete grid modules to occur, the only constraints imposed on the fixed-scale kernel W^f are: (a) the Fourier transform $\mathscr{F}W^f(k)$ must have a sufficiently large number of maxima (at least 4 maxima, corresponding to the 4 grid modules observed in experimental observations); and, (b) these maxima must be at scales smaller than $1/\sigma$ in k-space. Here we argue that this is generally true for arbitrary kernels, modulo a single scaling parameter.

We hypothesize and give support, without formal proof, that almost every arbitrarily chosen kernel $W^f(\Delta x)$ will have a Fourier transform with multiple maxima satisfying condition (a). We will then argue that this kernel can always be scaled to satisfy condition (b).

To motivate our hypothesis, we first note that it is actually possible to construct specific kernels $W^f(\Delta x)$ whose Fourier transform does not present multiple maxima. For example, the Gaussian kernel, $W_{gauss}(\Delta x) = \exp[-(\Delta x)^2/2]$, results in a Fourier transform that is unimodal. However, we hypothesize that such functions are rare in the space of all continuous functions in L^2. Indeed, we can construct a function that is arbitrarily close to the Gaussian kernel whose Fourier transform will have an infinite number of maxima: Let $f_0(\Delta x) = \mathbb{1}_{[-1,1]}$ be the box function. Define

$$f_n = f * f_{n-1}$$

for all $n \geq 1$, where $f * g$ represents the convolution of functions f and g. By the central limit theorem, $\sqrt{n} f_n(\sqrt{n}\Delta x)$ will approach $W_{gauss}(\Delta x)$. However,

$$\mathscr{F}f_n(k) = [2\sin(k)/k]^n, \tag{34}$$

which clearly has an infinite number of maxima. Thus, even though the Gaussian kernel has a unimodal Fourier transform, we can construct a function $g_n(\Delta x) = \sqrt{n} f_n(\sqrt{n}\Delta x)$ that is arbitrarily close to the Gaussian kernel (for sufficiently large n) but has a Fourier transform that presents an infinite number of maxima.

In this context, we claim that almost every arbitrarily chosen kernel $W^f(\Delta x)$ will have a Fourier transform with multiple maxima. This may be intuited as follows: First note that Fourier space is a dual space, and hence instead of considering arbitrary kernels in real space we may equivalently choose arbitrary kernels in Fourier space. Further assuming that $\mathscr{F}W^f(k)$ is a smooth function, we hypothesize that generically smooth functions that are in L^2 will almost always have multiple maxima and minima.

Thus condition (a) may be satisfied for arbitrary kernels $W^f(\Delta x)$. Next, note that scaling a function in real space results in an inverse scaling of the Fourier transform, i.e., $\mathscr{F}[W^f(a\Delta x) = \mathscr{F}W^f(k/a)$. Hence, we can always scale the function $W^f(\Delta x)$ to obtain a Fourier transform with maxima that are within any desired scale, allowing condition (b) to be satisfied.

In Fig. 10, we show examples of modularization arising from different combinations of graded pattern forming kernels (W^g) and fixed-scale kernels (W^f). In each case, we also present the expected periodicity in each module as a function of spatial position as given by the perturbative analysis Eq. (17). The analytical result based on linear stability provides an excellent prediction of the pattern periods per module (see also Main text, Fig. 3e). It also predicts the locations of the module boundaries (see also Main text, Fig. 3e) though not as accurately: module boundary predictions tend to be slightly but systematically offset relative to the simulated dynamics, due to the effects of nonlinearity in the later stages of pattern formation.

3 Simple kernels and period ratios

What kinds of fixed-scale interactions might be present in the medial-entorhinal cortex? As described in the main text, in the context of biology, we might expect *simple* interaction kernels W^f to be relevant i.e., the fixed-scale interaction profile W^f has the following characteristics: (a) there exists a *single* length-scale d that primarily characterizes the shape of W^f; (b) any other length-scales relevant to W^f, say scales $\epsilon_1, \epsilon_2, \ldots$ are each much smaller than the primary length scale d. Further, we assume that the primary length-scale associated with the fixed-scale interaction is larger than the length-scales of the pattern forming kernel, i.e., $d \gg \sigma_{E/I}(x)$.

We will demonstrate that *simple* fixed-scaled interaction kernels result in analytic expressions for grid periods that are characterized by a single angular variable ϕ

$$\frac{\lambda_{m+1}}{\lambda_m} = \frac{m + 1 + \phi/(2\pi)}{m + \phi/(2\pi)}. \tag{35}$$

Before filling in the details of our argument, we present an intuitive explanation of the general idea:

Consider the following basic classes of *simple* kernels that satisfy the above-described criteria corresponding to a length-scale d:

(a) $g(|\Delta x| - d)$, for arbitrary functions $g(\rho)$ that are nonzero only over scales $|\rho| < \epsilon_i$ (a *localized* kernel), and,

(b) A constant term, that is uniform everywhere up to $\Delta x = d$, after which it falls to zero (a *diffuse* kernel),

(c) A decaying term, that decreases from a constant value at $\Delta x = 0$ to zero at $\Delta x = d$ (a *decaying* kernel).

We also define *short-range* kernels, as any arbitrary function $h(\Delta x)$ that is nonzero only over scales $|x| < \epsilon_i$.

Any *simple* kernel $W^f(\Delta x)$ can be generally constructed as a linear combination of the above basic classes. In addition, *simple* kernels may also contain an added component of a *short-range* kernel.

To see that *simple* kernels will generally result in grid period ratios corresponding to Eq. (35), we will examine the approximate Fourier transform structure for each component of the linear combination of *simple* kernels corresponding to a given length-scale d. We first demonstrate that each of the basic *simple* kernels will result in Fourier transforms that are sinusoidal functions with phase shifts and decaying envelopes and hence each basic *simple* kernel will satisfy Eq. (35). We then show that short-range kernels present Fourier transforms that vary only at large scales, and can be ignored in our analyses of *simple* kernels. We then use these results to demonstrate that all *simple* kernels constructed as the above-described linear combination will have sinusoidal Fourier transforms and will satisfy Eq. (35).

3.1 Localized kernels

For a general localized kernel $W^f(\Delta x) = g(|\Delta x| - d)$ we obtain

$$\mathscr{F}W^f(k) = \Re[e^{-ikd}\mathscr{F}g(k)]. \tag{36}$$

Since $g(x)$ is supported over a scale ϵ, the Fourier transform $\mathscr{F}g(k)$ will only vary at scales $k \sim 1/\epsilon \gg 1/d$. Thus for $1/d \ll k \ll 1/\epsilon$, we can approximate Eq. (36) as

$$\mathscr{F}W^f(k) = |\mathscr{F}g(k)| \cos(kd - \psi), \tag{37}$$

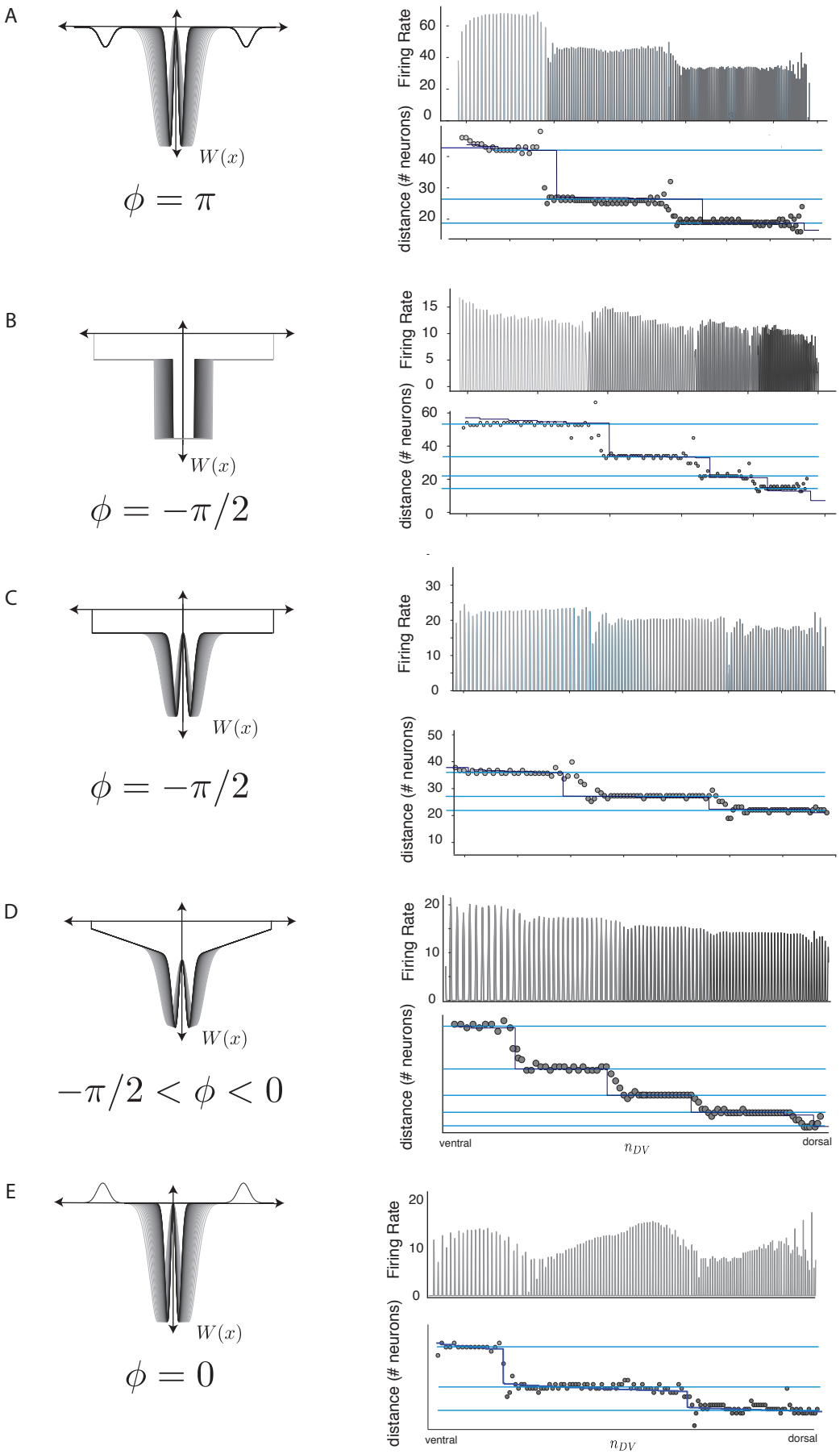


Figure 10: Examples of modularization and population activity (right column) with various pattern forming and fixed-scale lateral interactions (left column). In each case the dark-blue curve shows the predicted value of the grid period from Eq. (17), and is in close agreement with the numerical simulation of the population activity. Each of the fixed-scale interactions has a qualitatively different shape, spanning different values of ϕ (see Fig. 6)

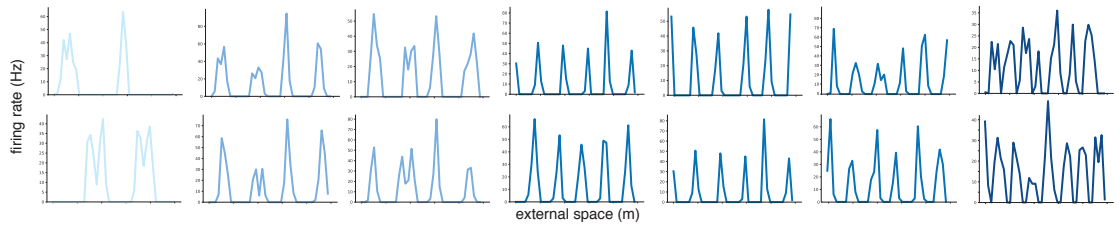


Figure 11: Sample tuning curves from several neurons in all modules from the network of Fig 2a.

where $\psi = \arg[\mathscr{F} g(k)]$. The local maxima of $\mathscr{F} W^f(k)$ will then occur at

$$S = \left\{ \frac{2m\pi + \psi}{d} \middle| m \in \mathbb{Z}^+ \right\}, \tag{38}$$

resulting in period ratios described by

$$\frac{\lambda_{m+1}}{\lambda_m} = \frac{m + 1 + \psi/(2\pi)}{m + \psi/(2\pi)}, \tag{39}$$

which is identical to Eq. (35) for $\phi = \psi$. We also note that we can now ascribe an interpretation to the phase angle ϕ — it is the phase difference between $\mathscr{F} W^f(k)$ and $\cos(kd)$.

3.2 Diffuse kernels

We model a diffuse interaction kernel $W^f(x)$ as

$$W^f(x) = -W_0 \mathbb{1}_{[-d,d]} = \begin{cases} -W_0 & \text{if } |x| \le d \\ 0 & \text{if } |x| > d \end{cases}. \tag{40}$$

Corresponding to the discussion above, we look at the Fourier transform $\mathscr{F} W^f(k)$

$$\mathscr{F} W^f(k) = \int_{-\infty}^{+\infty} -W_0 \mathbb{1}_{[-d,d]} e^{ikx} dx = \int_{-d}^{+d} -W_0 e^{ikx} dx \tag{41}$$

$$= -2W_0 \frac{\sin(kd)}{k} = -2W_0 d \ \mathrm{sinc}(kd). \tag{42}$$

Note that once again, similar to Eqn. (31), we obtain a functional form consisting of a periodic function ($\sin(kd)$) that is multiplied by a decaying envelope $1/(kd)$. Ignoring the effects of the envelope function, the maxima of this function occur at

$$S \approx \left\{ \frac{2m\pi - \pi/2}{d} \middle| m \in \mathbb{Z}^+ \right\}, \tag{43}$$

which immediately results in period ratios of the form

$$\frac{\lambda_{m+1}}{\lambda_m} \approx \frac{m + 1 - 1/4}{m - 1/4}, \tag{44}$$

which corresponds to the result in Eq. (35) for $\phi = \pi/2$.

More precisely, the extrema of $\mathscr{F} W^f(k)$ occur at $k_m d = q - 1/q - 2/3q^3 + O(q^{-5})$ where $q = \left(m + \frac{1}{2}\right)\pi$. Notably, the errors decay approximately as $1/(\pi m)$, and thus for modules generated corresponding to $m \gtrsim 2$ will result in period ratios that approximate Eq. (35) closely.

3.3 Decaying kernels

Decaying kernels with a scale d may be modeled as any monotonically decreasing function that decays from some constant W_0 at $\Delta x = 0$, to zero, at $\Delta x = d$. For simplicity, we consider the simplest linear approximation to such

a kernel, modeled as a triangular kernel. For additional subtleties in the treatment of other decaying kernels, see 3.5.1 The triangular kernel can be written as:

$$W^f(\Delta x) = \begin{cases} W_0(\Delta x - d)/d & \text{if } \Delta x < d \\ 0 & \text{if } \Delta x \geq d \end{cases} \tag{45}$$

This function can be written as the convolution of 2 diffuse box functions:

$$W^f(\Delta x) = (-W_0 \mathbb{1}_{[-d/2,d/2]}) * (W_0 \mathbb{1}_{[-d/2,d/2]}).$$

Thus, its Fourier transform is:

$$\begin{aligned} \mathscr{F}W^f(k) &= -W_0^2 d^2 \left(\frac{\sin(kd/2)}{(kd/2)} \right)^2 \\ &= -\frac{2W_0^2}{k^2}[1 - \cos(kd)]. \end{aligned}$$

Once again, we obtain a simple trigonometric function, with maxima at

$$S \approx \left\{ \frac{2m\pi}{d} \middle| m \in \mathbb{Z}^+ \right\}, \tag{46}$$

which immediately results in period ratios of the form

$$\frac{\lambda_{m+1}}{\lambda_m} \approx \frac{m+1}{m}, \tag{47}$$

which corresponds to the result in Eq. (35) for $\phi = 0$.

3.4 Short-range kernels

For the case of a short-range kernel $W^f(\Delta x)$ that extends upto a scale ϵ, we note from the Fourier uncertainty principle that the characteristic k-scales of $\mathscr{F}W^f(k)$ will $\sim 1/\epsilon \gg 1/d$. Thus, unlike the three other types of simple kernels discussed above, short range kernels do not have structure at the scale of $1/d$. Since all relevant scales are much larger than $1/d$, adding short range kernels to any of the other types of *simple* kernels will *not* change the structure of local maxima at scales of $1/d$.

3.5 Arbitrary simple kernels

We now consider a general form for *simple* kernels, by constructing linear combinations of the above described three basic classes of *simple* kernels each corresponding to the same length scale d and additional short-range kernels.

$$W^f = a_{\text{local}} W^f_{\text{local}} + a_{\text{diffuse}} W^f_{\text{diffuse}} + a_{\text{decaying}} W^f_{\text{decaying}} + a_{\text{short}} W^f_{\text{short}}. \tag{48}$$

As demonstrated in the preceding sections, the Fourier transform $\mathscr{F}W^f(k)$ will be given as

$$\mathscr{F}W^f(k) = a_{\text{local}} |\mathscr{F}g(k)| \cos(kd - \psi) - 2W_0 a_{\text{diffuse}} \sin(kd)/k - 2W_0^2 a_{\text{decaying}} (1 - \cos(kd))/k + \mathscr{F}h(k) \tag{49}$$

$$= H_0(k) + \sum_{i=0}^{3} H_i(k) \cos(kd + \phi_i) \tag{50}$$

for some constants ϕ_i, and some envelope functions $H_i(k)$ for $i = 0, 1, 2, 3$ that are slowly varying for $kd \gtrsim \mathscr{O}(1)$. Under this approximation, $\mathscr{F}W^f(k)$ is simply the sum of multiple sinusoidal waves with different phases and identical frequencies. Thus,

$$\mathscr{F}W^f(k) \approx \cos(kd - \phi) \tag{51}$$

for some ϕ and $kd \gtrsim \mathscr{O}(1)$. Hence, the maxima of $\mathscr{F}W^f(k)$ occur at

$$S \approx \left\{ \frac{2n\pi + \phi}{d} \middle| n \in \mathbb{Z}^+ \right\}, \tag{52}$$

which immediately results in period ratios of the form Eq. (35). Note that the approximations made above imply that there may be deviations from our results for the maxima corresponding to small k values — this may manifest as deviations in the largest period grid module away from Eq. 35.

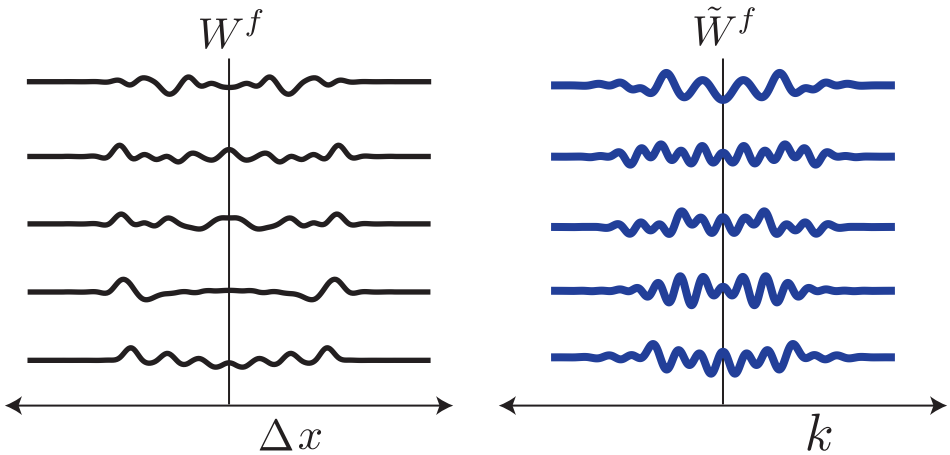


Figure 12: Randomly constructed fixed-scale interactions (left column) and their Fourier transforms (right column), in addition to the hand-designed ones in Fig.6a, that give $\phi = 0$.

3.5.1 Caveats

Clearly there exist *simple* kernels with Fourier transforms that are not given by $\mathscr{F}W^f(k) \approx \cos(kd - \phi)$. For example the Gaussian kernel, $W^f(\Delta x) = \exp[-\Delta x^2/(2d^2)]/(d\sqrt{2\pi})$ is a *simple* decaying kernel (since it has only a single scale d). Yet, its Fourier transform is simply $\mathscr{F}W^f(k) = \exp[-k^2d^2/2]$, which has only a single maximum! However, as we have shown earlier, there exist kernels that are arbitrarily close to the Gaussian kernel, whose Fourier transforms are given by powers of trigonometric functions, and hence have multiple regularly-spaced maxima with a spacing of $\sim 1/d$. Similarly, there exist additional *simple* functions[82, 83], $f(\Delta x)$, (like the Gaussian kernel) whose Fourier transforms $\mathscr{F}f(k)$ have a small number of maxima. We hypothesize that for all such functions $f(\Delta x)$ there exist *simple* kernels $g(\Delta x)$ that are arbitrarily close to $f(\Delta x)$ and possess regularly spaced maxima.

3.6 Period ratios

Having demonstrated analytically that *simple* kernels result in a sequence of period ratios given by Eq. (35), we now address the question of the mean period ratio over the sequence and over different values of ϕ. In the main text we have demonstrated that setting $\phi = 0$ results in a detailed period ratio sequence that is in close agreement with the sequence of experimentally observed values. Here we consider the period ratios obtained for other values of ϕ, to demonstrate that the experimental observation of mean period ratios being approximated by 1.4 [45] emerges naturally from our setup.

From Eq. (35), we obtained that the period ratio, $r_m = \lambda_{m+1}/\lambda_m$ can be written as

$$r_m = 1 + 1/(m + f), \tag{53}$$

where $f = \phi/(2\pi)$. We ignore $m = 1$, since that results in a period ratio close to 2, which does not correspond to experimental observations. Averaging the period ratio over the next 4 modules (corresponding to r_m for $m \in \{2 \ldots 4\}$) results in

$$\langle r_m \rangle_m = 1 + \frac{1}{3}\left(\frac{1}{f+2} + \frac{1}{f+3} + \frac{1}{f+4}\right) \tag{54}$$

As can be seen in Fig. 13, this mean period ratio lies in the range [1.3,1.45], indicating that at all values of ϕ, the period ratio obtained from Eq. (35) matches well with experimental observations. The average of these period ratios over all values of ϕ can also be calculated as

$$\langle r_m \rangle_{\phi,m} = 1 + \frac{1}{3}\left[\log\left(\frac{5}{3}\right) + \log\left(\frac{7}{5}\right) + \log\left(\frac{9}{7}\right)\right] \tag{55}$$

which is approximately equal to 1.37.

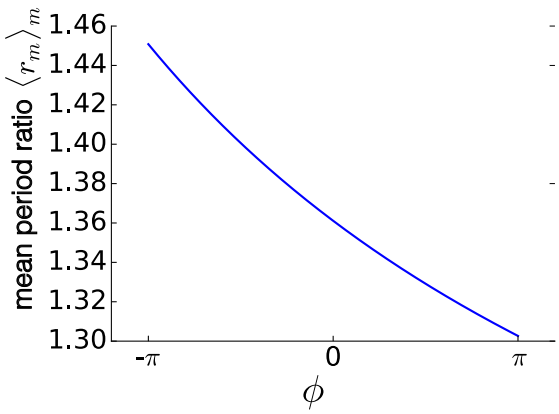


Figure 13: **Mean grid-period ratios** Ratios of grid periods averaged over 4 modules as a function of the phase shift ϕ in Eq. (35)

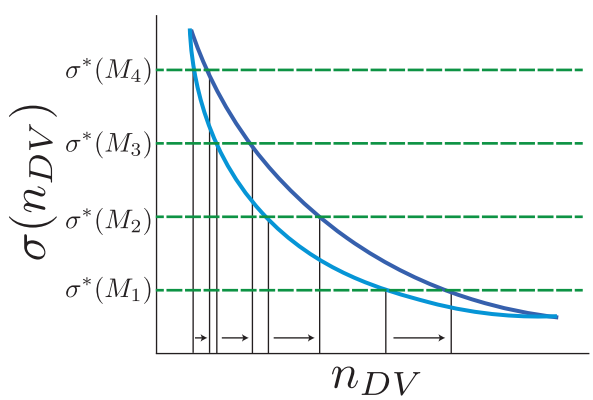


Figure 14: **The number of modules is a topological invariant and hence invariant to the gradient shape (the function $\sigma(x)$)** since it is set only by the fixed interaction width and the extremal/endpoint values of $\sigma(x)$, even though changing the gradient shape shifts the locations of module boundaries.

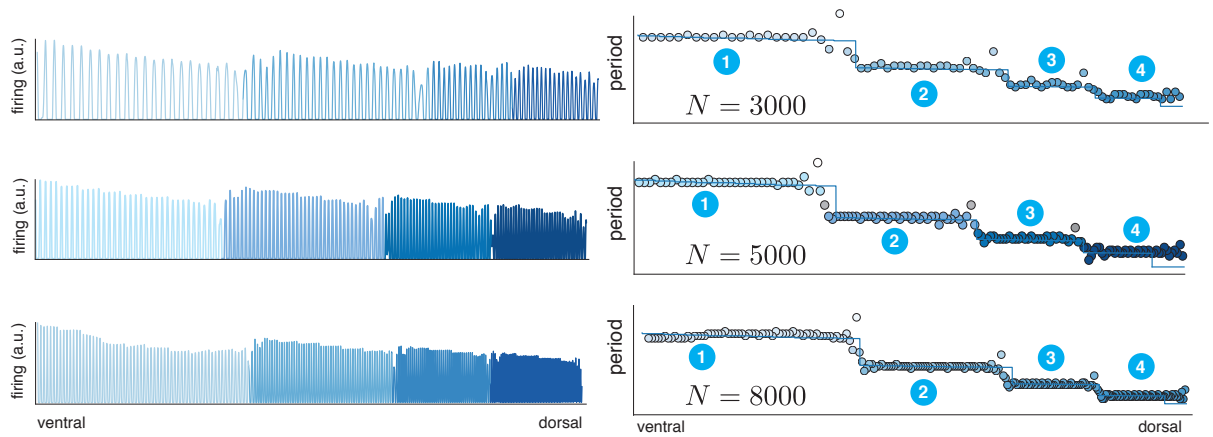


Figure 15: **The modularization process is independent of system size N and the size of formed module scales linearly with N**: 3 simulations corresponding to the same parameters as Fig.2d-f. The number of modules formed as well as the module periods remains the same as N is varied from 3000-8000.

3.7 Module size; number of modules as a topological quantity

As discussed in the main text, peak-selection for modularization is a highly robust mechanism that is largely indifferent to system parameters such as the the particular forms of the fixed-scale interaction and the shape of the gradient. Here we provide an analysis of the number of modules, the scaling of module sizes, and the positions of module boundaries, which also exhibit the same robustness. Further, we also describe how this robustness may be interpreted as arising from a topological origin, similar to topological robustness in other physical systems like the quantum hall effect.

Recall that for the continuously graded kernel $W_x^g(\Delta x)$ with characteristic spatial scale $\sigma(x)$ at position x, the wave-vector of the formed pattern was proportional to $1/\sigma(x)$:

$$k^{*g}(x) = \eta/\sigma(x), \tag{56}$$

where η is an x-independent constant that depends on only the particular form of the graded kernel. Let the spatial extent of the system be $x \in [0, L]$, with $\sigma(x)$ monotonic such that $\sigma_{\min} = \sigma(0) \leq \sigma(x) \leq \sigma(L) = \sigma_{\max}$.

We assume for simplicity that the fixed-scale lateral interaction is a *simple* kernel, such that $\mathscr{F}W^f(k) \sim \cos(kd - \phi)$. Thus, the local maxima generated by $\mathscr{F}W^f(k)$ occur at $k_n \approx (2n\pi + \phi)/d$, where n are the natural numbers. As discussed in the main text, each of these local maxima is 'selected' in turn by the moving broad peak of the Fourier transform of the graded kernel, whose position according to Eq. 56 occurs at $k^{*g}(x) = \eta/\sigma(x)$.

Notably, the selected maximum k_m will be robust to small perturbations in the selection function $\mathscr{F}W_x^g(k)$, since k_m will remain quantized to one of the discrete values prespecified by the set $\{k_n \| n \in \mathbb{N}\}$. In this sense, the chosen maximum k_m (and hence the corresponding module) presents the hallmarks of a topologically protected state[51]. The topological number corresponding to a given module is the module number m, which is a topological invariant similar to a winding number[51][1].

The set of modules expressed through the length of the system corresponds to the set of local maxima k_n that lie within the range $[\eta/\sigma_{\max}, \eta/\sigma_{\min}]$ that is delineated by the range of peak positions of the graded interaction. It follows that the maxima selected by the graded interaction obey:

$$\frac{\eta}{\sigma_{\max}} \leq \frac{2n\pi + \phi}{d} \leq \frac{\eta}{\sigma_{\min}}. \tag{57}$$

Thus, the set of formed modules are determined by the set of integers n that fit in the following interval:

$$\frac{-\phi + \eta d/\sigma_{\max}}{2\pi} \leq n \leq \frac{-\phi + \eta d/\sigma_{\min}}{2\pi} \tag{58}$$

and hence the number of modules ν_{mod} is:

$$\#\text{ modules} \equiv \nu_{mod} = \left\lfloor \frac{-\phi + \eta d/\sigma_{\min}}{2\pi} \right\rfloor - \left\lceil \frac{-\phi + \eta d/\sigma_{\max}}{2\pi} \right\rceil = \left\lfloor \frac{-\phi + k^{*g}(0)d}{2\pi} \right\rfloor - \left\lceil \frac{-\phi + k^{*g}(L)d}{2\pi} \right\rceil \tag{59}$$

[1] Note that in our convention the module number m is ordered such that the largest grid period module is the first module. This is opposite to the numbering usually used in the literature, such as in [45].

where $\lfloor\ \rfloor, \lceil\ \rceil$ indicate the floor and ceiling operations, respectively.

The above result leads to the following observations: First, the central quantity essential for determining the number of modules is the difference in the integer ratios of the fixed-scale interaction width to the extremal lateral interaction widths, $d/\sigma_{\min}, d/\sigma_{\max}$. Second, the number of modules depends only on the end-point values $\sigma_{\min}, \sigma_{\max}$ of the smoothly varying width $\sigma(x)$ the graded interaction; notably, it does not depend on the detailed shape of $\sigma(x)$. Moreover, if $\sigma_{\min}, \sigma_{\max}$ are varied smoothly (while d is held fixed), or if d is varied smoothly (while $\sigma_{\min}, \sigma_{\max}$ are held fixed), the number of modules will remain fixed, until the change becomes large enough to accommodate one additional or one less module. Thus, the number of modules is also a topological invariant of the system, through the module number m. Third, the number of modules does not depend on the system size L, or the number of neurons n_{DV} the system is discretized into (cf. SI Fig. 14). Fourth, since the average module size will be L/ν_{mod}, the module sizes are extensive in L. Thus, for sufficiently large L, the module sizes can be orders of magnitude larger than the scales of the lateral interaction d and σ.

Note that the above argument on topological robustness of the modularization of the system is not restricted to the case of *simple* fixed-scale kernels. Indeed, for any fixed-scale interaction W^f, the topological number m for any given expressed module will correspond to selecting the mth maximum of $\mathscr{F}W^f(k)$, for $k > 0$.

3.7.1 Module boundary locations

Following the peak-selection arguments made earlier, the module boundaries will occur at spatial locations that have $k^{*g}(x)$ in between k_n and k_{n+1} (the specific location will depend on the particular forms of the kernels). As a zeroth order approximation, we can assume that the module boundaries will occur near $(k_n + k_{n+1})/2$,

$$k^{*g}(x_{\text{boundary}}) \approx \frac{(2n+1)\pi + \phi}{d} \tag{60}$$

and thus

$$x_{\text{boundary}} \approx \sigma^{-1}\left(\frac{\eta d}{(2n+1)\pi}\right). \tag{61}$$

where σ^{-1} is the inverse function of $\sigma(x)$, $\sigma^{-1} \circ \sigma(x) = x$. Thus, while the specific positions of the module boundaries are dependent on the shape of the gradient $\sigma(x)$, qualitative features such as the number of modules, module periods and module sizes are indifferent to the particular forms of the gradient (cf. Fig. 14).

3.8 2D analysis

We have presented a majority of the above analysis for the case of one-dimensional grid cells. Here we briefly present the analogous computations for the Fourier transforms in two dimensions. We first demonstrate a classical result relating the Fourier transform of radially symmetric functions to the Hankel transform, which we shall then use to compute the relevant transforms. Consider the Fourier transform of a function $f(\mathbf{x}) = f(x, y)$

$$\mathscr{F}f(\mathbf{k}) = \int f(\mathbf{x})e^{i\mathbf{k}\cdot\mathbf{x}}d\mathbf{x}$$
$$\mathscr{F}f(k_x, k_y) = \int f(x, y)e^{ik_x x + ik_y y}dxdy.$$

Define polar coordinates in real and Fourier space such that:

$$\begin{aligned} x &= r\cos\theta \\ y &= r\sin\theta \\ k_x &= k\cos\phi \\ k_y &= k\sin\phi \end{aligned}$$

This leads to the dot product $\mathbf{k}\cdot\mathbf{x}$ to be simplified as

$$\begin{aligned} k_x x + k_y y &= rk(\cos\theta\cos\phi + \sin\theta\sin\phi) \\ &= rk\cos(\theta - \phi) \end{aligned}$$

Thus,

$$\mathscr{F}f(k_x,k_y) = \mathscr{F}f(k,\phi) = \int_0^\infty \int_0^{2\pi} r dr d\theta f(r,\theta) e^{ikr\cos(\theta-\phi)}$$

In all cases of interest, the function f is a kernel, and is hence a radially-symmetric real function $f(r,\theta) = f(r)$. Similarly, the Fourier transform $\mathscr{F}f$ will also be a real radially-symmetric function $\mathscr{F}f(k,\phi) = \mathscr{F}f(k)$. Thus

$$\mathscr{F}f(k) = \int_0^\infty \int_0^{2\pi} r dr d\theta f(r) e^{ikr\cos(\theta-\phi)}, \tag{62}$$

$$= \int_0^\infty r dr f(r) \int_0^{2\pi} e^{ikr\cos(\theta-\phi)} d\theta, \tag{63}$$

$$= 2\pi \int_0^\infty r f(r) J_0(kr) dr, \tag{64}$$

where J_0 is the Bessel function of the first kind, defined by

$$J_0(x) = \frac{1}{2\pi} \int_0^{2\pi} e^{ix\cos(\theta-\phi)} d\theta.$$

Equation (64) defines the Hankel transform (of order zero) of $f(r)$ — the radial component of the Fourier transform of the kernel $f(\mathbf{x})$ is simply the Hankel transform of $f(|\mathbf{x}|)$.

For the localized gaussian secondary interaction, we can calculate the Fourier transform analytically.

$$\begin{aligned}\mathscr{F}W_{\text{local}}(k) &= 2\pi \int_0^\infty r\left[\alpha_E e^{-r^2/2\sigma_E^2} - \alpha_I e^{-r^2/2\sigma_I^2} + \alpha_S e^{-(r-d)^2/2\sigma_S^2}\right] J_0(kr) dr \\ &= 2\pi\left[\alpha_E \sigma_E^2 e^{-k^2\sigma_E^2/2} - \alpha_I \sigma_I^2 e^{-k^2\sigma_I^2/2} + \alpha_S J_0(kd)\sigma_S^2 e^{-k^2\sigma_S^2/2}\right]\end{aligned}$$

We can also analytically calculate the Fourier transform for a box-like interaction:

$$\begin{aligned}\mathscr{F}W_{\text{diffuse}}(k) &= 2\pi W \int_0^d r J_0(kr) dr \\ &= \frac{2\pi W}{k^2} \int_0^{kd} \rho J_0(\rho) dr \\ &= \frac{2\pi W}{k^2} [kdJ_1(kd)] \\ &= \frac{2\pi W d^2 J_1(kd)}{kd}\end{aligned}$$

We can similarly also define a two-dimensional equivalent of the decaying kernel, as the convolution of the half-sized circular box kernel with itself. Thus, by applying convolution theorem to the result on diffuse kernels we obtain

$$\mathscr{F}W_{\text{decaying}}(k) = \left[\frac{\pi W d J_1(kd/2)}{k}\right]^2.$$

Note that $J_0(x)$ and $J_1(x)$ display qualitatively similar behavior to $\cos(x)$ and $\sin(x)$ respectively, apart from an amplitude modulation of the peaks — particularly, we note that the Bessel functions display approximately periodic maxima, which was the central property required for all of our results on modularization and peak selection to apply. We demonstrate this in Fig.16, where we show that the maxima of the Bessel functions are approximately periodic, and fit the form of Eq. (35) well. In particular, note that the best-fit value of ϕ for $J_0(k)$ is approximately 0, which is similar to $\cos(k)$, and the best-fit value of ϕ for $J_1(k)$ is approximately $\pi/4$, which is similar to $\sin(k)$.

We implemented a 2d simulation that generates 3 discrete modules as shown in Figure 18. For computational feasibility, the simulation was performed in 2 parts: one with $x \in [0, 0.6N_x^{2d}]$ and the other with $x \in [0.6N_x^{2d}, N_x^{2d}]$. The weight matrices for each network were of size 100x1000 each. The weight matrix for a single large 100x2000 network would have contained $4x10^{10}$ elements, which we found prohibitively difficult and slow to run.

Fig 19(a) shows another instance of a modular 2d network, the only difference being the value of d_{loc}, which changed from 50 to 45. Fig 19(b) shows the same simulation with 2 distinct random initializations. The pair of resulting modules in each simulation have different relative orientations. Because finite size effects from our simulations also partially constrain the orientations of the modules (data not shown), we cannot make predictions about the relative orientations of the grid modules found in experiments [45].

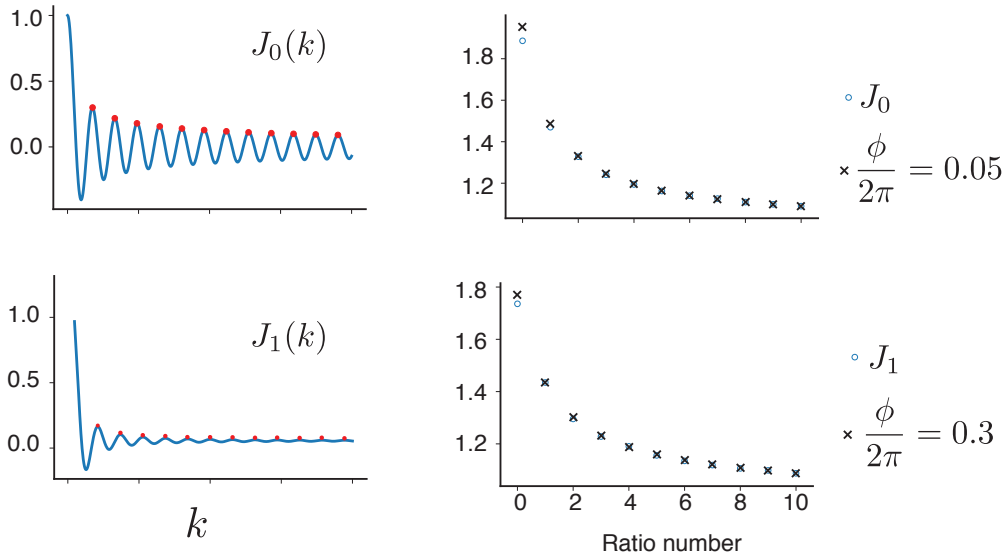


Figure 16: Bessel functions (left column) and period ratios for Bessel function maxima (right column) with their best-fit values of ϕ for the period ratios corresponding to Eq. (35)

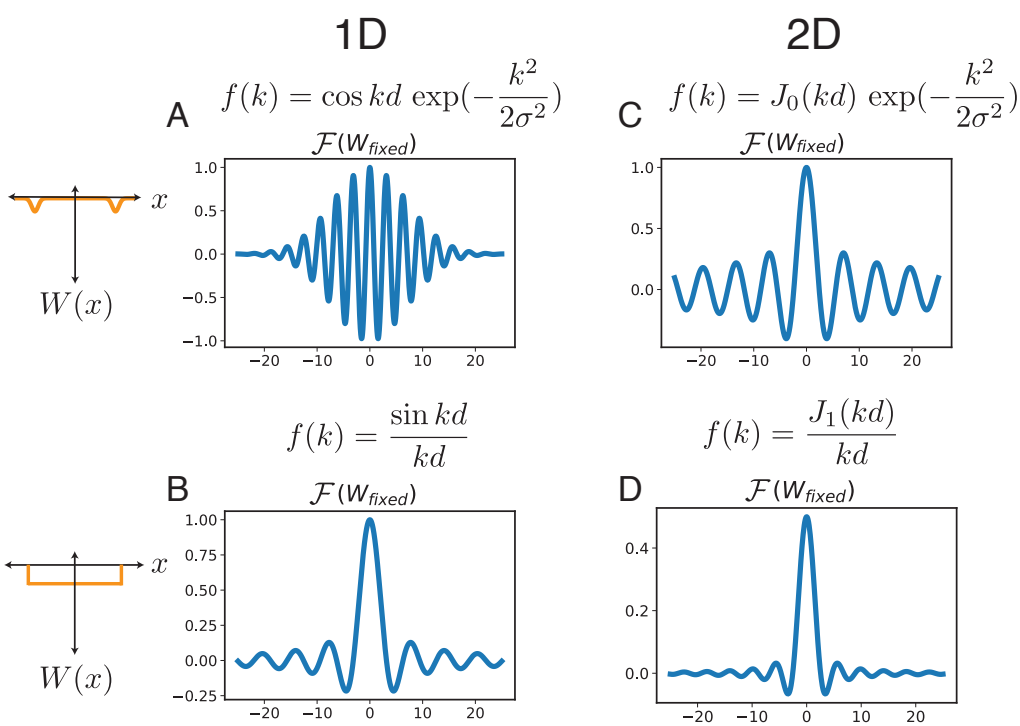


Figure 17: Fixed interactions(left, in orange) and their oscillatory Fourier transforms in 1D (left column) and 2D (right column).

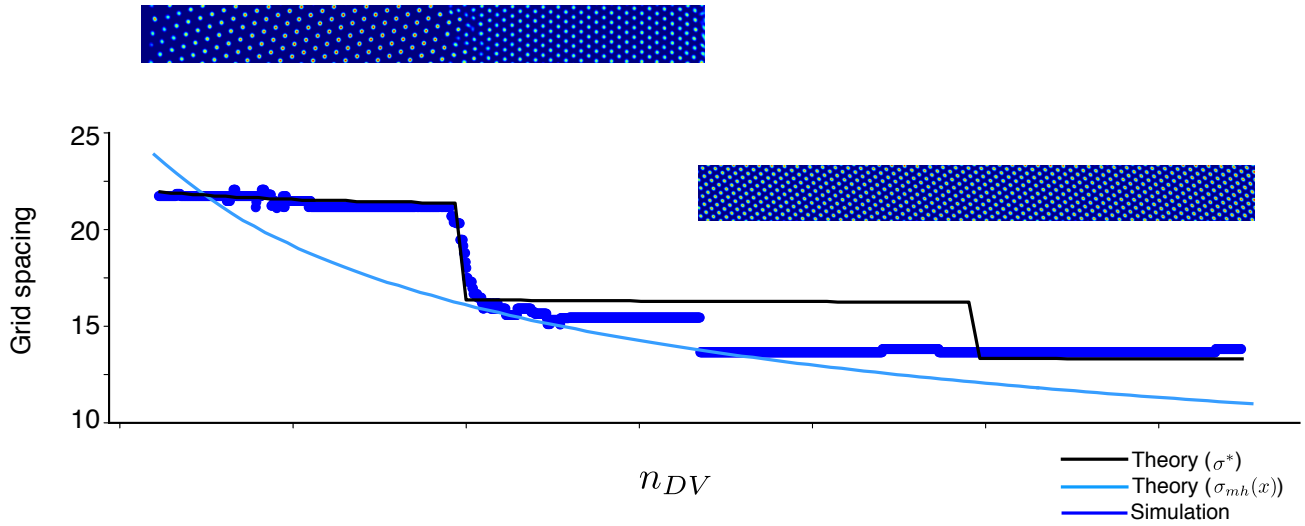


Figure 18: **2d simulation with 3 modules:** (top) Snapshots of population activity showing 3 discrete 2d grid modules, (bottom) plot of grid spacing and comparision with Hankel transform predictions. Grid spacing determined by calculating the (neural) spatial auto-correlation of the population firing activity.

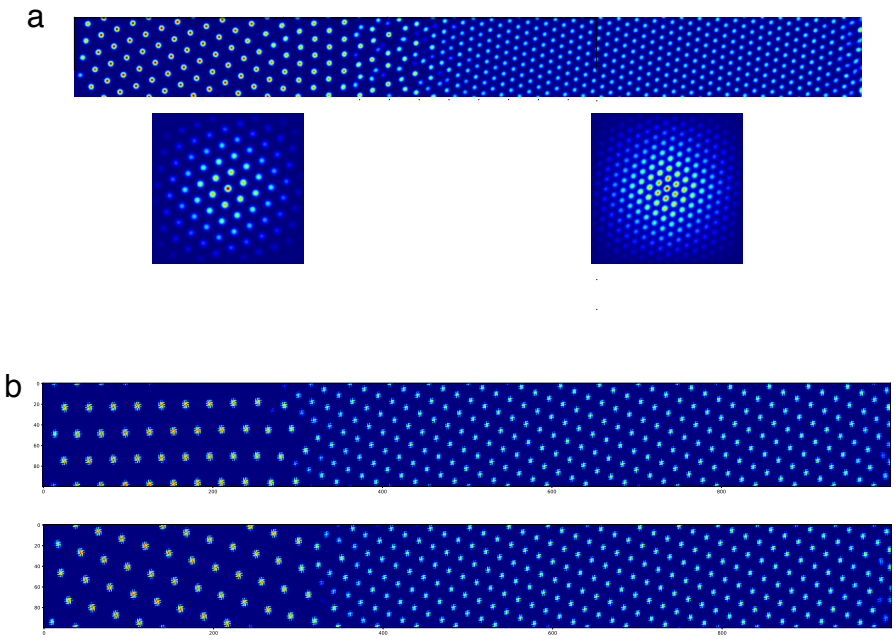


Figure 19: (a) Another instance of a spontaneously formed two dimensional network with parameters given in Table 4. (b) Two different random initializations of the network from Fig 2h show different relative orientations between the 2 formed modules.

3.9 Robustness to spatial noise

In the main text, we discussed how the topological robustness properties of peak selection result in the formed modules being stable to several forms of noise. Particularly, here we focus on the robustness to spatial heterogeneities in the lateral interaction kernels.

We first examine the robustness to spatial heterogeneities in the pattern forming kernel W^g. To construct such an inhomogeneous pattern-forming interaction, we construct the noisy kernel at location $\mathbf{x}$, by replacing the spatially homogeneous kernel $W^g[\mathbf{x},\mathbf{x}'] = W^g[\mathbf{x}-\mathbf{x}']$, with a spatially heterogeneous kernel $W^g_\xi[\mathbf{x},\mathbf{x}'] = W^g[(\mathbf{x}-\mathbf{x}')\times(1+\xi(\mathbf{x}'))]$, where $\xi(\mathbf{x}')$ is a random number sampled independently for each spatial location $\mathbf{x}'$ with mean zero and variance ϵ^2. In Fig. Fig. 20d we present examples of such kernels for the case of $W^g[\mathbf{x},\mathbf{x}']$ described by the box function Eq. (6). Note how the independent sampling of $\xi(\mathbf{x}')$ at each location results in a heterogenous kernel W^g_ξ that varies in scale at different $\mathbf{x}$, and is no longer radially symmetric.

Recall that peak selection entails that the grid period at any location $\mathbf{x}$ is dependent on the set of potential maxima defined by $\mathscr{F}W^f(k)$, with a selection between these maxima performed by the broader peak of $\mathscr{F}W^g(k)$. If noise in the form of spatial heterogeneities are only introduced in W^g (and hence introduced in $\mathscr{F}W^g$) this results in a noisy selection function. However, since the same maxima will be chosen for a range of selection functions (See Fig. 20a-b), the heterogeneity in W^g will not be manifested in the emergent grid period.

We next consider the addition of similar heterogeneities in the fixed-scale interaction as well, W^f (such as in Fig. 20c). Note that maxima induced by *simple* W^f are at $k_n \approx (2n\pi+\phi)/d$, where n are the natural numbers, and hence the grid periodicity of the nth module is given by $\lambda_n \approx d/(n+\phi/2\pi)$. If we consider $\mathscr{O}(\epsilon)$ noise added to W^f in the form of spatial heterogeneities, this would result in an $\mathscr{O}(\epsilon)$ error in the effective fixed-scale d. However, since λ_n is approximately d/n, thus the effective noise in periodicity of the nth module, λ_n, will be $\mathscr{O}(\epsilon/n)$. Thus, higher module numbers (corresponding to modules with smaller grid periods) have additional error correction beyond the robustness conferred by the topological nature of the peak selection process. This results in clean hexagonal firing fields despite inhomogeneities introduced in all lateral interactions as shown in Fig. 7.

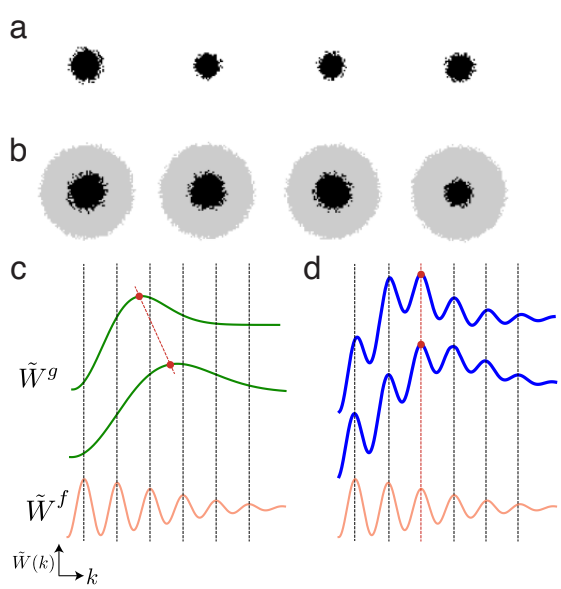


Figure 20: **Noise robustness in peak selection process** demonstrating how the additional of the smaller oscillatory fourier transform of the fixed interaction leads to no change in maxima despite smooth movement of the primary peak.

3.10 Comparison of experimental observations with predicted period ratios

The general mechanism of peak-selection presented above describes how discrete modules can spontaneously arise in the presence of continuous gradients, by consideration of an additional fixed-scale lateral interaction W^f. However, this mechanism does not provide any testable predictions for the ratio of grid periods unless additional assumptions are made. If indeed we assume that W^f is a *simple* kernel, i.e., W^f is primarily defined by a single spatial scale, then we demonstrated in SI Sec. 3 that the period ratios will be given by the simple formula, Eq. 35. In this section, we show that experimental observations of grid periods largely appear to match our predicted period ratios for *simple* kernels with $\phi = 0$.

For verification of our main results on the predicted form of period ratios, we examine the literature for grid period measurements for multiple simultaneously measured grid modules in rats[45, 84, 85, 86]. We note that a large fraction of experimental observations of grid cells with more than one module measure only two modules. For a single pair of grid periods λ_1 and $\lambda_2 > \lambda_1$, we can always explicitly solve for ϕ and m in Eq. (35), to obtain

$$\frac{\phi}{2\pi} = \left\{\frac{\lambda_2}{\lambda_1 - \lambda_2}\right\}, m = \left\lfloor \frac{\lambda_2}{\lambda_1 - \lambda_2} \right\rfloor, \tag{65}$$

where $\{x\}$ represents that fractional part of x, and $\lfloor x \rfloor = x - \{x\}$ represents the integer part of x. Thus, a single ratio, because it can always be fit by Eq. (35), imposes no constraints on the accuracy of the expression.

It is possible to obtain a value of ϕ from Eq. (35) and a single pair of periods; however, the estimate obtained from a single pair is not robust: r_m depends too sensitively on ϕ. For example, in [45], Rat 13388 exhibits grid periods of $\approx$ 53.24 cm and $\approx$ 43.00 cm (as estimated from SI Fig. 12b in [45]); Eq. (35) then yields $\phi/(2\pi) = 0.199$. Assuming a very small measurement error of $\sim 0.5cm$ in the larger period, such that if it were 53.75 cm instead of 53.24, would yield ϕ exactly equal to zero. A simple sensitivity analysis of the magnitude of error in estimating ϕ can be performed from Eq. (65):

$$\delta\phi = 3\epsilon \frac{\lambda_2}{\lambda_1 - \lambda_2} \approx 3\epsilon m, \tag{66}$$

where ϵ represents the fractional error in the estimate of grid period. Thus, particularly for smaller grid periods (corresponding to larger m), even small errors in grid period estimation can result in a large error in ϕ, making the errorbars in the estimation of ϕ from a single pair of periods large.

To obtain results with significant statistical certainty, we focus our analysis on published experimental studies that measure at least 50 grid cells per animal, spanning at least 3 distinct modules. This restriction results in grid period data sets for three rats — we present kernel density estimates of the module periods for each of them in Fig. 21 (Fig. 21c corresponds to the data presented in the main text in Fig. 5).

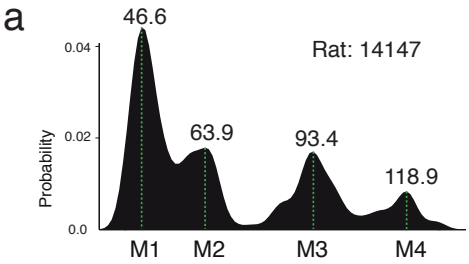
We have already demonstrated in Fig. 5 that Rat 14257 presents an extremely accurate match to the period ratio prediction for $\phi = 0$ (i.e., predicted period ratios of 2, 3/2, 4/3, 5/4,...); in addition, Rat 14147 (observed period ratios of 1.27 , 1.46 $\approx$ 3/2, 1.37 $\approx$ 4/3) and Rat 15708 (observed period ratios of 1.31, 1.49 $\approx$ 3/2, 1.32 $\approx$ 4/3) also match $\phi = 0$ very well (R^2 values of 0.999, 0.979, and 0.968 for Rats 14257, 15708, 14147 resp.) for all grid modules except for the module with the largest period.

Why is there an observed discrepancy for the grid module with the largest period? We propose four possible reasons for this discrepancy: Firstly, this discrepancy may be a result of the approximation made in arriving at Eq. (51) — since the approximation is particularly accurate for $kd \gtrsim \mathcal{O}(1)$, the potentialy mismatch would primarily affect only the largest grid period module. Secondly, as demonstrated in Sec. 3.9, the grid module corresponding to the largest grid period will have the least robustness to noise in the fixed-scale interaction, potentially introducing a large variance in the grid period for that module. Thirdly, as can be seen in Fig. 6c and Eq. (66), the error in estimating the grid period for the first module ($m = 1$) is the most susceptible to errors in the value of ϕ Lastly, our predictions for grid period ratios Eq. (35) are for the case of *simple* kernels that have a single spatial scale. A discrepancy at only the largest grid module may thus be suggestive of fixed-scale interactions that are primarily described by a single scale, with an additional low frequency perturbation at a larger spatial scale.

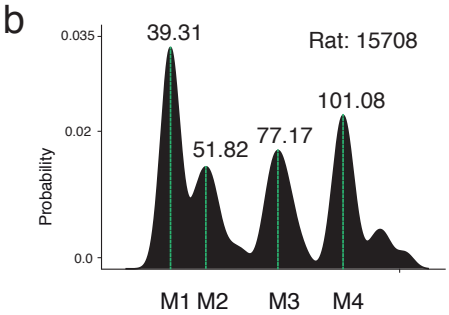
However, note that (particularly for Rats 14147 and 14257) there are relatively few grid cells observed from this largest period module, and the resulting uncertainty in period estimation may instead contribute to the error. In sum, apart from the possibility of some additional low frequency perturbations, the experimental data for rats with several simultaneously observed grid modules is largely consistent with the predicted period ratios for simple kernels with $\phi = 0$.

Skipped modules: Sometimes, neural recordings can miss a module. This can cause a large deviation from our predictions. For example, for a set of 5 modules following period ratios M4/M5 = 1.20, M3/M4 = 1.25, M2/M3 = 1.33, M1/M2 = 1.5. If recordings had missed module M4, the measured ratios would be M1/M2 = 1.5, M2/M3 = 1.33, M3/M5 = 1.5.

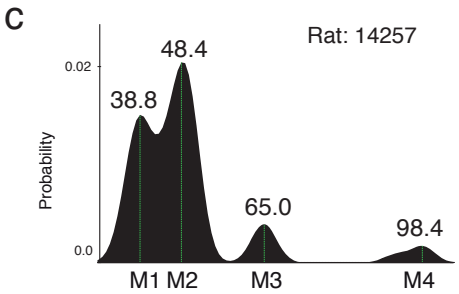
However, we do note that available data on multiple modules with a statistically large number of grid cells per module are quite sparse. To obtain further verification of our theoretical results, including the prediction of Eq. (35) and even more specifically the hypothesis that ϕ is close to zero, additional data with multiple simultaneously observed grid modules will be important.



observation	$r_m(1.26)$prediction	deviation
1.273	1.83	30.%
1.462	1.46	0.13%
1.371	1.31	4.65%



observation	$r_m(0.7)$prediction	deviation
1.310	1.90	31.%
1.489	1.48	0.61%
1.318	1.32	0.15%



observation	$r_m(0)$ prediction	deviation
1.514	3/2 = 1.5	0.93%
1.343	4/3 = 1.33	0.75%
1.247	5/4 = 1.25	0.24%

Figure 21: The 3 rats from Stensola *et al.* with 4 modules and their corresponding periods.

4 Lyapunov Function

The energy function of continuous time neural networks can be written as [87]:

$$E(\mathbf{s}) = -\frac{1}{2}\sum_{ij} s(i)W_{ij}s(j) + \sum_i \frac{1}{R_i}\int_0^{s(i)} \phi^{-1}(s)\,ds - \sum_i I_i s(i), \tag{67}$$

where $\mathbf{s}$ represents a vector of the synaptic activation at each neuron in the network, and I_i is the input bias to neuron i. For simplicity and since linear analysis does a remarkably good job in predicting the formed modules, let us restrict ourselves to the case of $\phi(x) = x$. Also, since the system is locally translationally invariant, we know that the dominant modes are going to be periodic. Hence, we may evaluate the energy function of the network dynamics (in the linearized regime) by assessing the energy of the periodic neural activity modes:

$$\mathbf{s}_k(\mathbf{x}) = A\sin(\mathbf{k}\cdot\mathbf{x} + \delta) + B, \tag{68}$$

where $\mathbf{k} = k\hat{\mathbf{k}}$ is an arbitrary Fourier space vector, and A,B and δ are arbitrary constants. For these modes, we can write the energy function in the continuum limit as:

$$E[s_{\mathbf{k}}(\mathbf{x})] = -\frac{1}{2}\int d\mathbf{x}d\mathbf{x}' W(\mathbf{x},\mathbf{x}')s_{\mathbf{k}}(\mathbf{x})s_{\mathbf{k}}(\mathbf{x}') + \frac{1}{2}\int d\mathbf{x}s_{\mathbf{k}}(\mathbf{x})^2$$

Assuming that the system size L is large,

$$\begin{aligned}
2E[s_{\mathbf{k}}(\mathbf{x})] &= -\int W(\mathbf{x}-\mathbf{x}')[A\sin(\mathbf{k}\cdot\mathbf{x}+\delta)+B][A\sin(\mathbf{k}\cdot\mathbf{x}'+\delta)+B]d\mathbf{x}d\mathbf{x}' + \int [A\sin(\mathbf{k}\cdot\mathbf{x}+\Delta)+B]^2 d\mathbf{x} \\
&= -A^2\int d\mathbf{u}d\mathbf{v}W(\mathbf{u})\cos(\mathbf{k}\cdot\mathbf{u}) + A^2\int d\mathbf{u}d\mathbf{v}W(\mathbf{u})\cos(2\mathbf{k}\cdot\mathbf{v}+\delta) + B^2\int d\mathbf{x}d\mathbf{x}'W(\mathbf{x}-\mathbf{x}') + L(A^2/2+B^2) \\
&= -A^2L\int d\mathbf{u}e^{i\mathbf{k}\cdot\mathbf{u}}W(\mathbf{u}) + A^2\int d\mathbf{u}W(\mathbf{u})\int d\mathbf{v}\cos(2\mathbf{k}\cdot\mathbf{v}+\delta) + B^2\int d\mathbf{u}d\mathbf{v}W(\mathbf{u}) + L(A^2/2+B^2)/2 \\
&= -A^2L\tilde{W}(k) + LB^2\bar{W} + L(A^2/2+B^2), \\
&= -\text{constant}_1 \times \tilde{W}(k) + \text{constant}_2
\end{aligned}$$

where have used the simple trigonometric identity, $2\sin(C)\sin(D) = \cos(C-D) - \cos(C+D)$, and a change of variables, $\int d\mathbf{x}d\mathbf{x}' = (1/2)\int d(\mathbf{x}-\mathbf{x}')d(\mathbf{x}+\mathbf{x}') = \int d\mathbf{u}d\mathbf{v}$, with $\mathbf{u} = \mathbf{x}-\mathbf{x}'$ and $\mathbf{v} = \frac{1}{2}(\mathbf{x}+\mathbf{x}')$.

Thus, we obtain that the energy function $E[s_{\mathbf{k}}]$ is a simple linear function of the Fourier transform $\tilde{W}(k)$ of the recurrent weight matrix. The minimum energy solution corresponds to the Fourier mode that maximizes $\tilde{W}(k)$. In other words, the dynamics is dominated by the k^* that maximizes $\tilde{W}(k)$. This result, derived from an energy landscape perspective, is equivalent to the result in Eq. (17), which we obtained earlier via perturbation analysis.

5 General formulation of module formation dynamics: Discrete peak selection via loss minimization

In Sec. 4, we demonstrated how the pattern formation on the neural sheet can be derived via an energy minimization approach. Here, we use an energy landscape view to describe how loss function minimization results in modular solutions.

The key components for spatially modular solutions to arise from energy minimization are as follows: 1) A spatially-independent loss function $f(\theta)$ with multiple local maxima and minima; 2) A gradient in a spatially-dependent variable, $\theta_0(x)$; and 3) A coupling between the system parameters θ and θ_0, that results in a combined loss function

$$L(\theta, x) = f(\theta) + \alpha\|\theta - \theta_0(x)\|^2 \tag{69}$$

Under appropriate constraints on $f(\theta)$, solving the following optimization at each x

$$\theta^*(x) = \arg\max_\theta L(\theta, x) \tag{70}$$

will produce discrete, step-like changes as a function of x. This happens because the smooth minimum given by the $||\theta - \theta_0(x)||^2$ term effectively selects one of the local minima in $f(\theta)$ as the global minimum. As the function $||\theta - \theta_0(x)||^2$ slides smoothly along with x,the peak of $f(\theta)$ selected as the global minimum remains the same for some time, then jumps abruptly. These step-like changes are modular solutions to the global optimization problem. The energy function defined in Eq. (69) can be viewed as a regularized optimization problem, with the spatially-dependent regularizer $||\theta - \theta_0(x)||^2$ acting as a prior that selects one of the minima of $f(\theta)$ at each location (Fig. 22).

The correspondence of this general picture with the peak selection mechanism described in the main text follows directly with the following identifications: the spatially independent nonlinear loss function $f(\theta)$ with the fixed-scale interaction W^f; the spatially varying parameter prior $\theta_0(x)$ with the graded scale $\sigma(x)$ of the pattern-forming kernel; the combined loss $L(\theta, x)$ with the full kernel W_x; and the spatially-varying, multi-step-like set of optima $\theta^*(x)$ with the grid periods $\lambda^*(x)$, respectively. Similar to peak selection for grid cells, the formed modules in this generalized setting will also inherit topological robustness and stability.

Although we primarily focused on the peak selection process in Fourier space for multi-periodic patterning in grid cells, we also showed that it has a general formulation in terms of dynamics on an energy landscape: One (spatially invariant) interaction sets up an optimization problem with multiple local minima, while a second (spatially graded) interaction defines a locally shallow single-optimum landscape, with a smoothly shifting optimum as a function of space. Thus, the shallow optimum selects one of the narrow local optima as the global optimum, with discontinuous jumps to the next local minimum even as the parameters vary smoothly. This analytical formulation provides a simplifying mathematical perspective on how smooth gradients could lead to discrete patterning and modular specialization in the brain and body [52, 53, 54].

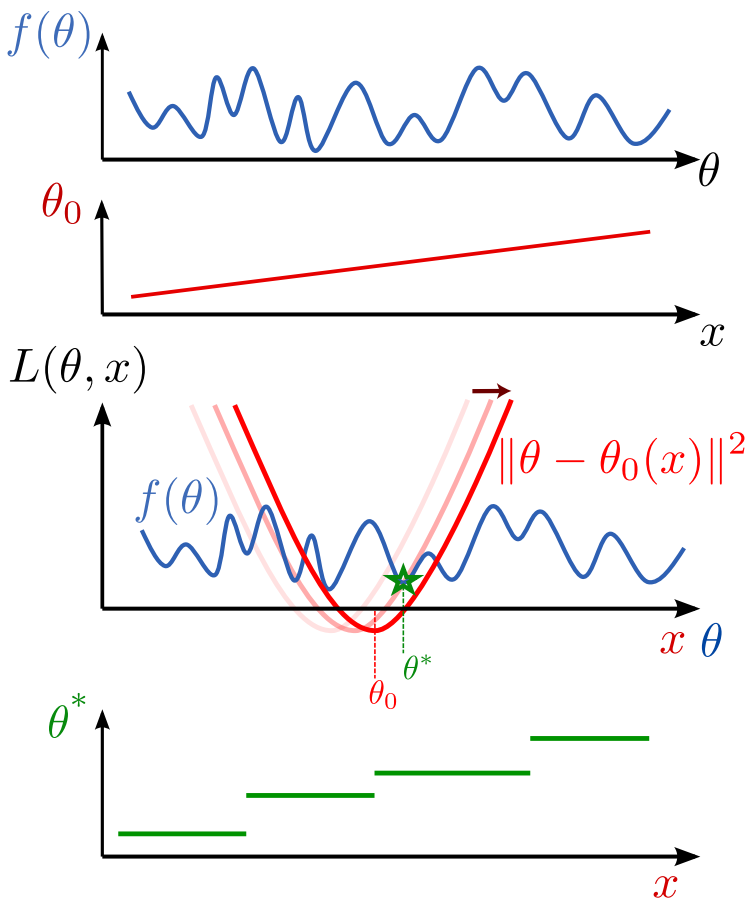


Figure 22: **A general setting for peak-selection** Assuming a loss function $f(\theta)$ (blue) and a spatially dependent quantity θ_0 (red), a combined loss function $L(\theta, x)$ can be constructed such that the x-dependent optimizer of $L(\theta, x)$ will be modular (green), since it will be constrained to correspond to one of the minima of $f(\theta)$.

6 The emergence of modules corresponds to the formation of localized eigenvectors

As has been observed before [88], a neural network endowed with slowly varying local interactions shows diverse timescales that are spatially localized: different parts of the network respond with disparate temporal dynamics.We also find a localization of eigenvectors in our multi-module grid network, Fig. 23A. Similar to [88], our interaction matrix has a locally circulant form (due to the slowly varying gradient in lateral inhibition width).

We find that in the resulting set of localized eigenvectors, each has a different but constant period, Fig. 23B. These periods exactly match the spatial periods of the modules formed in steady state. In sum, the locally circulant matrix gives rise to eigenvector localization, and the localized eigenvectors correspond to the modules.

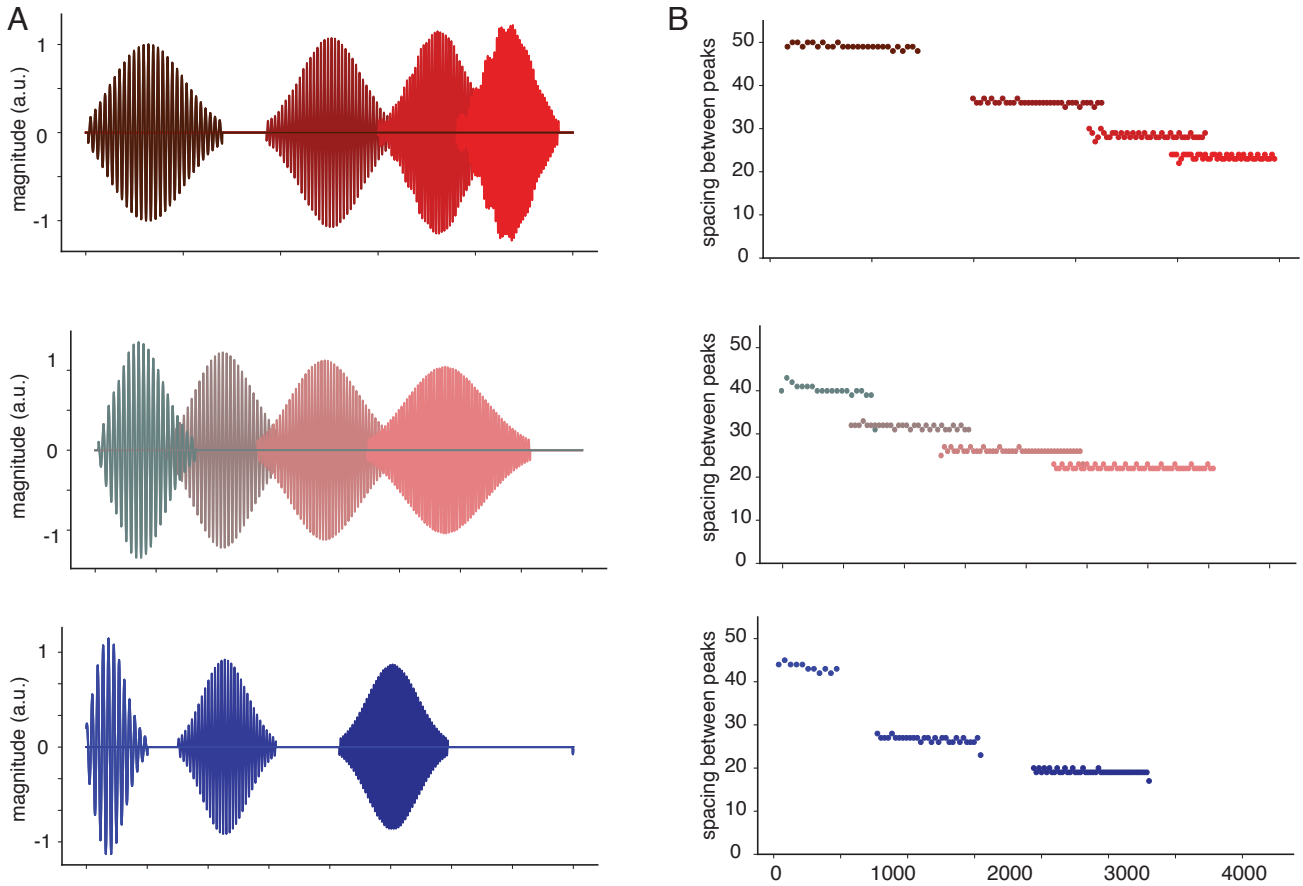


Figure 23: **Localization of eigenvectors**: A) Eigenvectors of various one-dimensional interaction weight matrices along with the corresponding inter-peak spacings are localized, B) The periodicity within an eigenvector is constant.