Review

### *Special Issue: The Connectome*

# Cortical dynamics revisited

**Wolf Singer**[1,2,3]

[1] Max Planck Institute for Brain Research (MPIB), Frankfurt am Main, Germany
[2] Ernst Struengmann Institute for Neuroscience in Cooperation with the Max Planck Society (ESI), Frankfurt am Main, Germany
[3] Frankfurt Institute for Advanced Studies (FIAS), Frankfurt am Main, Germany

**Recent discoveries on the organisation of the cortical connectome together with novel data on the dynamics of neuronal interactions require an extension of classical concepts on information processing in the cerebral cortex. These new insights justify considering the brain as a complex, self-organised system with nonlinear dynamics in which principles of distributed, parallel processing coexist with serial operations within highly interconnected networks. The observed dynamics suggest that cortical networks are capable of providing an extremely high-dimensional state space in which a large amount of evolutionary and ontogenetically acquired information can coexist and be accessible to rapid parallel search.**

## Extending classical views of information processing in the brain

The research strategy for analysing the connectivity of brains and the transformation of response properties of individual neurons along processing streams extending from sensory organs to executive structures has been extremely successful and has provided support for the notion of serial processing across hierarchically organised cortical areas [1]. However, advances in the analysis of the cortical connectome, the introduction of multisite recording techniques, and the development of imaging methods assessing whole-brain activity have generated data that necessitate extension of classical views, raise novel questions, and are likely to provide new solutions to old problems.

Here I review anatomical and functional data suggesting that, as the prevailing organisational principle, distributed processing in densely coupled, recurrent networks with nonlinear dynamics is capable of supporting high-dimensional states. I argue that this organisation requires precise temporal coordination of distributed processes and that special mechanisms are implemented to dynamically bind local processes into coherent global states. The putative computational power of such dynamical systems is illustrated by referring to the concept of 'reservoir computing'. Finally, I review data from studies on developmental plasticity, resting state activity, stimulus–response functions, and attention and examine their compatibility with concepts that emphasise the high-dimensional state space provided by complex systems with nonlinear dynamics as the basis for neuronal computations in highly evolved brains.

## Evidence requiring extension of concepts

### *Anatomical evidence*

(i) Within processing streams, including thalamic relays, feedback projections are in general more numerous than feedforward projections, emphasising the importance of top-down control.

(ii) Intracortical tangential connections cross the boundaries between areas [2]. Thus, at least the supragranular and to some extent the infragranular layers of the cerebral cortex appear as continuously coupled sheets, the different cortical areas being distinguished mainly by their input and output connections.

(iii) From primary sensory areas onwards, processing streams diverge into numerous parallel pathways whose nodes are linked by massive reciprocal connections both within and across modalities [3,4].

(iv) The rule that feedforward connections originate in supragranular and feedback projections in infragranular layers does not hold for nearby cortical areas [3,4]. Together with electrophysiological evidence [5], this questions the strict distinction between feedforward driving and feedback modulatory connections.

(v) Finally, statistical analysis of interareal connectivity suggests an organisation resembling small-world, rich-club networks (see [6]) that minimises path length between nodes (areas) [7,8]. However, analysis of projections with cellular resolution suggests as one reason for short path length the surprisingly high degree of connectedness among cortical areas. Statistical analysis suggests that more than 60% of possible links are realised [3].

### *Functional evidence*

(i) Even in early sensory areas, neurons lose their simple feature-specific responses when challenged with complex stimuli [9,10]. Moreover, responses are influenced by stimuli in other modalities, by attention, reward expectation, and contents in working memory, sug-

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*Corresponding author:* Singer, W. (wolf.singer@brain.mpg.de).

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## Glossary

**Assembly:** introduced by Donald Hebb in the context of his seminal proposal that neuronal representations of composite cognitive objects should comprise coherent assemblies (ensembles) of neurons whereby the responses of the individual neurons represent only subcomponents (one of many features) of the object. By introducing this notion of a combinatorial code, Hebb intended to overcome the 'combinatorial explosion' that would be the consequence of representing complex contents by individual, highly specific neurons because individual neurons can participate at different times in different assemblies representing different objects that have certain features in common. An important property of assemblies is their cohesion, because they need to remain identifiable as a coherent whole within the network of distributed neurones. Hebb's initial concept was that assemblies are distinguished by the simultaneity of their responses and that cohesion is assured by selective strengthening of connections between simultaneously active neurons via Hebbian synapses that increase their gain when pre- and postsynaptic responses are positively correlated in time. Thus, assemblies require reciprocal interactions between the constituting neurons to stabilise and to remain coherent. This feature distinguishes them from other distributed codes such as population codes that can be realised in purely feedforward architectures. Here the principle is to encode information about a stimulus or a motion trajectory in the joint but graded responses of a population of neurons with overlapping receptive or motion fields. This joint activity is termed a population vector.

**Hopfield net:** a one-layered artificial neuronal network in which all neurons (usually of the McCulloch–Pitts type) are reciprocally coupled with one another but not with themselves through connections with symmetrical weight distribution. The synaptic weights of the coupling connections are modified as a function of activity according to the standard Hebb rule und updated in an unsupervised way either simultaneously or sequentially. For a particular activation pattern (conveyed by inputs to the units), the network reaches a stable state after numerous repeated adjustments of the synaptic weights. Depending on the number of units and the statistical similarity of patterns, the network can, after such learning trials, store a certain number of patterns and complete (recognise) them even if fed only with partial or noised patterns. Thus, the nets have autoassociative properties and resemble in this aspect certain layered structures in nervous systems (olfactory bulb, area CA1 of hippocampus, layers of neocortex).

**Laminar organisation:** aggregations of neurons take the form of either densely packed clusters, in which case they are referred to as ganglia or nuclei, or sheets that usually assemble into multilayered structures (neocortex, hippocampus, olfactory bulb, tectum, retina). In multilayered structures, cells within the same layers tend to share functional properties and to have similar input–output connectivity. In general, cells are coupled more tightly within than across layers. Structures with laminar organisation are well suited to form maps for the representation of concrete (e.g., space, sensory features) or abstract (e.g., categories) contents.

**Oscillations:** processes that repeat periodically or aperiodically, ranging from perfectly regular (e.g., sinusoidal) oscillations to highly irregular, chaotic oscillations. Neuronal oscillations tend to lie between these extremes and typically comprise discharge sequences characterised by rather regular alternations between epochs of enhanced and reduced firing probability that lead to autocorrelograms with satellite peaks. These oscillations tend to occur in characteristic frequency bands that cover a wide range (from $<$1 Hz to $>$200 Hz: delta $<$2 Hz; theta 4–7 Hz; alpha 8–12 Hz; beta 15–30 Hz; low gamma 30–60 Hz; high gamma 60 to $\sim$90 Hz; ripples $\sim$200 Hz). The frequency, power, duration, and regularity of these oscillations strongly depend on brain states (arousal, attention, sleep, expectancy) and stimulation conditions and can vary from long stretches of frequency-stable oscillations to highly non-stationary, brief bouts of a few cycles. In most (analysable) conditions oscillations are a population phenomenon because adjacent coupled neurons tend to oscillate in synchrony. In this case the currents produced by synchronous inward and outward membrane currents summate sufficiently to be detectable as oscillatory fluctuations of so called local field potentials (LFPs). If these summate sufficiently (i.e., if the groups of synchronised neurons are large enough and synchronisation is sufficiently precise), oscillating currents can be detected with remote sensors (epicortical electrodes, EEG, or MEG). In individual neurons the autostructure of the discharge sequences often does not exhibit oscillatory signatures even if the cells participate in an oscillatory population, because cells tend to not discharge at every cycle (cycle skipping). In this case participation in an oscillatory process can be disclosed only by correlating the cell's discharges with the LFP and calculating spike field coherence.

**Synchronisation:** to determine whether the discharges of neurons are synchronised, one computes cross-correlograms between the activities of simultaneously recorded neurons. If these correlograms show a significant peak, the responses are synchronised and the temporal offset of the peak from the midpoint of the correlogram indicates the time lag between the correlated discharges. If the cross-correlogram shows additional satellite peaks, this indicates synchronisation of oscillatory spike trains, and the offset of the centre peak from the midpoint reflects the phase offset of the respective oscillations. Synchronisation can have several reasons and it is critical for functional interpretations to distinguish between them. (i) Discharges of different neurons can be synchronous because the respective neurons receive common input from bifurcating fibres or because one neuron drives the other. This type of synchrony is little influenced by states or stimuli and can be used for the analysis of anatomical connectivity. (ii) The timing of discharges of distributed neurons can become coordinated by temporally structured stimuli. In this case the correlations are manifest not only among the simultaneously recorded responses but also among responses evoked by successive stimuli because the timing of spikes is locked to the stimulus. One refers to this synchrony as evoked synchrony. The synchronous currents associated with this type of evoked synchronisation are the substrate of evoked potentials. (iii) Discharges become synchronised because neurons are embedded in a reciprocally coupled network and when activated entrain one another into synchronous firing. In this case the synchrony is called induced. This type of synchrony depends on cooperative network dynamics and hence is self-organising. It is greatly facilitated if the embedding networks oscillate and, like the oscillations, depends strongly on central states. It is this type of synchrony that is thought to assure the cohesion of Hebbian assemblies and dynamically formed functional networks. Oscillations concentrate discharges to a narrow window of the oscillation cycle and this temporal parsing of discharge sequences has many putative functions in neuronal processing.

gesting contextual modulation not only by intrinsic connections but also top-down projections [11–15].

(ii) The notion of strictly serial processing from input layer 4 via layers 3 and 2 to the output layers 5 and 6 needs to be revised because of the evidence that vigorous infragranular responses can be elicited by direct thalamic input in the absence of supragranular activity [16]. The possibility that supra- and infragranular compartments can operate in parallel is further supported by the evidence that the two subdivisions engage in oscillatory activity (see Glossary) in different frequency bands (gamma in supragranular and alpha or beta in infragranular layers [17,18]).

(iii) Multisite recordings indicate that 'spontaneous' fluctuations in the responsiveness of individual neurons are often the reflection of coordinated, highly structured spatiotemporal activity patterns rather than the result of noise [19,20].

(iv) Widely distributed cortical areas exhibit coherent fluctuations of their spontaneous activity, forming functionally coupled networks that change in their composition in a state-dependent way [21–24]. Thus, cortex and, in a wider sense, the brain appears as a highly active, pattern-generating system rather than just a stimulus-driven device.

(v) Analysis of whole-brain activity with functional MRI (fMRI), electroencephalography (EEG), and magnetoencephalography (MEG) measurements indicates that virtually all cognitive and executive functions are associated with activation of networks of often widely distributed cortical areas [25–29]. This suggests distributed networks as the substrate of functions rather than individual specialised structures.

(vi) Finally, analysis of the brain's dynamic signatures indicates that neuronal populations can engage in oscillatory activity in characteristic frequency bands and synchronise their discharges, whereby the respective frequency bands and the composition of coherently active cell groups depends on central states, attention, cognitive tasks, and goals of action [30].

## Dynamic coordination of distributed activity

The dense connectome allows for virtually unconstrained interactions among any pair of neurons in the cortical mantel, either through direct connections or via a few switching nodes. This necessitates dynamic coordination of interactions at all scales, global to configure functional networks on the fixed backbone of anatomical connections and local to flexibly associate object attributes in distributed representations (assemblies in the Hebbian sense). In both cases mechanisms are required to dynamically gate signal flow between selected nodes [31]. The concept of assembly (distributed) coding posits that the attributes of a composite object and the relations among them are encoded by the distributed responses of cells tuned to the respective attributes and temporarily associated into a coherent representation [32]. Hence, neurons constituting the assembly need to interact selectively with one another to assure cohesion of the assembly and identify themselves as members of that assembly. Thus, both the configuration of functional networks and the formation of assemblies have in common that relations between neuronal responses have to be established fully reversibly and on the fly, requiring gating of coupling on a very fast timescale. Task switching, shifts of attention, and changes of stimulus configurations (e.g., by saccadic eye movements) occur at intervals of a few hundred milliseconds, implying that the configuration of functional networks and assemblies has to be accomplished at a similar pace.

An obvious mechanism capable of opening and closing transmission links at fast timescales is inhibition. Dendrites cannot effectively summate incoming excitatory postsynaptic potentials (EPSPs) when they are shunted by inhibition and cells cannot transmit signals when soma and axon hillock are inhibited. However, to exploit inhibition for the selective routing of signals and the dynamic configuration of functional networks, it is required that the windows of opportunity for communication be temporally coordinated between sender and receiver, so that the partners that are to be functionally coupled discharge at times at which the respective other is susceptible. As proposed by Fries [33] and supported by multisite recordings in the visual system [34,35] and hippocampus [36], such coordination can be realised by synchronising oscillating cell clusters at the appropriate phase because cells embedded in oscillating circuits are exposed to precisely timed, periodically repeating volleys of inhibition [37,38]. As revealed by numerous *in vitro* [39–41] and *in vivo* studies [42–44] the networks of reciprocally coupled inhibitory interneurons and here especially the fast-spiking, parvalbumincontaining basket cells play a crucial role as pacemakers for oscillatory activity and its synchronisation. This principle also holds for the hippocampus, which shares numerous features with the neocortex and whose dynamics have been thoroughly investigated (for reviews, see [30,45]).

One of the first demonstrations of a task-dependent association of cortical areas into a functional network by synchronisation was obtained in cats trained to respond to the change of a visual stimulus. Following an auditory stimulus announcing a new trial, cortical areas required for the task (visual, parietal, somatosensory, and motor) engaged in precisely synchronised beta oscillations before the appearance of the visual stimulus, probably in anticipation of the need to ensure effective communication among processing stages [46]. Since then, numerous studies have used measures of temporal coherence for the identification of functional networks and provided ample evidence for the notion that cortical areas become dynamically bound into functional networks by synchronisation in a task- and state-dependent way [21,25,34,47–51].

Increases in coherence (synchrony) among distributed responses have also been observed in conditions likely to be associated with the formation of Hebbian assemblies [49,52–54]. Here synchronisation of oscillatory responses has several functionally relevant consequences. (i) It selectively enhances the interactions between the assembly members (see above and [35]), thereby increasing the cohesion of the assembly. (ii) It focuses spikes to a narrow window of the oscillation cycle and this enhanced synchronicity of firing facilitates propagation of signals from assembly members, increasing the likelihood of their further joint processing. The reason is that synchronised EPSPs summate more effectively in target neurons than temporally dispersed inputs [55,56]. (iii) It facilitates selective readout of responses originating from the same assembly and segregation from responses of other assemblies because synchronised responses arrive within the same window of opportunity in downstream structures. If these also oscillate, selection can be achieved by phase adjustment. (iv) It favours selective consolidation of connections among the assembly members and thereby their long-term cohesion, because use-dependent synaptic modifications follow a correlation rule [57–59].

In conclusion, there is evidence that selective gating of signal transmission, configuration of functional networks, and the binding of the different attributes of composite objects in distributed representations (temporary as well as lasting formation of assemblies) is achieved through temporal coordination of activity that often involves synchronisation of oscillatory activity. Interestingly, inhibitory processes play a major role in this dynamic coordination, both in the generation of oscillations and in the vetoing of transmission, suggesting that the function of inhibitory interneurons extends well beyond gain control, shaping of receptive fields, and improvement of signal-to-noise ratios. This notion agrees well with the increasing evidence that interneurons constitute an extremely heterogeneous population and form highly specific networks [45,60].

When discussing mechanisms of network and assembly formation, it is worth emphasising that all of the functions attributed to dynamic coordination are also attributed to attentional mechanisms [61]. Because attention and expectancy have been shown to enhance synchronised oscillatory activity in the gamma and beta frequency band [34,49,50,62,63], it is likely that temporal coordination of discharge sequences is used as a mechanism to implement attentional control.

The importance of temporal coordination for brain functions is further underlined by the increasing evidence that disturbances of cognitive functions are associated with abnormal dynamics. Diseases such as schizophrenia and autism go along with deficits in functions requiring flexible association of distributed processes such as feature binding, attention, polymodal integration, task switching, and working memory. In patients suffering from these diseases, task-related gamma oscillations are reduced, phase locking of beta oscillations between cortical areas is impaired, and the patterns of resting-state dynamics are altered (for reviews, see [64,65]).

## The nature and role of resting-state activity

The evidence that the resting-state activity of the brain is highly structured raises the question of whether this activity contains information and, if so, what this information represents and how it is encoded. The dynamics of resting-state activity must somehow reflect the functional architecture of cortical networks. Because this architecture is determined by genetic factors and modified by experience, spontaneous activity patterns should contain information about evolutionary and epigenetically acquired knowledge about the world and serve as a covert internal model for perception and action (see [66] for a review on predictive coding). This then raises the question of how the immense amount of knowledge accumulated throughout evolution and by experience throughout life can be mapped into the networks and – even more challenging – how it can be read out on the fly within a couple of hundred milliseconds. This question is closely related to the conundrum that memories are retrievable irrespective of their storage date within comparably short search times. It seems as if all of these memories (inborn and acquired knowledge about the world) are coexisting in the functional architecture of networks and equidistant for the search mechanism. A space in which such coexistence is possible must have an exceedingly high dimensionality and allow for very rapid readout (i.e., convergence towards the state representing the result of the search process) (see Box 1 for putative computational solutions and [67] for a concrete implementation).

Analysis of cortical dynamics indicates that resting-state activity exhibits characteristic correlations at widely differing timescales and reflects the coupling among neurons [22] (for a review, see [68]). Ultra-slow covariations of activity in the range of seconds have been found for areas belonging to the so-called default network [23] and diffusion tensor imaging (DTI) studies confirm strong anatomical connections between the respective areas [7,8]. In the visual cortex, Grinvald and colleagues [19] have shown with optical recording correlated activity fluctuations in the system of orientation columns and Fries *et al.* [20] found with field-potential and single-cell recordings that cells in orientation columns with the same orientation preference oscillate in synchrony in the gamma frequency range. These correlation patterns agree well with the functional architecture; in this case, the selectivity of tangential intracortical connections that preferentially link columns with similar response properties [69–71]. The study of Fries *et al.* [20] further revealed that the resting-state oscillations are responsible for the substantial intertrial variability of cortical response latencies. Neurons respond early (late) when retinal signals arrive during the peak (trough) of the oscillations. Because columns sharing the same orientation preference oscillate in synchrony before stimulation, cells sharing the same orientation preference discharge at the same time (i.e., in synchrony if activated by contours of the same orientation). This and the evidence that cells sharing the same orientation preference also synchronise their tonic responses when activated with coherent stimuli [52,72] led to the

### Box 1. Computational strategies to create high-dimensional coding space

Artificial networks of the Hopfield type are capable of simultaneously representing different relational constructs (objects defined by relations) due to reciprocal coupling and make them accessible to parallel search. However, such systems with symmetric connections cannot cope easily with the representation of large numbers of superimposed relational constructs, particularly if temporal relations also need to be stored. One reason is their restricted temporal dynamics, which limits the dimensionality of states [111,112]. Another class of models capable of dealing with relational constructs and providing high-dimensional spaces for coding is derived from concepts of reservoir computing, also termed echo-state or liquid computing. These networks comprise self-active, nonlinear units with random recurrent coupling that maintain their own dynamics and are engaged in active processing [113–117] (Figure I).

In this computational framework, the reservoir comprises a network of self-active, randomly coupled neurons (nodes). If a specific input constellation is driving a subset of these nodes, a complex, transient, high-dimensional and stimulus-specific activity pattern emerges in this recurrently coupled network, the liquid, and is then further propagated by waves of recurrent interactions among neurons. Such reverberation provides the liquid with a fading memory of recent inputs that allows it to integrate input sequences (e.g., several frames of visual input) while keeping track of sequence order. The readout of the relational code is achieved with a linear or nonlinear classifier (e.g., support-vector machines with linear or nonlinear kernels). This readout function can again be implemented by neuron-like elements that sample activity from the nodes in the liquid and adjust the coupling strength of the sampling lines through supervised learning until they become optimally activated by a particular state of the liquid [118]. In these simple cases, the readout cells act like 'grandmother cells' [119]. However, the readout stage could also comprise cell assemblies that are in turn ignited by specific states of the liquid after appropriate adjustment of the synaptic weights of the connections between the liquid and the readout stage. This strategy increases the robustness of decoding and at the same time generates low-dimensional readout patterns that can directly be used to control effectors (e.g., orchestrate the population vector for a composite movement). The principle of this computing strategy is simple and powerful: a low-dimensional input configuration is transformed into a high-dimensional dynamic representation. In this high-dimensional state space, stimulus-evoked vectors remain compact, cluster in well-segregated subspaces, and can be more easily discriminated based on their spatiotemporal signatures. The segregation of clusters can be improved further if the network is endowed with Hebbian synapses and given the opportunity to 'learn' in an unsupervised fashion about the features of the stimulus sample by repeated presentation of the stimuli [120]. As a matter of principle, the performance of the liquid increases with the dimensionality of the space it is able to explore. Thus, if the nodes are configured as oscillators (e.g., relaxation oscillators or damped harmonic oscillators), phase also comes into play, which allows further expansion of the dimensionality of the liquid (see also [88]). However, at the same time the amount of training data has to be increased to fill the high-dimensional space. Because of their high dimensionality, such liquids are in principle capable of storing and superimposing very large numbers of 'memories' and learnt associations that can be accessed and readout nearly instantaneously. The astounding ability of our brains to solve with such ease problems that are still computationally intractable (e.g., the segmentation of complex scenes) suggests that the brain indeed capitalises on computational algorithms that permit parallel storage and fast readout of complex relational constructs.

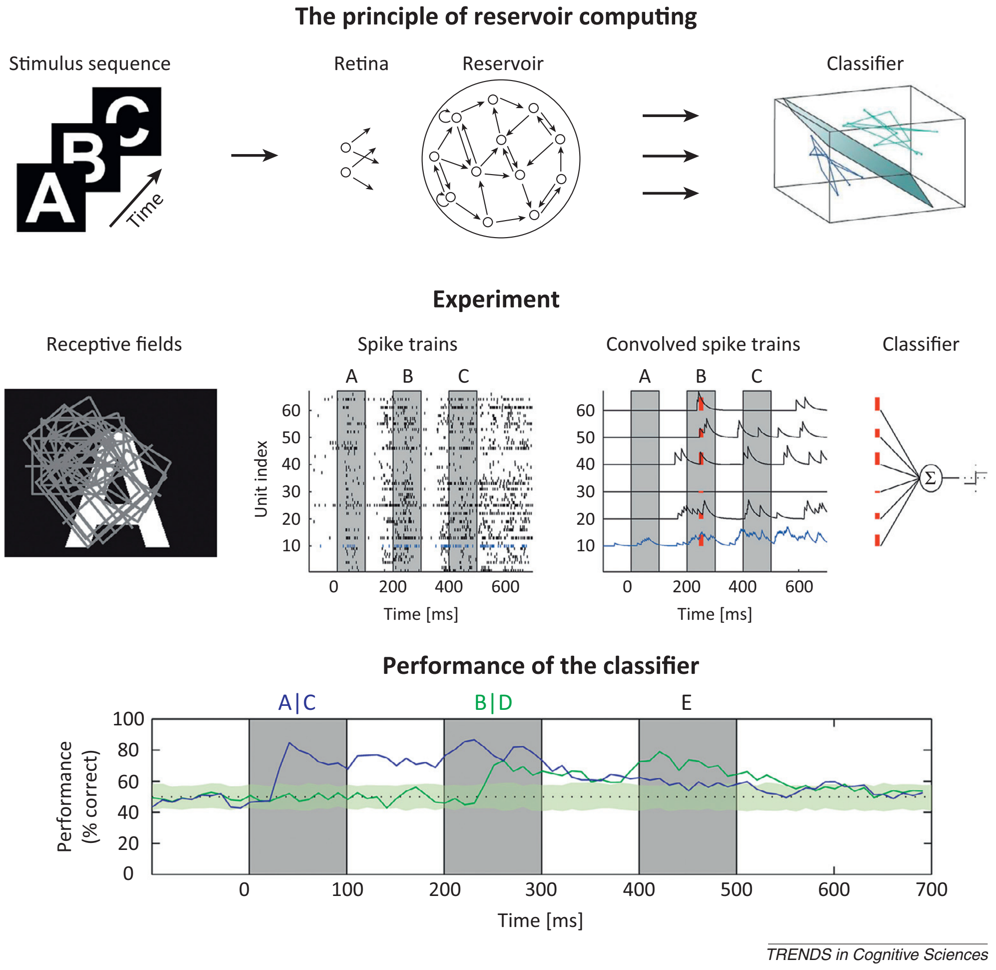

**Figure I**. Computation in recurrent networks, theory, and experiment. Upper row: A sequence of low-dimensional stimuli (A, B, C) is encoded in parallel spike trains by an artificial retina. Signals are then distributed to a subset of nodes in a recurrent network in which they are transformed into stimulus-specific, high-dimensional dynamic states. These states are then classified by a linear or nonlinear classifier. Middle row: A sequence of stimuli (A, B, C) is presented over the receptive fields of many simultaneously recorded neurons, randomly sampled from cat primary visual cortex. The recorded spike trains, displayed as raster plots (second panel), are then convolved with a sawtooth function to generate continuous signals (third panel). Shaded columns indicate time and duration of stimulus presentation. The activity vector sampled from a short time window placed over the responses to stimulus B (red bars) is used to train a linear classifier by adjusting the weights of inputs from individual neurons to recognise the signatures of the stimuli. Bottom panel: Experimental results. A sequence of three stimuli was presented. The first was either A or C, the second either B or D, and the third always E. Data were split into a training set and a test set and the classifier was trained at the different time bins (5 ms duration) to identify stimuli A–D. The black and green curves show classification performance (% correct on ordinate) in the test set for the distinction between A/C (black) and B/D (green), respectively. Identification of the first stimulus is significantly above chance (green-shaded region) as soon as responses to the first stimulus appear, remains high (~80% correct) during the responses to the second stimulus, and slowly drops to chance level during the responses to the third stimulus. Identification of the second stimulus rises above chance (~70% correct) during the responses to the second stimulus, drops slowly to nearly chance level before the third stimulus, and rises again during the responses to the third stimulus. Thus, the responses to the second stimulus contain information about the identity of both the first and the second stimulus and the increase of discharge rate caused by the third stimulus facilitates retrieval of information about the second stimulus. Jittering of the spike sequences revealed that the classifier evaluated both the actual discharge rates and the precise timing of individual spikes (data not shown). If only a single stimulus is shown, information about stimulus identity can persist for up to 1 s (fading memory). For more details see [118]. By courtesy of D. Nikolic and A. Lazar.

suggestion that the rules for perceptual grouping, in this case the gestalt criteria of continuity and colinearity, reside in the architecture of corticocortical connections and are translated into synchronisation probabilities [11,20,53]. These data indicate that the most prevalent features of the cortical architecture are already detectable in resting-state activity [73]. Ample evidence for the strong impact of ongoing synchronised oscillations on sensory responses is also available from studies in the primate auditory cortex [74,75].

Developmental studies indicate that the statistics of feature conjunctions in the outer world are translated into the strength of coupling between cells tuned to the respective features. Early evidence for such internalisation of contingencies has been obtained in kittens that had exclusive experience with vertically oriented, unidirectionally moving gratings that had a constant stripe separation of 10° visual angle [76]. As expected, this selective rearing biased the numerical distribution of orientation- and direction-selective neurons towards the experienced stimulus (see also [77]). However, most importantly, a substantial fraction (~30%) of the neurons in supragranular layers of area 17 developed multiple, well-segregated receptive fields whose spacing frequently corresponded to the spacing of the experienced stripes (Figure 1). Because intercolumnar connections are shaped by experience according to a Hebbian mechanism [70], the ectopic receptive fields are most likely due to selective strengthening of

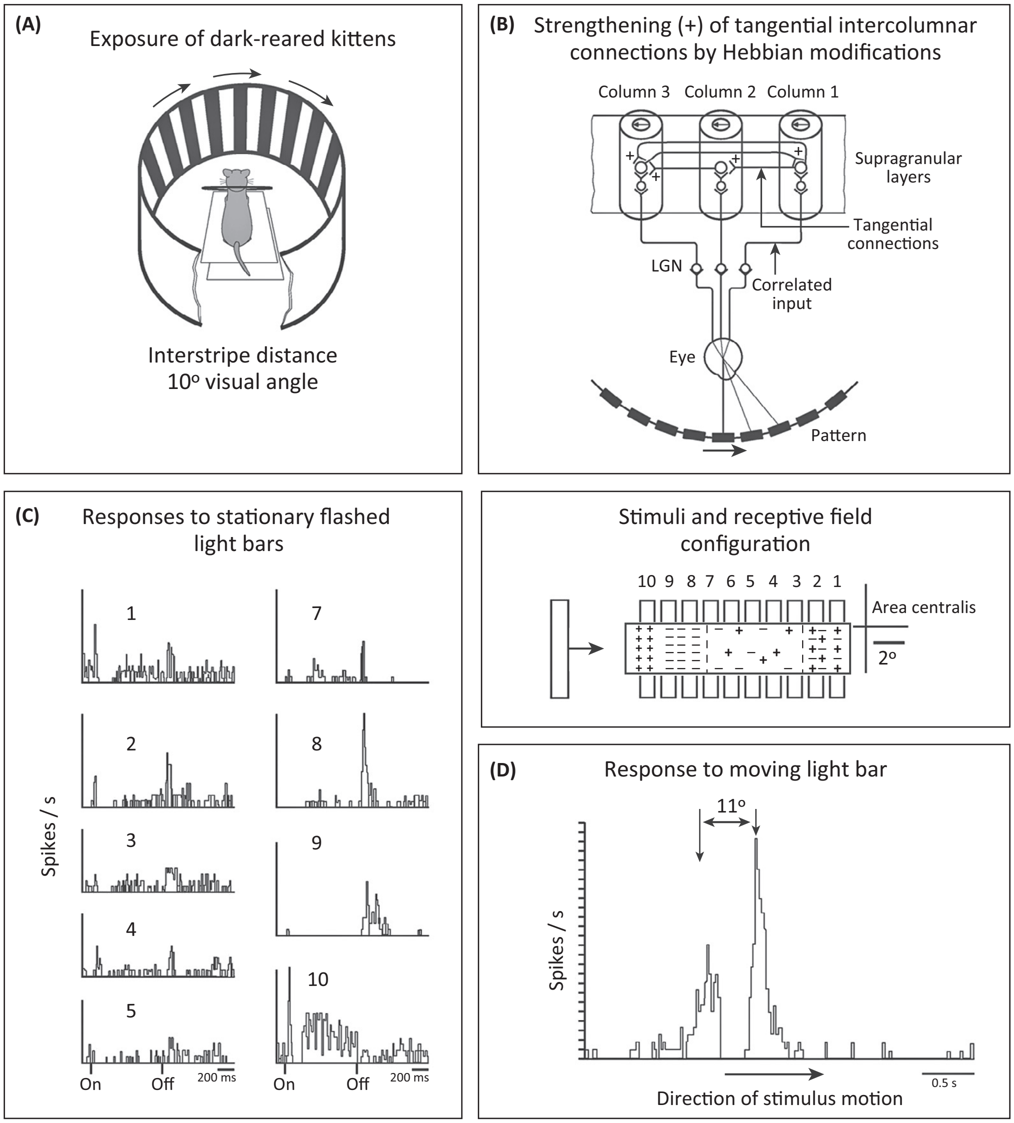

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**Figure 1**. Imprinting environmental statistics in cortical architecture. (**A**) Selective exposure of dark-reared kittens to unidirectionally moving vertical gratings of constant spatial frequency (10° interstripe distance). (**B**) Simplified sketch of tangential intracortical connections linking columns whose response properties match the stimulus and whose spacing in the retinotopic map corresponds to the spatial frequency of the grating. It is hypothesised that tangential connections linking neurons that are activated synchronously by the grating patterns increase their gain (see **+** at respective synapses). (**C**) Peristimulus time histograms (PSTHs) of responses of a neuron in supragranular layers to stationary flashed light bars at positions in the visual field indicated in the graph to the right. The neuron has two well-segregated receptive fields; one is ectopic (positions 7–10), the other is located at the position corresponding to the retinotopic location of the recording site close to the area centralis (positions 1–4). (**D**) Response of the same neuron to a vertically oriented light bar moving from the periphery towards the area centralis as indicated in the graph above. Note the clear separation of the two response regions, the more vigorous response being elicited from the medial (the normal) receptive field, which has complex response properties. Modified from [76].

intrinsic cortical connections linking those columns that were activated synchronously by the grating. Whether these modifications of functional architecture had also affected resting-state correlation patterns has not been explored, but there is recent evidence that learning can indeed modify the covariance structure of spontaneous activity [78,79].

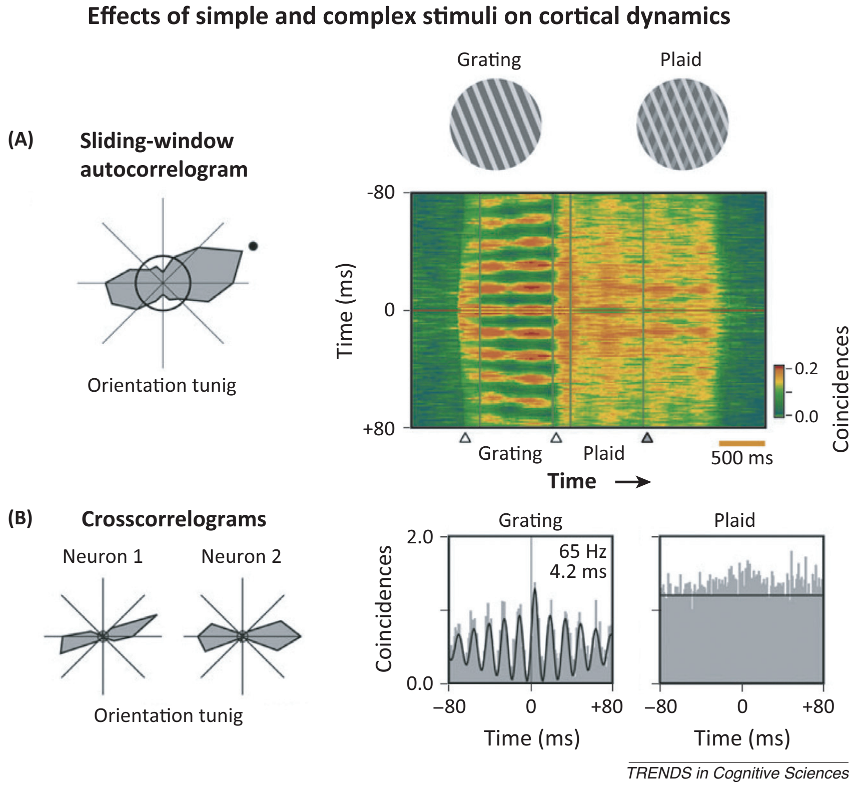
In conclusion, the weight distributions of the connections among cortical neurons are likely to reflect not only evolutionary adaptation to regularities but also the immensely complex statistics of the feature relations experienced throughout life [73]. Somehow, these countless, content-specific weight distributions must coexist in a very high-dimensional space to remain flexibly addressable as contextual priors [80,81]. As discussed in the following section, certain properties of resting-state activity suggest that the dynamics emerging from cortical networks are indeed high dimensional, allowing for the coexistence of a large number of potentially realisable states [82].

## The fingerprints of network dynamics

The dynamics of complex systems can vary between two extremes. All elements of the system could be active independently and exhibit stochastic activity (high dimensionality) or all elements could be synchronised (low dimensionality). Both extreme states have low computational potential. However, under normal conditions the cerebral cortex operates in an intermediate regime where the emergent dynamics are complex and computational power is high (see below). Interestingly, this is also true for the architecture of the connectome. The connectivity graph constitutes a compromise between randomness and regularity where complexity and dimensionality are high [83,84].

Analysis of the resting-state dynamics of cortical networks suggests that they operate close to a self-organised critical (SOC) state [68,85–88]. The SOC state provides favourable conditions for computations: its memory capacity is maximal [89]; the information transfer is most reliable [90,91]; it can optimally separate between different inputs [89]; and it shows the largest dynamical range [90,92]. This intermediate regime and the associated spatiotemporally scale-free avalanche dynamics is maintained in states characterised by a broad-frequency spectrum of oscillatory activity that leads to the typical 1/*f* distribution of spectral power (i.e., the power of the respective oscillations is inversely related to their frequency). However, the system can also operate in SOC states when oscillating in narrower frequency bands [93,94].

Sensory stimulation or top-down mechanisms related to attention, expectancy, or action preparation tend to cause a widespread reduction in the variability of the dynamic state. Often this reduction is associated with an increase of oscillations, synchrony, and coherence in distinct frequency bands that leads to deviations from the 1/*f* power distribution (see above and [62,95]). This change in the dynamics is equivalent to the reduction of the dimensionality of the dynamic state and a signature of an increasingly constrained dynamical space in which the maximally informative assemblies come to dominate the dynamics. It appears as if there is a relation between the complexity of stimuli and the degree of dimensionality reduction, the latter being more pronounced for simple than for complex stimuli. In the case of vision, simple, low-dimensional stimuli such as single moving contours or gratings induce sustained narrow-band oscillations that can synchronise over large distances [52]. One likely reason is that such simple stimuli represent feature constellations that are particularly frequent in real-world objects such as colinearity, continuity, and coherent motion and therefore match well with the prevalent architecture of intracortical connections whose layout does reflect the statistics of contingencies in the outer world (see above and [70]). By contrast, complex stimuli such as natural scenes induce much more complex and time-varying patterns that are difficult to analyse with conventional methods of time-series analysis based on stationarity assumptions [96–98] (for an extreme example, see Figure 2). However, this



Effects of simple and complex stimuli on cortical dynamics

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**Figure 2**. Relationship between stimulus complexity and dynamic states. (**A**) Sliding-window analysis of the autocorrelation of responses of a neuron (receptive field shown in the insert to the left) recorded in the primary visual cortex of an awake, fixating monkey to sequentially presented drifting-grating stimuli of different complexity. The first stimulus (insert above) comprises a simple grating that drifts in the direction preferred by the neuron orthogonal to its orientation. This stimulus evokes responses with sustained oscillatory modulation in the gamma frequency range (onset indicated by first arrow on the x-axis of the time–frequency plot). The second stimulus (insert above) comprises two superimposed gratings (a plaid) with different orientations, each drifting in the direction orthogonal to its orientation (one of the two gratings is identical with stimulus 1). This second stimulus evokes responses with a much more complex autostructure (onset and offset marked by arrows 2 and 3 on the abscissa). The ordinate represents the shift intervals for the computation of the autocorrelograms (altogether ±80 ms). (**B**) Cross-correlations between responses of two neurons (receptive fields in inserts on the left) recorded simultaneously from primary visual cortex and stimulated with a simple drifting grating similar to the first stimulus in (A) (left correlogram) and with a plaid similar to the second stimulus in (A) (right correlogram). The simple grating evokes sustained oscillatory responses in the gamma frequency range (65 Hz) that are precisely synchronised with a phase offset of 4.2 ms, as indicated by the periodically modulated cross-correlogram (left). With the complex stimulus, this correlation breaks down, as shown by the flat cross-correlogram (right). Modified from [96].

does not imply that the more complex dynamics no longer contain information about the stimulus. Moreover, there is experimental evidence from monkeys freely exploring natural scenes that gamma oscillations are still robustly elicited when the animals direct their gaze to individual objects in a cluttered scene [99]. The analogy with a 'liquid' is obvious. A single stone thrown in a pond will produce propagating coherent waves the frequency of which is determined by the properties of the liquid (in the case of networks, e.g., the time constants of interacting elements) whereas a sequence of temporally and spatially distributed impacts, even if well structured, will evoke a much more complex interference pattern. However, in both cases the emerging patterns contain comprehensive information about the stimuli. The response properties of individual neurons undergo similar changes. When exposed to simple stimuli, neurons exhibit well-defined receptive fields (RFs), as described by Hubel and Wiesel [100] half a century ago. However, when presented with complex stimuli, it often becomes impossible to retrieve the original RF structure [9]. The reasons are intracortical interactions that render local responses dependent on global context.

## Epiphenomenal or computationally relevant signatures

The observations on dimensionality reduction bear on the question of whether system properties disclosed with simple stimuli are computationally relevant or only epiphenomena. The canonical RFs resulting from selective recombination of input connections and oscillations are an emergent property of recurrent networks. The functional roles of input recombination and recurrency are undisputed but oscillations are often considered maladaptive epiphenomena because they create instabilities and, by favouring synchrony, may reduce coding capacity. However, in dynamic systems oscillating nodes may be advantageous. In addition to increasing the dimensionality of state space (Box 1), they are essential for the implementation of 'central pattern generators' [101–105], extend coding space by introducing phase as a variable [106,107], and permit exploitation of resonance for matching operations [108,109]. These could be the reasons why nature has endowed most of the neurons in the simple nervous systems of invertebrates with pacemaker currents that make these neurons function as autonomous oscillators. When coupled, these oscillating neurons generate complex, well-coordinated, and metastable spatiotemporal activity patterns. Because of their nonlinear dynamics, such systems can undergo rapid state transitions (bifurcations) and generate different stable patterns on the backbone of fixed anatomical connections depending on changing cognitive or executive demands [102,105] (for a review of pattern generation in cortex, see [110]).

## Concluding remarks

The novel data on the structural and functional organisation of the cerebral cortex support concepts that emphasise distributed coding and information processing in self-organised complex systems with nonlinear dynamics. As outlined above, there is now sufficient empirical evidence to warrant targeted experimental testing of a set of hypotheses derived from these concepts (Box 2).

To test the hypotheses listed in Box 2 will require in-depth analysis of dynamic states across scales and the establishment of close – and ideally causal – relations between dynamic signatures and cognitive as well as executive functions. This calls for massive parallel recordings

### Box 2. Hypotheses suggested by novel findings on cortical organisation and dynamics

(i) Cortical networks potentially provide an extremely high-dimensional space for coding due to the complex dynamics emerging from the recurrent coupling of nodes.

(ii) The propensity of nodes to oscillate and to engage in synchrony has numerous computational advantages. It increases the dimensionality of states, introduces phase for coding, can be used to selectively gate communication among nodes, facilitates through phase locking the formation, identification, and stabilisation of functional networks and assemblies, endows the networks with hysteresis and the capacity to resonate, facilitates long-term stabilisation of assemblies by Hebbian plasticity, and last but not least provides the option for cross-frequency coupling to encode nested relations in the concatenation of rhythms.

(iii) An internal model of the world stored in the networks by both genetic specification and experience is implemented in the architecture and weights of corticocortical connections and generates an immense repertoire of coexisting potential states.

(iv) The complex spatiotemporal dynamics of resting-state activity reflects to some extent the superposition of the prior expectations generated by this internal model.

(v) Low-dimensional input signals are transformed into high-dimensional internal states due to their interaction with the network's dynamics.

(vi) Input signals cause selective stabilisation of substates that are often distinguished by enhanced coherence and reduced dimensionality, suggesting that an initially unconstrained dynamic state of coexisting solutions (the internal model) is forced towards the most likely substate, given the structure of the internal model and the specific input constellation.

(vii) These stimulus-constrained, low dimensional substates constitute the solution to the respective computational problem.

(viii) The reduced dimensionality of these substates, in particular their increased coherence (synchrony), increases their saliency, thereby enhancing their impact on downstream processes, and promotes their long-term stabilisation by facilitating Hebbian modifications of synaptic connections.

(ix) A selection of substates is also caused by attention, expectancy, and behavioural goals because these reduce the dimensionality of resting-state activity patterns by increasing coherence in subnetworks.

(x) These modifications of dynamics are facilitated by SOC states because these facilitate the rapid emergence and dissolution of neuronal assemblies (synchronised oscillatory populations), requiring minimal 'effort' because of the intermediate level of existing correlations.

(xi) The advantages of performing computations in a high-dimensional space are: the option to superimpose many information priors simultaneously, which allows for parallel search and fast matching with input signals; and the option to generate multiple selected substates in parallel and to keep them segregated, which facilitates classification.

(xii) Numerous mental diseases are associated with characteristic alterations of brain dynamics, suggesting the possibility of using these dynamic signatures as endophenotypes for further disease classification and the exploration of pathophysiological mechanisms.

from large domains of the cortical mantle and for the development of novel mathematical tools that permit the analysis of high-dimensional, non-stationary time series and the detection of behaviourally relevant patterns (trajectories). Currently there is a rapid development of electrode technology permitting long-term recordings of large numbers of neurons in awake, behaviourally trained animals. These approaches are complemented with optical recording methods based on fluorescent calcium- or voltage-sensitive sensors that are either supplied by incubation or expressed in selected cell populations by genetic-engineering tools. These powerful techniques will soon provide the high-dimensional time series required for the analysis of trajectories. However, in parallel mathematical tools will have to be adopted that can cope with the non-stationarity and nonlinear dynamics of neuronal processes. The currently applied methods are capable only of disclosing rather stationary and regular patterns of long duration (sustained oscillations of constant frequency and low-order correlations). It is therefore likely that we presently see only selected, low-dimensional substates of the system. The methodological and intellectual challenges ahead are enormous as we seem to enter a new era in systems neuroscience.

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