

Synchronization: The Computational Currency of Cognition

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Abstract

Spatiotemporal codes, such as synchronization of neuronal activity, offer significant computational advantages over traditional rate codes, and our recent simulation studies suggest a role for synchronization in a broad range of cognitive processes, from contour detection to associative memory. We suggest that synchronization mediates Gestalt-based perceptual organization in striate cortex, and that the degree of synchronization represents the perceptual salience of an object. Spatiotemporal coding provides an efficient representation for recognition, and we propose a medial point hypercolumn representation of object shape. Finally, we consider the effects of neuromodulation on synchronization and temporal dynamics in the hippocampal memory system. Together, these processes suggest that the control and coordination of synchronization may be a basic component of many cognitive processes.

Introduction

It is a common observation that computational efficiency depends upon the coding system used to represent information--multiplication in roman numerals is difficult, auditory localization via binaural time difference is straightforward. In

considering the role of temporal coding in the nervous system, we should therefore focus on how such codes can be used to expedite neural computation. Several recent studies have argued that, in comparison to traditional rate-based codes, spike-based temporal coding—which makes use of the precise spike timing relationships among populations of neurons—offer improved signal/noise properties, vastly greater informational capacity, and faster processing speeds [1]. Simple temporal coding schemes, such as converting the intensity of a stimulus into a phase delay in firing [2] have proven efficient in demanding network applications such as continuous stream speech recognition.

We would like to consider the question of how one such spatiotemporal code—synchronization of neuronal activity—may provide a common computational framework for cognition. The range, diversity, and species-specific nature of cognitive processes suggests that the brain has evolved a “bag of tricks” [3] to carry out the processes underlying perception, attention, learning, and reasoning. The command, control, and coordination of these quasi-independent processes into a seamless, integrated system requires a common underlying representation—such a representation is provided by synchronization. Synchronized activity occurs throughout the nervous system, and across species—the interpretation of its function has been the subject of a number of experimental and theoretical studies (reviewed in [4]). Considerable work has been devoted to the possible role of synchronization as a mechanism for representing binding relations [5, 6] and as the medium of higher brain function [7]. Recent experiments [8, 9] show a direct correlation between synchronization and visual perception.

One of the frustrations of trying to model these processes is that current network systems just don’t seem to capture the essence of biological systems. No matter how complex the architecture or how detailed the cellular model, there is something organic missing. Part of what is missing is provided by closing the sensory-motor loop [10] to allow real-time interaction with the environment. Another critical element is a neural-based control structure, e.g. attention, which dynamically reallocates computational strategies and which gates learning-based changes in system properties. The core of the problem, however, is that such systems are still ultimately stimulus-driven, their responses correspond more to sensation rather than perception.

One of the defining characteristics that distinguishes perception from sensation is Gestalt-based perceptual organization. The Gestalt laws describe how stimulus features are bound and segmented into perceived objects [11]. The array in Figure 1 is perceived as alternating rows of open and closed circles, and it is difficult to perceive the array in any other possible manner, e.g., vertical columns. A system which, in response to a stimulus, exhibits this type of grouping and binding behavior must be characterized as active and intelligent—it has crossed the boundary from sensation to perception. According to Gestalt principles, binding is based on the spatiotemporal relationships between elements: proximity, similarity, common motion, colinearity and continuity (good continuation), closure, and symmetry. These basic laws predict a perception of figure versus ground that is consistent with top-down predictions based on a

generic/accidental viewpoint or Bayesian inference theory [12]. However, regardless of the level of description--Gestaltist or Bayesian--perceptual organization must ultimately arise from the properties of visual cortex.

Over the past few years, we have developed a series of models [13, 14] which suggest synchronization-based cortical mechanisms for the Gestalt laws. For example, long-range horizontal connections between oriented cells in supragranular layers [15, 16] may mediate the law of good continuation as well as the law of common motion [17]. The anatomy (together with intrinsic neuronal properties) determines which neurons will synchronize in response to a particular stimulus; the resulting pattern of synchronization represents the Gestalt-based binding. This pattern of synchronization can be modulated by top-down, attentional, or local context-dependent inputs.

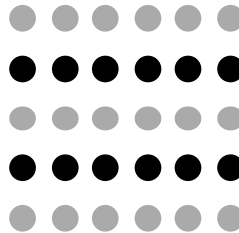


Figure 1: Perceptual organization forces stimulus to be grouped as alternating rows of light and dark dots.

One of the most influential and intriguing studies in the Gestalt tradition was carried out 25 years ago by Johansson and colleagues at Uppsala University. Johansson [18] attached small lights to a subject's joints (elbow, knee, etc.) and viewed the resulting point motions as the subject walked or ran in a dark room. Johansson found that, despite the sparse information provided, it was possible to recognize a human body walking or running, and, in fact, all observers immediately perceived the moving dots as a moving human form. The key to solving the Johansson problem lies in discovering the hidden correlations between the motions of individual lights. Spatiotemporal codes, such as synchronization provide an effective and efficient means of detecting and representing such correlations. In this case, spatiotemporal correlations in the stimulus signal the presence of object components (e.g. a limb). Recognition of a human form in motion requires detecting spatiotemporal patterns of synchronization among groups of cells. More generally, one might argue that the detection and amplification of correlation is the central principle of learning and recognition in the brain. The cortical architecture is therefore designed to translate spatiotemporal correlations in the stimulus into patterns of synchronization of cell responses. Complex synchronization patterns have been observed in olfactory recognition[19, 20] and throughout cortex [4, 21]. Related patterns are seen in central pattern generators [22, 23] responsible for production of motion.

Synchronization and the Gestalt Laws

In thinking about the Johansson problem, it is useful to first consider the simpler case of synchronization in response to static visual displays, focusing on the recent work of Ilona Kovács and her colleagues. It is well known [24] that subjects can detect a form or contour in a random array of dots, provided that the dots comprising the contour are spaced more closely together than those in the background. [This reflects the Gestalt law of grouping based on proximity]. If, instead of dots, oriented line segments or Gabor functions are used, elements arranged along a smooth contour can be detected at spacings greater than the spacings of the randomly oriented background elements [25]. [This reflects the Gestalt law of good continuation]. Most interestingly, if the line segments or gabor functions are arranged so that the elements lie along a smooth closed contour, the elements can be spaced at significantly greater distances (roughly 1.5 times background spacings) compared to elements on an open contour [26]. Closed curves are therefore more salient than open curves¹ [reflecting the Gestalt law of closure].

The most relevant studies, in this regard, have been carried out by Kovács and colleagues [24, 26, 28], who have shown that the critical parameter is the ratio of contour element to background element spacing. For example, in Figure 3, when elements on the contour are spaced more closely than the average background spacing, the circular contour pops-out immediately. However, when the contour elements are spaced at twice the average background spacing, it is nearly impossible to locate the contour. Psychophysical and physiological experiments have shown that the salience of a contour depends on the relative orientation, alignment and spacing of elements [25, 29, 30]. These parameters affect the balance of excitation/inhibition between cells responding to the contour elements, and must therefore, in our view, affect neuronal synchronization.

In line with the Johansson experiment, we propose that neurons responding to elements on a static contour synchronize, and that the amount of synchronized activity generated by a contour determines its perceptual salience. Kovács and Julesz have carried out psychophysical experiments that can be interpreted as strong evidence for the involvement of such a synchronization process. The experiment is carried out with closed and open contours in which the elements are at threshold spacing—i.e., for a given background density, the contours are detectable at a 75% performance level. Under these conditions, if elements are successively added to an open contour, the detectability of the contour increases proportionally. However, the threshold spacing for elements on a closed contour is much greater, and if one begins with an open contour with elements at this greater spacing, the contour is essentially undetectable until the final elements is added and the contour is closed, at which point it suddenly and reliably pops-out [26].

¹ Straight lines are roughly equivalent in salience to circles; thus *predictability* may be an important factor in determining salience [27].

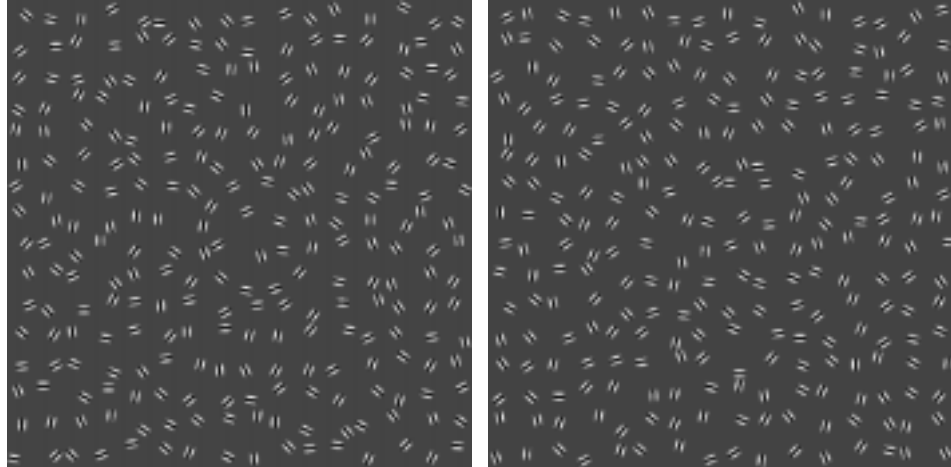


Figure 2: Detection of contours composed of individual gabor elements depends upon the relative spacing and orientation of contour elements relative to elements in the background. Figure on left has a circular contour with elements spaced more closely than background elements-it is very salient and pops out. Figure on right has circular contour spaced at twice the separation of background elements-it is difficult to detect (Based on [24]).

We interpret this experiment as reflecting the onset of synchronization. In a theoretical study of synchronization among phase-coupled oscillators, Kopell and Ermentrout [31] showed that closed chains of oscillators will reliably synchronize with nearest-neighbor coupling, whereas open chains require nearest and next-nearest neighbor coupling. If contour elements are maximally spaced so as to limit effective connections to nearest neighbors, then a closed contour will synchronize whereas an open contour will not. Until, the final element is added to a closed contour, it is, by definition, an open contour, and thus will not synchronize (unless the element spacing is reduced)—however, once the final element is added, synchronization occurs spontaneously.

As shown in figure 3, we have replicated these findings in a detailed, cellular level simulation of cortical orientation columns interconnected via anatomically correct horizontal connections. This network consists of 6 orientation columns, each containing eight 66-compartment pyramidal cells [32] and eight 51-compartmental interneurons [33]. AMPA, NMDA and $GABA_A$ synapses are compartment specific. Within a column all cells are interconnected with no axonal delay; 50% of cells are connected between columns with an average axonal delay of 5ms and a peak conductance that decreases with receptive field separation. When a contour (closed or open) is salient, the responding neurons synchronize, and the degree of synchronization changes in proportion to the psychophysical detectability.

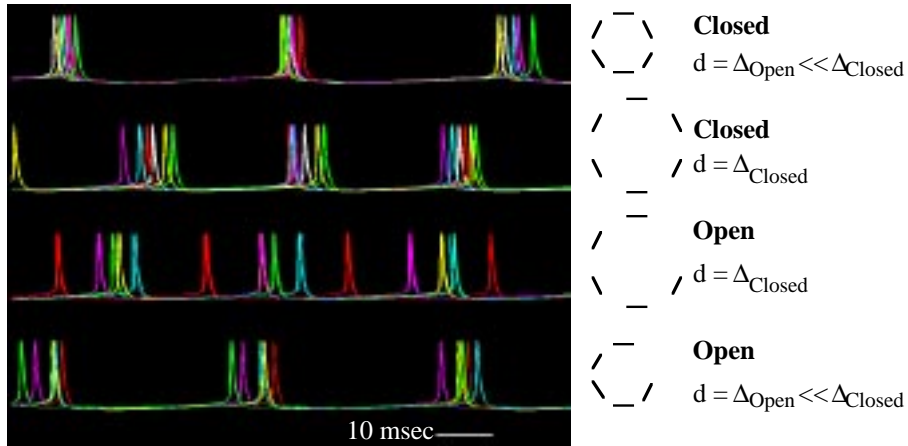


Figure 3: Spike synchronization in a detailed cellular model [34]. Degree of synchronization corresponds to salience of contour. Spikes recorded from 48 pyramidal cells in 6 orientation columns, spikes from cells within an orientation column superimpose exactly, different shaded spikes correspond to different orientation columns stimulated by the contour elements. (Top) Tight synchronization to closed contour. (2nd row) Degree of synchronization decreases as contour elements are spaced farther apart. (3rd row) Removing one element from closed contour destroys synchrony, (4th row) Halving element spacing on open contour restores synchrony.

This approach [14] is able to quantitatively account for a large body of physiological and psychophysical data on the salience of contours in reduced and complex images [24, 25, 29, 30, 35]. When confronted with an image, as shown in Figure 4, the model extracts those contours which are most salient to human observers.

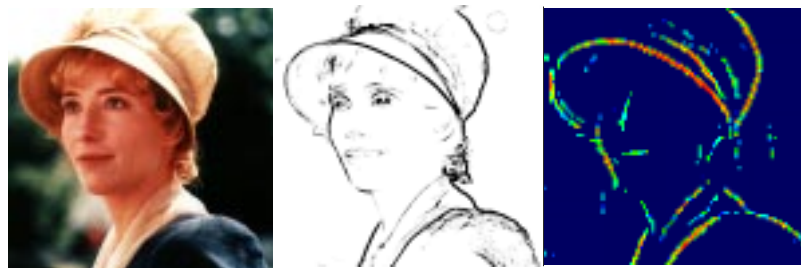


Figure 4: Perceptual salience estimated by a synchronization mechanism. Results of cortically-based network processing of real image (left). Traditional edge extraction (middle) emphasizes highest contrast edges. (Right) Synchronization mediated by long-range horizontal cortical connections [36] extracts salient contours based on Gestalt factors.

These results suggest that the properties of synchronization transcend the synchronization mechanism, and arise directly from the boundary conditions. Synchronization can thus serve as a means of detecting closure--but more generally, it may reflect a number of Gestalt-based factors and provide a measure of the overall Pragnanz of the stimulus

Synchronization provides a natural mechanism for mediating perceptual grouping. The stimulus in Figure 5 is perceived as 3 columns of vertical bars (due to the Gestalt law of proximity). We created a network with nine interconnected orientation columns, similar to the one described above. However, here axonal delays increase with receptive field separation. Axonal delays between cells in closely spaced orientation columns (i.e., those arranged vertically in the stimulus) average around 5 ms; delays between other orientation columns average 15 ms. Studies have shown that short delays allow synchronization whereas long delays introduces phase lags between cell firing [37]. Simulation results show the 9 orientation columns synchronize into 3 distinct groups, corresponding to the perceptual grouping of the stimulus. Interestingly, once one group of columns is synchronized, the desynchronizing connections actually promote synchronization in other neuronal populations. This mechanism may thus play a role in propagating transient groupings in metastable stimulus perception.

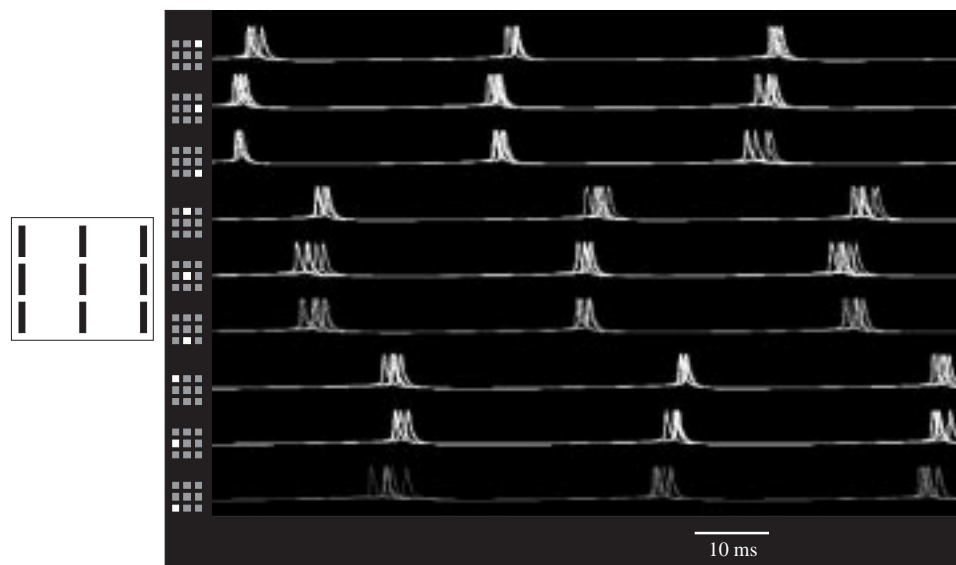


Figure 5: Gestalt-based perceptual grouping. Stimulus (shown on left) is made up of vertical bars arranged so that the dominant percept is of 3 vertical columns. Simulation results of the 72-cell network. Pattern of synchronization reflects perceptual grouping.

Synchronization-Based Recognition

Returning again to the Johansson problem, we consider the implications of a Gestalt-based front-end (e.g., striate cortex) for the process of recognition. In his original paper, Johansson posed the question of how the motions of 10 little dots could signify the motion of a dynamic human form. Part of the answer to this question can be drawn from the work of Nowlan and Sejnowski [38], who pointed out that due to the aperture problem [39], most motion information is concentrated at the discontinuities in a moving object's boundaries. A possibly related idea has been suggested recently by Kovács [40] as a result of her psychophysical studies--namely, that the visual system in its normal operation, reduces objects to a sparse and compact representation, similar to that discovered by Johansson, and consistent with the idea of a medial point representation. The medial points of an object are the maximally activated positions on the medial axis [40]. Medial axes--the set of points minimally distant from two or more edges--were proposed by Marr [39] as a useful representation for recognition, and have been extensively investigated in computer vision. The advantage of a such a skeleton-based representation is that it reduces surfaces to contours while capturing the relationship between object components--it is therefore useful for shape categorization.² Mumford and colleagues have recently reported theoretical and physiological evidence supporting the existence of medial axis representations in the visual system [41, 42]. These experiments suggest that during the first 60-100 ms of neural processing in striate cortex, cells respond directly to the stimulus, but immediately afterwards, responses are accentuated along the medial axis of the stimulus. It is presently unclear to what degree these delayed responses arise from feedback, but their time course is consistent with such a mechanism. Kovács and Julesz [28] observed a similar enhancement at medial axis locations in psychophysical studies. Using the stimulus shown in Figure 2, they found a region of increased contrast sensitivity along the rim and at the center of the circle. When gabor elements were aligned so as to form an ellipse, increased sensitivity was found at the two foci of the ellipse. More recent experiments show increased contrast gain along the medial axes of rectangles, cardioids, and other shapes [40].

Blum [43] originally suggested a "grassfire" model for determining the medial axis of a surface. Activation originating at the boundary of the contour diffuses across the surface, but like a fire in a field of grass, once burned, a location can no longer be activated. The medial axes are the last activated regions. A number of alternative models for generating the medial axes have subsequently been proposed [40]. At the risk of further theoretical speculation in an experimentally-deprived area, we offer a biological implementation for such models. In addition to the facilitation between elements on a contour discussed above, psychophysical studies have documented changes in contrast sensitivity induced in directions orthogonal to the local contour orientation [35]. It has

² One disadvantage of medial axis representations is that they are sometimes very sensitive to small perturbations in shape

also been shown that contour-based facilitation only occurs in cells which receive direct thalamic stimulation—e.g., cells whose receptive fields lie in the gaps between contour elements are not facilitated, at least in striate cortex [44, 45]. Finally, it has recently been observed, that stimulation of the thalamus can result in waves of activation which slowly propagate across the thalamus [46, 47].

Presentation of a stimulus results in thalamic and cortical activation, transiently accentuated at the boundary. If the stimulus is perceptually salient, cortical cells responding to the boundary will receive facilitation from their neighbors responding to the bounding contour, and as discussed above, will become synchronized. Synchronized activity spreads from supragranular to infragranular cortical layers, and is then fed back to the thalamus, where possibly through T-type calcium channels, it ignites bursting in geniculate cells. This represents the initiation of a “grassfire” in the geniculate, which eventually terminates at the medial points of the retinotopically projected representation of the surface.

To carry this speculation further, an analogous process could occur simultaneously in the cortex, with ongoing feedback between the thalamus and cortex. In the cortex, we envision a set of orientation-specific connections which measure the distance from each cell to the nearest border. In the cortical hypercolumn corresponding to each medial point, the activity in each orientation column represents the distance to the object border. The distribution of activity across the hypercolumn is a local representation of object shape. This spatial representation can be converted into a temporal representation by translating input strength (relative border distance) into a delay in spike timing, similar to a scheme proposed by Hopfield [2]. To read this code, neurons in higher cortical areas (e.g. IT) must detect a temporal pattern of delays among inputs from a hypercolumn. Use of a temporal code allows a single IT cell to “listen” to inputs from hypercolumns over a large visual field. By backprojecting this temporal pattern over V1, a cell in IT could prime recognition of particular structure in a translation, rotation, and scale invariant manner.

This medial point hypercolumn representation offers several benefits for a recognition system. First, it provides a compact representation of object shape—all information is coded within a single hypercolumn through the relative activation of different orientation columns. The representation reduces the problem of scale invariant recognition to local normalization, and the problem of orientation invariance to a simple time shift. Symmetries in the object will be manifested as symmetries in the representation, transforming the problem of symmetry detection into something akin to auditory localization. Since the representation also reflects the effects of proximity, continuity, and closure, it serves as an objective function over the Gestalt laws—providing a measure of the object’s salience in addition to a representation of its shape. Such a representation provides a bridge between perception and recognition, and indicates how attention and learning could be additionally integrated.

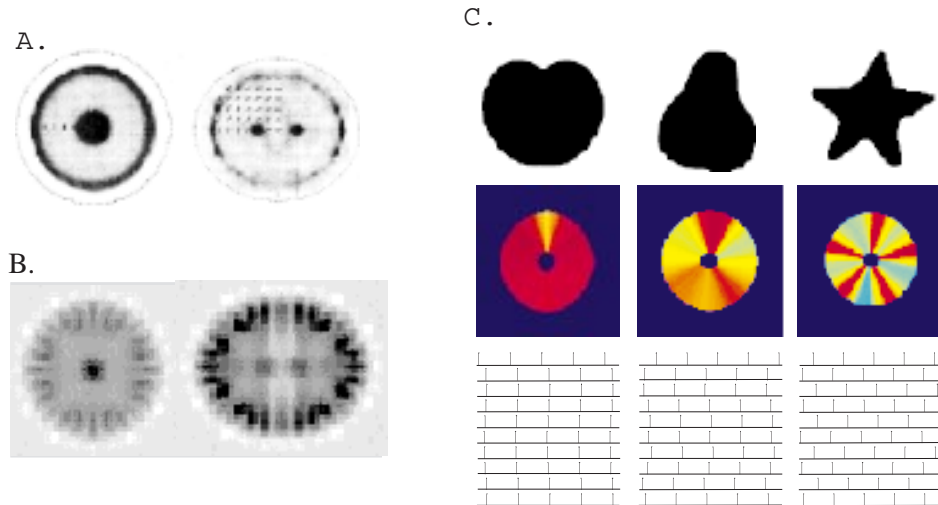


Figure 6: Medial Point Hypercolumn Representation. A. Experimental data from Kovács and Julesz [28] showing increased contrast sensitivity at medial points of circle (left) and ellipse (right) Reprinted with permission from Nature (370, 645, Fig. 2) Copyright (1994). Macmillan Magazines Ltd. B. Simulation results [14] accounting for medial point facilitation by cortical connections. C. Proposed hypercolumn representation for 3 shapes (top), middle row shows activation in orientation columns around the medial point (intensity codes border distance), bottom shows hypothetical translation into spatiotemporal code across orientation columns (see text).

The chief benefit of such a representation is that it makes the spatial relationships between features, e.g., the geometry, explicit. One can imagine composing hierarchies of network representations that describe the spatial relation between object components. For example, representation of a face would involve coding the relative distances and positions of each of the major facial features, as well as the overall shape of the head. This representation would be linked with hypercolumns devoted to the details of each individual feature and subfeature. The entire representation would be an extended spatiotemporal firing pattern, that could be “detected” by a single, well-tuned cell. Activation of this cell could induce, perhaps at a subthreshold level, stirrings of the spatiotemporal pattern, thus predisposing us to see the “man in the moon” as a result of partial activation of the system.

Synchronization-Based Memory

As a final example of how synchronization may provide a common framework for cognitive processes, we consider a synchronization-based mechanism for memory

storage and recall. With slight modification, the same cellular mechanisms used above to model orientation columns in visual cortex are used here to model the CA3 region of the hippocampus. The hippocampus and associated structures are known to play a critical role in the consolidation of memory, and are the structures first and most severely damaged in Alzheimer's disease. The hippocampus is also known to exhibit complex temporal dynamics in the theta (6-10 Hz) and gamma (20-80 Hz) frequency range. The behavioral correlation of these rhythms is clearer in the hippocampus than in the visual cortex. Buzsáki, for example, has proposed that the hippocampus operates in two different rhythmically-characterized states [48]. During active exploration of the environment, as new information streams in from cortex, the hippocampus exhibits prominent gamma and theta frequency oscillations. Every so often, in rats at least, behavior switches to a quieter state characterized by grooming or feeding; during these periods the theta oscillations disappear and the hippocampus switches to a predominantly bursting mode. Buzsáki argues that in the exploratory state, the hippocampus is engaged in active information processing and memory recall; whereas, in the quiescent state, new memories are being consolidated.

The gamma oscillations seen in hippocampus (and neocortex) are intimately connected to the synchronization process. The gamma oscillations arise from synchronized firing, and conversely, synchronization often occurs with gamma frequency periodicity. For example, in Traub's model of mutual interneuron inhibition [49] (which is the basis of the simulations presented here), the gamma frequency nature of the synchronization is due to the ratio of NMDA, AMPA and GABA_A conductance decays. Buzsáki's data suggests that synchronization underlies the function of the hippocampal memory system, and we envision the following model. A "memory" can be defined as a synchronized pattern of neuronal activity, extending over time. As illustrated in Figure 7, a memory is represented in the CA3 network as the spatial pattern of pyramidal cell spikes during the time window defined by a single gamma cycle. Gamma-band synchronization is induced by a mechanism of mutually inhibitory interneurons [37, 49, 50]. Theta-band oscillations, generated by septal interneurons, clock new perforant input to the network from entorhinal cortex, terminate each attractor state, and reset the network for the next set of entorhinal inputs. Lastly, cholinergic input from the medial septum is responsible for maintaining otherwise bursting pyramidal cells in a single spike firing mode.

This network can function as an attractor-based associative memory network, analogous in operation to a Hopfield network [51, 52]. A memory is reached when the network converges to a fixed-point attractor state. Using a small, 24-cell version of this network, we have shown [53] that attractor states directly correspond to those in a traditional Hopfield network constructed with a similar synaptic matrix. In a larger, 136-cell network (64 pyramidal cells, 64 chandelier cells, and 8 basket cells) it is possible to examine both the fidelity of auto-associative recall as well as the effects on memory storage of the pathological depletion of cholinergic neuromodulation as is seen in

Alzheimer's disease [54].

For these purposes, we randomly chose five 64-bit binary strings to store as memories (viz. firing pattern of the 64 pyramidal cells), used Hopfield's [51] algorithm to calculate synaptic weights, and then used these weights to scale the maximal conductances of the excitatory and inhibitory recurrent synapses. Network performance was evaluated by measuring the correlation between the network state and each of the stored patterns as a function of time. The overlap m_p with a pattern is defined by

$$m_p(t) = 1 - \frac{2d_H(t)}{N} \quad (1)$$

where d_H is the Hamming distance between the current network state and the stored pattern. With this metric, an exact match (i.e. the network has reached the attractor state) will give $m_p=1$ while the inverse of the stored pattern will give $m_p=-1$.

Corrupted memories were created by randomly flipping some percentage of the bits of the original pattern. The degree of corruption is shown in Figure 7B as the overlap between the network state on the first gamma cycle and the stored memory. The top trace in the figure shows the network dynamics for the presentation of corrupted versions of one of the five stored memories. The correlation between corrupted inputs and the stored memories ranges from 90% down to about 50%, yet the network still reaches the appropriate attractor demonstrating error correction as well as recall of memories.

Simulations of the effects of decreasing cholinergic input show that the network function is quite robust, in that it is capable of performing pattern completion/correction on highly degraded input patterns even with [ACh] lowered by 50%³. This is demonstrated in the second trace of figure 7B where, at 50 μ M of ACh, the network is still able to reach the appropriate attractor state for various corrupted inputs. One of the major effects of decrease cholinergic input is a slowing of the gamma rhythm. For example, at 50 μ M the gamma frequency slows to the point that there are only 7 or 8 gamma cycles per theta cycle. The drop in gamma frequency stems from two sources: 1) decreased depolarization of pyramidal cells and interneurons, and 2) the increase in both I_{AHP} and I_{Ca} causes a lower spike frequency in pyramidal cells for a given depolarization.

As cholinergic input declines even further however, network performance deteriorates. The bottom two traces of Figure 7B demonstrate the results of reducing [ACh] to 25 and 10 μ M respectively. The gamma frequency continues to drop and eventually the network not only lacks enough gamma cycles to reach the attractor, but

³ Cholinergic inputs inhibit several intrinsic membrane currents and act to generally depolarize cells. Cholinergic inputs also alter the balance of intrinsic/extrinsic synaptic efficacies (Hasselmo, 1995). We calculated the degree of cholinergic current inhibition from dose-response curves [54].

its ability to reconstruct the pattern declines as well.

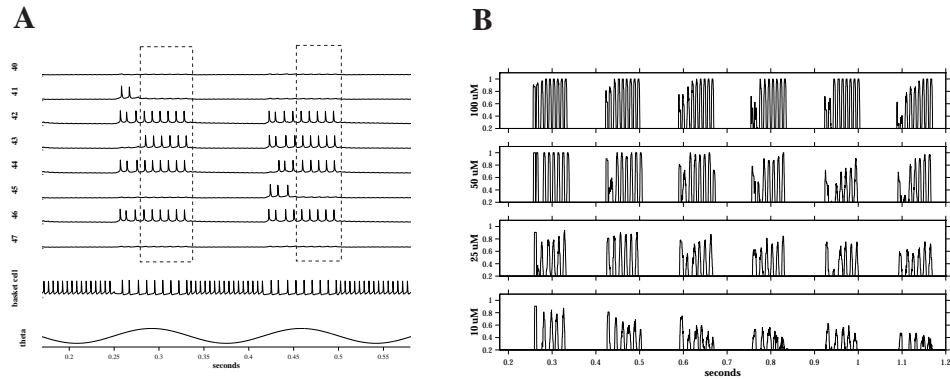


Figure 7: Synchronized hippocampal network. (A) Spike traces of eight CA3 pyramidal and one basket cell (from a network simulation of 64 pyramidal, 64 chandelier, and 8 basket cells) with idealized theta (6 Hz) population rhythm shown for reference. The state of the network is defined by the spatial pattern of temporally-precise spikes during the time window defined by a single gamma cycle (indicated by spiking of basket cell). Arbitrary patterns are input to network at the start of a theta cycle; a memory is reached when the network converges to a fixed attractor state (indicated by dashed box). (B) Functional consequences of decreased cholinergic input. Plots, at various concentrations of acetylcholine, of the correlation between network state and attractor state (1.0 implies perfect recall, 0.0 implies no correlation). Oscillations are at gamma frequency. At the start of each theta cycle, a degraded version of a memory (i.e. $0 < \text{correlation} < 1$) is presented to the network. Over subsequent gamma cycles, the network attempts to recall the uncorrupted memory. At normal physiological levels of Ach (top trace) highly degraded input patterns are correctly recalled by the network in only a few gamma cycles. As the [ACh] drops, the gamma frequency decreases, and the network has fewer cycles with which to reach the attractor state.

Conclusions

We have discussed synchronization-based models for perceptual organization, recognition, and memory recall. Our argument for the central role of synchronization arises from three sources. (1) The Johansson problem requires a mechanism for detecting extended spatiotemporal correlations, and synchronization provides such a mechanism. Consideration of how Gestalt-based processing could be implemented in striate cortex leads to a synchronization-based view of visual processing. (2) Synchronization in the hippocampus is well documented experimentally, and provides a mechanism for an attractor-based memory system. (3) Recognition must be coupled to both perception and memory, as well as attention and learning, and a similar synchronization-based

mechanism provides a compact representation of object shape. These arguments all rest on the growing body of experimental support for synchronization throughout cortex. The models discussed make use of similar cellular and network mechanisms, and might be suitable for use in an integrated system. The use of a common representational framework makes sense from both an engineering and evolutionary viewpoint. It is also reasonable from an ecological view, since spatiotemporal correlations in the world are detected by Gestalt-based circuits and represented by spatiotemporal correlations in the brain.

One common feature of the models discussed is the possible role for neuromodulation in the control of synchronization. In the thalamus and hippocampus, acetylcholine has documented effects on cell activity and its behavioral consequences. In visual cortex evidence suggests that acetylcholine activates “chattering cells” in supragranular layers [55]—anatomically, these pyramidal cells give off the long-distance horizontal connections discussed above, and physiological data indicates that they are involved in the generation of synchronized activity. Koch [56] and others have proposed that attention may operate by enhancing or suppressing the ability to achieve synchronization. The close association between attention and learning [57] and the necessity of correlated inputs for inducing synaptic plasticity, suggest a role for synchronization in a various forms of learning. In this regard, Merzenich and colleagues [58] have found that cholinergic inputs to neocortex enable rapid stimulus-dependent reorganization of receptive field properties and topographic representations. Acetylcholine is one of a number of modulators which may carry out such functions [59]. The take-home message is that there may be an interesting relationship between neuromodulation and synchronization in a wide range of cognitive phenomena.

For example, recent evidence [60] suggests that the interactions between contour elements in the perceptual pop-out experiments discussed above are dependent upon stimulus contrast: at low contrasts, interactions are facilitatory, at higher contrasts, interactions are predominantly suppressive. Several recent models have attributed this result to contrast-dependent changes in the relative activation of excitatory versus inhibitory cells [61]. Such phenomena may, however, be indications of the existence of different behaviorally-related system states, perhaps related to attention. Changes in functional connectivity could be controlled by neuromodulation, akin to the changes seen in hippocampus or invertebrate ganglia.

Clearly, the ideas here are premature, and there are significant unresolved questions. It is unclear whether the medial point hypercolumn representation discussed above makes sense for 3-D objects, or how it might function in real-world recognition problems. More fundamentally, it is difficult to reconcile the synchronization hypothesis with the notion of population coding. In the classic Gray and Singer [62] experiment two colinear bars moving in tandem evoke synchronization among cells of roughly appropriate orientation preference as the bars pass through their receptive fields. It is difficult to envisage how cells with different orientation preferences, firing at a range

of rates in response to the bars, can all be synchronized. Recent results from Singer and Kreiter [63] show that cells of non-preferred orientation are indeed synchronized if their preferred orientations can be linked by a smooth contour. Synchronization may thus be limited to a portion of the stimulus representation.

In conclusion, we should ask what does synchronization offer that cannot be fulfilled by a traditional rate code. The answer, although incomplete, is most importantly, that synchronization integrates the representation with the computation. As in AI systems in which the operation (e.g. multiplication) and the data have the same representation, this is a fundamental step towards autonomous intelligence. The goal now is to understand better, through theory and experiment, how such processes are carried out in the brain.

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