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Neural Oscillations for Coding, Communication, and Computation in the Visual System

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## **Neural Oscillations and Synchrony as Mechanisms for Coding, Communication, and Computation in the Visual System**

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### **Early Investigations of the Visual System**

Oscillatory structure in the mass activity of neurons is prevalent throughout the nervous system and across a wide variety of species. The phenomenon was already discovered in the nineteenth century by neurophysiologists who recorded from the exposed brain with mirror galvanometers. The recorded rhythms were unrelated to structure in the stimuli, as well as to heart or breathing rhythms, and thus correctly identified as an intrinsic feature of brain activity (Caton, 1875). Beck (1890) investigated the visual system by recording in occipital areas of rabbits and dogs during visual stimulation. He reported visually evoked potentials as well as ongoing oscillatory signals that could be suppressed by the arrival of stimuli, a phenomenon that is now referred to as stimulus-dependent desynchronization (Zayachkivska, Gzegotsky, & Coenen, 2011). While the functional interpretation was straightforward for the stimulus-evoked potentials, it remained elusive for the oscillatory signals.

In the 1950s and 1960s, single-cell physiology in visual areas provided a more detailed picture of stimulus-evoked and rhythmic activity. Stimulus-dependent spike rate changes

revealed the specific responses to localized visual stimuli (Hubel & Wiesel, 1962; Kuffler, 1953) in retina, lateral geniculate nucleus, and primary visual cortex. The experimental findings in primary visual cortex led to a powerful conceptual model of the two main types of excitatory cells involved in visual coding, simple and complex cells. In this model, a simple cell receives direct thalamic input and responds selectively to a conjunction of active inputs, thereby detecting specific features, such as localized, oriented edges. In contrast, a complex cell pools over several simple cells that coincide in certain features, such as a specific orientation, but differ in other features, such as location. The response of a complex cell is a disjunctive combination of its inputs. Specifically, the cell fires if any of the simple cells it is connected to is active, thereby signaling a specific orientation, somewhat independent of its exact location (or spatial phase) (Hubel & Wiesel, 1962). This conceptual model of consecutive layers of simple and complex cells within a cortical area has led to a canonical hierarchical model of visual processing (Fukushima, 1980; Riesenhuber & Poggio, 1999b; Serre, Oliva, & Poggio, 2007a) that will be important in what follows. The model describes the visual system as a feedforward cascade of processing modules, each consisting of simple-cell-like units that feed into complex-cell-like units. The idea is that cascading conjunctive and disjunctive feature combinations could produce specific yet invariant visual representations suited for object recognition and other functions performed by biological visual systems.

Single-cell physiology in early stages of the visual system also revealed that spike trains often exhibit peaks in the autocorrelation function, in the interspike-interval histogram, or in the Fourier transform, even without stimulation. These peaks reflect a dominant periodicity in the spiking—a hallmark of neural oscillations. For example, in ganglion cells, oscillatory activity is found in both anesthetized (Laufer & Verzeano, 1967; Ogawa, Bishop, & Levick, 1966;

Rodieck, 1967) and unanesthetized preparations (Heiss & Bornschein, 1966; Steinberg, 1966).

While anesthesia can increase neural oscillations, the presence of oscillations in the awake brain suggests that they could serve a function in vision. This intrinsic organization discovered in neural activity raised the question of its purpose and function. However, it was not until the mid-seventies that concrete hypotheses about the function of intrinsically paced periodic firing of neurons were proposed.

## **Correlation Theory of Brain Function**

Based on earlier ideas of Milner (1974) and Grossberg (1976), Christoph von der Malsburg (1981) published a technical report entitled “Correlation Theory of Brain Function,” possibly one of the highest impact technical reports in scientific history. The report started by identifying potential problems with the canonical hierarchical model of visual processing. Two problems were highlighted that hamper the model to reproduce the capabilities of biological visual systems. First, it cannot explain how the brain solves the problem of identifying objects in images. If one stage in the canonical model extracts some set of features, the next higher stage loses access to the relative spatial relationships or context between features that would be critical to identify objects. For example, if the lower stage extracts local edge and color features in a picture of a red triangle and a green square, the higher stage cannot access the information that the triangle was red and not the square. This problem of visual feature binding is one instance of the more general neural binding problem (Feldman, 2013).

A second problem of the canonical hierarchical model lies in supporting invariant object recognition; that is, the inability to produce representations unique to an object but independent of incidental variables, such as position, pose, or scale. As a consequence of the pooling in

complex cells, their response is somewhat independent from the exact position of the edge structure. For instance, if the stimulus is the character L, its representation, produced by complex cells with vertical and horizontal orientation, is invariant under small shifts of the L. However, the set of complex cells that represent L's will also be activated by other shapes with vertical and horizontal edges, such as a letter T and other combinations of a vertical and a horizontal edge. Thus, representations in the canonical model are invariant but not unique because, like above, context is discarded, in this case the exact relative positions of the edge features.

Von der Malsburg's report proceeded by sketching how the correlation theory offers a solution to these problems. The pivotal proposition of the theory is that the intrinsic structure of neural signals is not noise but essential for capturing the otherwise lost contextual information between features. This theory, like the canonical model, is only conceptual, not a full-fledged computational model. By proposing a set of coherent hypotheses, it became a manifesto about potential roles of intrinsic rhythmic activity in the visual system and the brain, spurring, guiding, and sometimes also biasing varied experimental and modeling work over the ensuing decades. For this reason, I will use four essential elements in the correlation theory as a scaffold to structure the material in the remainder of this chapter.

## **Is Feature Binding a Problem in Vision?**

The first hypothesis of the correlation theory is that there is a binding problem in vision. It is conjectured that in addition to visual features the (contextual) relationships between the features have to be encoded for modeling the functions of the visual stream of humans and animals, such as producing invariant object recognition or actions. It is further conjectured that it is practically

impossible to capture context by just adding contextual features in the canonical hierarchical model because of the combinatorial explosion of such features.

Some researchers argue that there is no binding problem in vision. Barlow (1985) has postulated that the visual system might be able to operate if it contained a manageable number of “cardinal cells” that represent context between visual features. Since this claim is hard to address directly in vision, it has first been investigated in another domain, the representation of text documents. It would be quite ambiguous to encode words just by the sets of their characters without representing feature context, in this case, the order of letters. For example, word pairs like “stare” and “tears” could not be distinguished. However, the use of features that represent some limited order information, such as n-tuples of subsequent characters, can decrease the ambiguity of the representations drastically and still result in a manageable number of features (Wickelgren, 1969). The representation of the above example words by letter pairs is ‘st,’ ‘ta,’ ‘ar,’ ‘re,’ and ‘te,’ ‘ea,’ ‘ar,’ ‘rs,’ respectively. This representation is already easy to disambiguate since there is only one common feature. This result has been used to propose that the binding problem of vision could be fully solved by adding a manageable number of disambiguating midlevel features in the canonical model (Mel & Fiser, 2000).

Another argument in support of this view comes from modeling studies. Riesenhuber and Poggio (1999a) demonstrated that a simulation of the canonical standard model for vision combined with state-of-the-art classifiers can reach high performance in a classification task even if the images contain background clutter (i.e., paperclip stimuli, similar to those used in Missal, Vogels, and Orban, 1997). Some recent studies further amplified this view by demonstrating that the canonical model of vision can reach human-level performance in image classification, for example, the task of determining whether or not there is an animal in the scene

(Serre et al., 2007b). Criticism has been raised against these demonstrations. For example, a method was developed that can trace back which features in an individual image were strongly indicative for the presence of animals. In some instances, these features were located in the background and not part of the animal (Landecker et al., 2010). Furthermore, it has been argued that although classification might be solvable without the full contextual information, other behaviorally relevant tasks of the visual system, such as interacting with objects in arbitrary poses or producing actions, may not.

From the perspective of perceptual psychology, Treisman (1999) and Wolfe and Cave (1999) argue that a hard binding problem exists in human vision. Illusory conjunctions are exquisite examples of this. When subjects must report on the identity of items in briefly presented arrays of colored shapes, they often report seeing a stimulus made up of the color from one array element and the shape from a different array element (e.g., Prinzmetal, 1981; Treisman & Schmidt, 1982). These experiments demonstrate that perceptual features can become unbound from their original objects and can be spuriously recombined to form a new object representation.

### **Is There Feature Binding by Synchrony in the Brain?**

The second hypothesis in the correlation theory proposes a specific neural coding scheme whereby the information about feature binding is represented in the brain. It is postulated that the synchronous structure of intrinsic fluctuations in neural signals encodes the relationship between features. This statement of the correlation theory, often referred to as binding by synchrony, was the first to gain strong traction in the field. Starting in the late eighties and continuing for about a decade, numerous studies tested this hypothesis in primary visual cortex. Some of the different

positions in the field about the validity and usefulness of the binding-by-synchrony hypothesis were captured in a series of review articles appearing in a special issue of *Neuron* (Roskies, 1999).

A first wave of experiments reported evidence for the binding hypothesis in primary visual cortex of anesthetized cats (Eckhorn et al., 1988; Engel et al., 1991; Gray et al., 1989). During visual stimulation these studies reported prominent gamma-band activity (30–60 Hz). The coherence of these oscillations in simultaneously measured cells was larger if the cells represented features that were part of a common object than if the cells represented features of two independent objects. A second wave of experiments investigated the existence of stimulus-evoked gamma-band oscillations in visual areas of monkeys, with somewhat mixed results (for reviews see Gray, 1999; Shadlen and Movshon, 1999). Oscillatory activity was not evident either in inferotemporal cortex in alert monkeys (Tovee & Rolls, 1992) or in striate cortex or middle temporal visual cortex of anesthetized monkey (Young, Tanaka, & Yamane, 1992). On the other hand, it was demonstrated that gamma-band activity is a robust property of neural responses in V1 and V2 of alert and also anesthetized monkey (Eckhorn et al., 1993; Friedman-Hill, Robertson, & Treisman, 1995; Frien et al., 1994).

Another line of experiments argued against the idea that binding takes place specifically in the cortex because high gamma-band activity is often not stimulus dependent and can be driven by gamma-band activity in the lateral geniculate nucleus (LGN) (Ghose & Freeman, 1992, 1997).

Reynolds and Desimone (1999) acknowledge that the binding problem exists for illusory conjunctions. However, they argue that most experimental evidence suggests that the problem is

solved by top-down mechanisms of attention rather than by a bottom-up binding-by-synchrony mechanism.

A number of theoretical studies have proposed alternative memory-based models of how the binding problem in vision could be solved without resorting to neuronal synchrony. One is the shifter circuit or routing circuit model (Anderson & Van Essen, 1987; Olshausen, Anderson, & Van Essen, 1993); another related model is the map-seeking circuit (Arathorn, 2002). The map-seeking circuit is able to solve challenging invariant recognition tasks in real images. However, there has been no direct experimental evidence for either of these models.

### **Do Neural Oscillations Enable Signal Communication?**

The correlation theory makes an important statement about signal communication between different sets of neurons. It suggests that fast intrinsic signal fluctuations carry contextual information in a frequency band that is separated from the frequency band corresponding to feature changes in stimuli which occur at a slower, behaviorally relevant time scale. It also describes how correlations of signal fluctuations can route the contextual information specifically to downstream targets that receive convergent input from features grouped within the same context. Von der Malsburg hypothesized different signal propagation paths that could benefit from such multiplexing of information: bottom-up, conveying sensory information from lower to higher visual areas, and top-down, such as in visual attention. In the last 15 years, this communication aspect of the correlation theory has probably received the most attention from neuroscience.



## Multiplexing

Various multiplexing schemes have been developed in engineering to communicate multiple messages separately in a single information channel. They fall under two broad classes. In time division multiplexing, the time axis is divided into interleaved nonoverlapping time windows, each exclusively reserved for one of the messages. This scheme works if the sampling rate of the time window is above the Nyquist limits of the signals to be communicated. In frequency division multiplexing, the frequency domain is divided into nonoverlapping frequency bands, each carrying one of the messages. If the transmitted signals occupy overlapping frequency bands, frequency-division multiplexing relies on methods for shifting signals to nonoverlapping bands in the frequency domain.

It is instructive to apply these definitions from engineering to the communication with spike trains in the brain. Clearly, the correlation theory proposes a form of frequency-division multiplexing, as it assumes that the intrinsic fluctuations used for coding context are in a higher-frequency regime than the signal changes directly reflecting sensory inputs. At the same time, the mechanisms postulated for synchronizing periodic fluctuations between neurons introduce a scheme of time-division multiplexing within the high-frequency band. If a group of neurons represents features with a common context, their rhythmic activity synchronizes and confines the neurons' firing to narrow time windows within the oscillation cycle. If the integration window of downstream neurons is small enough, this temporal patterning allows neurons with a common context to recruit downstream neurons preferentially. This selection effect has been called feedforward coincidence detection (Fries, 2009) and has been observed experimentally in cortical neurons (Bruno & Sakmann, 2006). Furthermore, it has been revealed that the activity of

inhibitory interneurons in cortical areas can exhibit strong power in the gamma range. Thus, the alignment or de-alignment of the phases of inhibition with the time windows of synchronized excitatory input provides a mechanism for how neurons can actively select which inputs they are sensitive to (Fries, Nikolic, & Singer, 2007). For simulation experiments exploring feedforward coincidence detection and input selection by inhibition, see Tiesinga, Fellous, and Sejnowski (2008).

There is evidence in various sensory systems that the meaning of a spike can depend on the phase of a reference signal (Friedrich, Habermann, & Laurent, 2004). For a theoretical model showing how the relative phase of a reference oscillation can be used to multiplex multiple visual signals in one spike train, see Nadasdy (2009).

### **Gamma Enhancement during Visual Attention**

Strong evidence has been presented supporting the idea that coherence in neuronal fluctuations might be crucial in mediating top-down effects of attention (Engel, Fries, & Singer, 2001). For example, in a study where alert monkeys attended to behaviorally relevant stimuli while ignoring distractors, it was shown that V4 neurons activated by attended stimuli exhibited increased gamma activity compared to neurons nearby in V4 that were activated by distractors (Fries et al., 2001). Another study reported a direct correlation between gamma-band synchrony and visually triggered behavior. The response time to a stimulus change can be predicted by the degree of gamma-band synchronization among those neurons in monkey visual area V4 that are activated by the behaviorally relevant stimulus (Womelsdorf et al., 2006).

## Bottom-Up Communication in the Visual System

In addition to endogenous rhythms, the cortex also seems to inherit oscillations that emerge in retina and LGN (Castelo-Branco, Neuenschwander, & Singer, 1998; Ghose & Freeman, 1992, 1997; Neuenschwander & Singer, 1996) and which are present both with and without anesthesia (Heiss & Bornschein, 1965, 1966). In spike trains from retina and LGN, the gamma oscillations and the stimulus-evoked changes are well separated in the frequency domain. The visual information encoded by spike rate occupies only the lower 25 Hz of the frequency spectrum, reflecting the fact that the spectral power of natural visual signals decays as the inverse of the frequency (Dong & Atick, 1995).

A recent study investigated how oscillations in the retina might be used by the thalamus to transmit information downstream (Koepsell et al., 2009). It was shown that the spike trains of a single thalamic relay cell can transmit two separate streams of information, one encoded by firing rate and the other in gamma oscillations (Koepsell et al., 2009). The study combined computational methods (Koepsell & Sommer, 2008) with the technique of whole-cell recording in vivo (Wang et al., 2007), which allowed the detection of both retinothalamic synaptic potentials and the action potentials they evoke from single relay cells. In other words, it was possible to reconstruct the spike trains of the inputs and outputs of single relay cells. In many cells, it was found that both spike trains had an oscillatory component. To explore whether or not these oscillations were transmitted by the thalamic cell, the phase of the oscillation of the retinal inputs was used to dejitter the timing of thalamic spikes across repeated trials of the stimulus. The result of the realignment was dramatic, as illustrated in figure 89.1A. Although the

oscillation was not visible in the raw peristimulus histogram (PSTH), it generated a pronounced modulation in the amplitude of the PSTH made from the dejittered signal (see [figure 89.1B](#)).

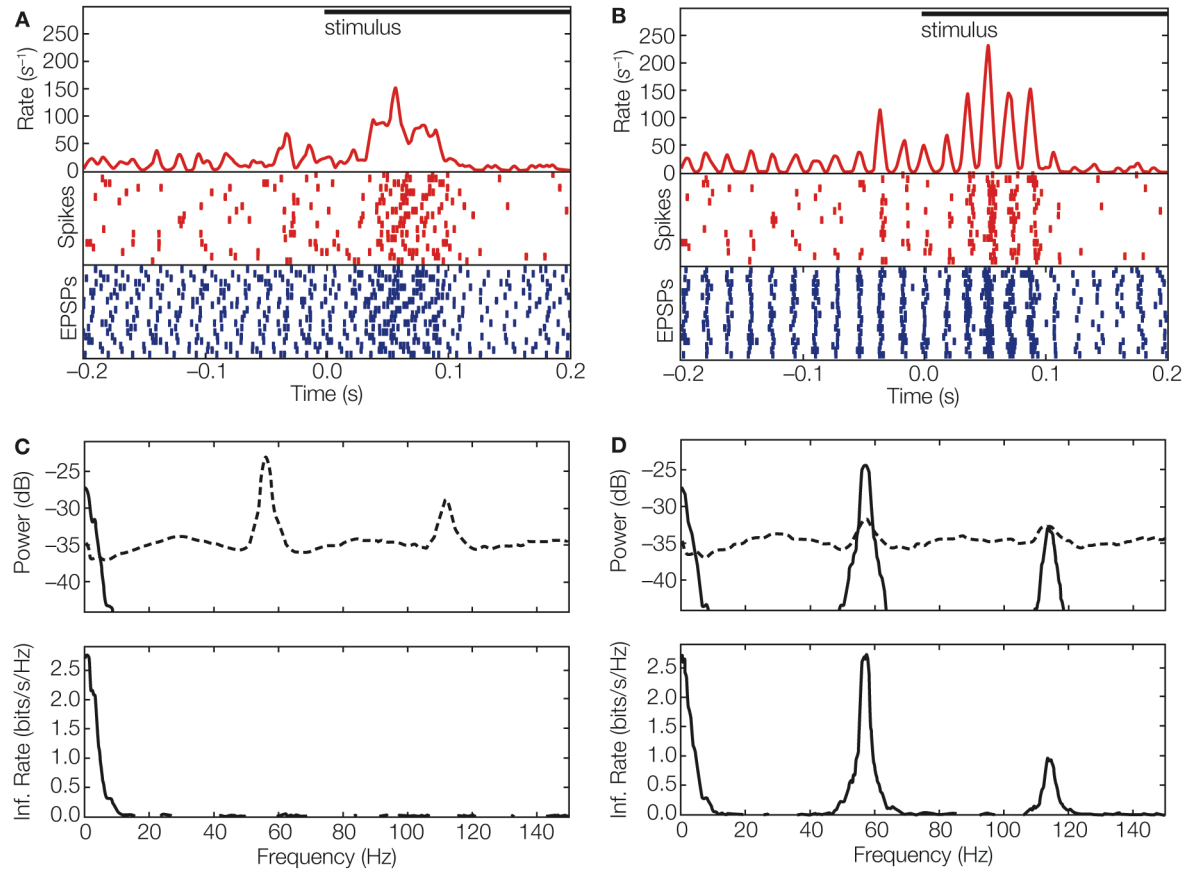


Figure 89

By estimating the amount of information conveyed by the dejittered spike train, it was shown that most relay cells receiving periodic synaptic inputs transmitted a significant amount of information in the gamma frequency band. For some cells, the amount of information in the oscillation-based (high-frequency) channel was several fold higher than that conveyed by the rate-coded channel (1.2 vs. 0.4 bits/spike in the example shown in [figures 89.1C and 89.1D](#)).

Thus, gamma oscillations in retina and thalamus provide a channel for conveying information through LGN to the cortex.

There are various possibilities for how this channel could contribute to visual function. One is the case in which the retinal oscillations do not contain information about the visual stimulus. Even if the oscillations are an uninformative carrier, they might increase the amount of information about local retinal features transmitted by the thalamic rate code. They would do so by a process akin to amplitude modulation, in which information about the retinal feature is reproduced in the frequency band of the oscillations. This redundant information could be read out and decoded in the cortex by mechanisms such as feedforward coincidence detection. A specific role for the oscillation-based channel could be denoising. Further, the modulation of the afferent spike train with a carrier might enable cortical oscillations to route the incoming sensory information or to direct attention to a particular feature.

A second possibility is that retinal oscillations are influenced by the stimulus, specifically, by displacements of the retinal image caused by eye movements. Thus, periodic activity in the retina might encode spatial information in the temporal domain, similar to the whisker system (Ahissar & Arieli, 2001; Rucci, 2008). This idea is motivated by the similarity between the dominant frequency bands in the local field potential recorded from primary visual cortex and fixational eye movements (note also that oscillatory eye movements are found in species ranging from turtle to humans; Greschner et al., 2002; Martinez-Conde, Macknik, & Hubel, 2004).

A third potential role for retinal oscillations involves computational analysis of visual stimuli. Since retinal oscillations are formed by distributed networks, they might be sensitive to spatially extensive features and/or context. In fact, there are many models of oscillatory neural

networks that are able to transform spatial structure from visual input into temporal structure in neural activity. These models, which were originally developed to simulate cortical computations, are built with phase-coupled oscillatory neurons, for example, Baldi and Meir (1990), Schillen and Koenig (1994), Sompolinsky, Golomb, and Kleinfeld (1991), Sporns, Tonioni, and Edelman (1991), Ursino et al. (2006), von der Malsburg and Buhmann (1992), and Wang and Terman (1997). It would be worthwhile to further develop such models for describing and exploring possible roles of oscillations in retinal and thalamic function. What needs to be tested experimentally is whether the oscillation-based channel might transmit large-scale information such as segments in the retinal image, conveying the gist of a scene (Navon, 1977). Through feedforward coincidence detection the oscillations could preferentially activate cells in V1 whose features are most consistent with the image segments. Thus, retinal and thalamic oscillations could help select cortical visual representations that not only carry fine-grained image information but are also helpful for guiding behaviors like object recognition or the interaction with objects (Koepsell et al., 2010).

A behavioral role for retinal gamma oscillations along those lines has been clearly established in the frog. Specifically, looming stimuli designed to simulate shadows cast by predators evoke synchronous oscillatory discharges in neural “dimming detectors.” By contrast, small dark spots that mimic prey fail to induce such activity (Ishikane, Kawana, & Tachibana, 1999). The consequence of the synchronous oscillations among retinal dimming detectors is important for an animal’s survival since it triggers escape behavior (Arai et al., 2004). Further strengthening the link between synchronous retinal activity and behavior, it was shown that pharmacological suppression of gamma oscillations abolishes escape responses but spares the slower modulation of spike rate evoked by small objects (Ishikane, 2005). Thus, in the frog,

information about different types of visual signals seems to be multiplexed in different frequency bands of neural spike trains.

### **Cross-Frequency Coupling**

Studies in a variety of sensory systems have shown that the power of gamma oscillations is modulated by the phase of lower-frequency intrinsic brain rhythms, such as theta waves (Canolty et al., 2006; Lakatos et al., 2005) and alpha waves. It is believed that this modulation of the gamma power could shape the brain activity into cycles for selection and processing of a particular aspect of sensory input (Fries, 2009; Schroeder & Lakatos, 2009) (see also Freeman, 2000).

### **Biological Mechanisms Supporting Visual Processing with Neural Oscillations**

The correlation theory makes a very specific hypothesis about the basic computational mechanism involved in visual processing. It postulates that a fast form of synaptic plasticity (or learning) is crucial for encoding of context information and for forming invariant visual representations (Bienenstock & von der Malsburg, 1987; Wiskott & von der Malsburg, 1996).

Such fast synaptic plasticity could easily interact with neuronal oscillations to introduce correlations between neurons for representing related items. Interestingly, this postulate predated the discovery of fast types of synaptic plasticity such as spike-timing dependent plasticity (STDP) (Bi & Poo, 1998; Markram et al., 1997). However, although some studies have reported response changes of visual neurons induced by STDP during vision (Yao & Dan, 2001), currently there seems to be little evidence that the interaction between oscillations and STDP is a crucial mechanism for visual perception.

There is a large body of literature studying the mechanisms for the production and synchronization of oscillations in cortical circuits (Bartos, Vida, & Jonas, 2007; Tiesinga & Sejnowski, 2009). Specifically, three mechanisms have been proposed for producing synchrony in a cortical region (Tiesinga & Sejnowski, 2009). First, by inheritance of synchrony from upstream areas via their feedforward projections (Ghose & Freeman, 1997; Koepsell et al., 2009; Neuenschwander & Singer, 1996; Tiesinga, Fellous, & Sejnowski, 2008); second, by activation of inhibitory networks via the interneuron gamma (ING) mechanism (Whittington, Traub, & Jeffreys, 1995); and third, by activation of reciprocally connected networks of excitatory and inhibitory neurons via the pyramidal-interneuron gamma (PING) mechanism (Börger & Kopell, 2005) as reviewed in Whittington et al. (2000). In the ING mechanism, only small effects are expected from activating the excitatory cells whereas activating inhibitory cells will increase the inhibitory cell firing rate and synchrony. Recent optogenetic methods allow for testing these proposed mechanisms quite directly. Studies that selectively modulated the activity in interneurons with optogenetic methods favored the PING mechanism (Cardin et al., 2009; Sohal et al., 2009). However, there is also experimental support for ING (Whittington, Traub, & Jeffreys, 1995), and the current evidence for PING is not strong enough to rule out ING entirely (Tiesinga & Sejnowski, 2009).

## **Conclusions: The Rise and Fall, and Rise Again, of Oscillations**

More than a generation after the appearance of von der Malsburg's technical report, opinions and viewpoints regarding the significance of oscillatory activity for visual processing in the brain have undergone several fundamental shifts. In the late nineties, the discussion was quite narrowly focused on two aspects of gamma oscillations, evidence for the binding-by-synchrony



hypothesis and assessments of how reliably stimulus-evoked gamma oscillations occur during visual perception. Following this first wave of experiments and modeling, it appeared that the evidence for binding by synchrony, though existent, was not conclusive. Likewise, stimulus-evoked gamma oscillations were reported in some experimental configurations but not in others.

In the face of these quite inconclusive results, it might appear surprising that studies of oscillatory neural activity would increase throughout the 2000s rather than die out. These newer studies differ from those of the first generation by a shift in perspective and also by taking a broader outlook. For example, Pascal Fries and colleagues (see chapter 71) have studied how the coherence of gamma oscillations in higher visual areas is correlated with focused attention necessary to solve a visual task in the presence of distractors (Fries et al., 2001). Rather than considering attention as a competitor to oscillation-based computations, the question here is how oscillatory mechanisms might be involved in creating attention-dependent biased competition between different sensory inputs. The involvement of oscillatory activity in focused attention and its impact on behavior has now become well established in the field.

Renewed interest in gamma oscillations has also come about as the result of new methods and findings in neuroscience. First, new optogenetic techniques allow for dissecting the mechanisms for how pyramidal cells and interneurons are involved in the generation of gamma oscillations and their synchronization (Sohal et al., 2009). Second, the coupling of gamma oscillations to other, slower and more global brain waves has become an active field of research (Canolty et al., 2006). Third, there is now increased awareness that gamma oscillations in primary visual cortex have multiple origins, and so there is probably not a unique functional interpretation, such as binding by synchrony. To disentangle the puzzle, the reexamination of

oscillations in the early visual pathway (Ghose & Freeman, 1997; Neuenschwander & Singer, 1996) may be crucial.

The strong impact of correlation theory in driving the investigation of oscillatory neuronal activity in vision is a striking example of the lasting power that a computational theory can have. However, since its inception, many new experimental methodologies and observations have emerged, and our appreciation of the challenges of visual processing has matured. Thus we may seek to extend the original theory to address the current incarnations of some fundamental open questions: How can oscillatory structure as observed in brain activity contribute to the powerful parallel and recurrent computations that neural circuits seem to perform? Can oscillation-driven schemes close the performance gap between brains and computer algorithms? To approach these questions, theorists should design models of how oscillations, as observed in brain activity, can produce, organize, and drive distributed computation. Such models can be tested on technical benchmark problems, for example in image recognition. In tasks that biological visual systems can solve, these models should favorably compare to state-of-the-art computer algorithms and clearly outperform the canonical feedforward model of vision. In addition to influencing technology, such computational models might motivate and guide future experiments to yield a deeper understanding of the periodic structure of brain activity.

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## References

- <jrn>Ahissar, E., & Arieli, A. (2001). Figuring space by time. *Neuron*, 32, 185–201.</jrn>
- <jrn>Anderson, C. H., & Van Essen, D. C. (1987). Shifter circuits: A computational strategy for dynamic aspects of visual processing. *Proceedings of the National Academy of Sciences of the United States of America*, 84, 6297–6302.</jrn>
- <jrn>Arai, I., Yamada, Y., Asaka, T., & Tachibana, M. (2004). Light-evoked oscillatory discharges in retinal ganglion cells are generated by rhythmic synaptic inputs. *Journal of Neurophysiology*, 92, 715–725.</jrn>
- <bok>Arathorn, D. (2002). *Map-seeking circuits in visual cognition: A computational mechanism for biological and machine vision*. Stanford, CA: Stanford University Press.</bok>
- <jrn>Baldi, P., & Meir, R. (1990). Computing with arrays of coupled oscillators: An application to preattentive texture discrimination. *Neural Computation*, 2, 458–471.</jrn>
- <jrn>Barlow, H. B. (1985). The Twelfth Bartlett Memorial Lecture: The role of single neurons in the psychology of perception. *Quarterly Journal of Experimental Psychology*, 37, 121–145.</jrn>
- <jrn>Bartos, M., Vida, I., & Jonas, P. (2007). Synaptic mechanisms of synchronized gamma oscillations in inhibitory interneuron networks. *Nature Reviews. Neuroscience*, 8, 45–56. doi:10.1038/nrn2044.</jrn>

- <jrn>Beck, A. (1890). Die Stroeme der Nervencentren. *Centralbibliothek Physiologie*, 4, 572–573.</jrn>
- <jrn>Bi, G. Q., & Poo, M. M. (1998). Synaptic modifications in cultured hippocampal neurons: Dependence on spike timing, synaptic strength, and postsynaptic cell type. *Journal of Neuroscience*, 18, 10464–10472.</jrn>
- <jrn>Bienenstock, E., & von der Malsburg, C. (1987). A neural network for invariant pattern recognition. *Europhysics Letters*, 4, 121–126.</jrn>
- <jrn>Börgers, C., & Kopell, N. (2005). Effects of noisy drive on rhythms in networks of excitatory and inhibitory neurons. *Neural Computation*, 17, 557–608.</jrn>
- <jrn>Bruno, R. M., & Sakmann, B. (2006). Cortex is driven by weak but synchronously active thalamocortical synapses. *Science*, 312, 1622–1627.</jrn>
- <jrn>Canolty, R. T., Edwards, E., Dalal, S. S., Soltani, M., Nagarajan, S. S., Kirsch, H. E., et al. (2006). High gamma power is phase-locked to theta oscillations in human neocortex. *Science*, 313, 1626–1628. doi:10.1126/science.1128115.</jrn>
- <jrn>Cardin, J. A., Carlen, M., Meletis, K., Knoblich, U., Zhang, F., Deisseroth, K., et al. (2009). Driving fast-spiking cells induces gamma rhythm and controls sensory responses. *Nature*, 459, 663–667. doi:10.1038/nature08002.</jrn>
- <jrn>Castelo-Branco, M., Neuenschwander, S., & Singer, W. (1998). Synchronization of visual responses between the cortex, lateral geniculate nucleus, and retina in the anesthetized cat. *Journal of Neuroscience*, 18, 6395–6410.</jrn>
- <jrn>Caton, R. (1875). The electric currents of the brain. *British Medical Journal*, 2, 278.</jrn>

- <jrn>Dong, D. W., & Atick, J. J. (1995). Statistics of natural time-varying images. *Network*, 6, 345–358.</jrn>
- <jrn>Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M., et al. (1988). Coherent oscillations: A mechanism of feature linking in the visual cortex? Multiple electrode and correlation analyses in the cat. *Biological Cybernetics*, 60, 121–130.</jrn>
- <jrn>Eckhorn, R., Fries, A., Bauer, R., Woelbern, T., & Kehr, H. (1993). High frequency (60–90 Hz) oscillations in primary visual cortex of awake monkey. *Neuroreport*, 5, 2273–2277.</jrn>
- <jrn>Engel, A. K., Fries, P., & Singer, W. (1991). Dynamic predictions: oscillations and synchrony in top-down processing. *Nature Reviews*, 2, 704–716.</jrn>
- <jrn>Engel, A. K., Koenig, P., Kreiter, A. K., & Singer, W. (1991). Interhemispheric synchronization of oscillatory neuronal responses in cat visual cortex. *Science*, 252, 1177–1178.</jrn>
- <jrn>Feldman, J. (2013). The neural binding problems. *Cognitive Neurodynamics*, to appear, Online First publication: DOI 10.1007/s11571-012-9219-8.</jrn>
- <jrn>Freeman, W. J. (2000). Mesoscopic neurodynamics: From neuron to brain. *Journal of Physiology, Paris*, 94, 303–322.</jrn>
- <jrn>Friedman-Hill, S. R., Robertson, L. C., & Treisman, A. (1995). Parietal contributions to visual feature binding: Evidence from a patient with bilateral lesions. *Science*, 269, 853–855.</jrn>

- <jrn>Friedrich, R. W., Habermann, C. J., & Laurent, G. (2004). Multiplexing using synchrony in the zebrafish olfactory bulb. *Nature Neuroscience*, 7, 862–871.</jrn>
- <jrn>Frien, A., Eckhorn, R., Bauer, R., Woelbern, T., & Kehr, H. (1994). Stimulus-specific fast oscillations at zero phase between visual areas V1 and V2 of awake monkey. *Neuroreport*, 5, 2273–2277.</jrn>
- <jrn>Fries, P. (2009). Neuronal gamma-band synchronization as a fundamental process in cortical computation. *Annual Review of Neuroscience*, 32, 209–224.  
doi:10.1146/annurev.neuro.051508.135603.</jrn>
- <jrn>Fries, P., Nikolic, D., & Singer, W. (2007). The gamma cycle. *Trends in Neurosciences*, 30, 309–316. doi:10.1016/j.tins.2007.05.005.</jrn>
- <jrn>Fries, P., Reynolds, J. H., Rorie, A. E., & Desimone, R. (2001). Modulation of oscillatory neuronal synchronization by selective visual attention. *Science*, 291, 1560–1563.  
doi:10.1126/science.291.5508.1560.</jrn>
- <jrn>Fukushima, K. (1980). Neocognitron: A hierarchical neural network capable of visual pattern recognition. *Neural Networks*, 1, 119–130.</jrn>
- <jrn>Ghose, G. M., & Freeman, R. (1997). Intracortical connections are not required for oscillatory activity in the visual cortex. *Visual Neuroscience*, 14, 963–979.</jrn>
- <jrn>Ghose, G. M., & Freeman, R. D. (1992). Oscillatory discharge in the visual system: Does it have a functional role? *Journal of Neurophysiology*, 68, 1558–1574.</jrn>
- <jrn>Gray, C. M. (1999). The temporal correlation hypothesis review of visual feature integration: Still alive and well. *Neuron*, 24, 31–47.</jrn>

- <jrn>Gray, C. M., Konig, P., Engel, A. K., & Singer, W. (1989). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature*, 338, 334–337. doi:10.1038/338334a0.</jrn>
- <jrn>Greschner, M., Bongard, M., Rujan, P., & Ammermuller, J. (2002). Retinal ganglion cell synchronization by fixational eye movements improves feature estimation. *Nature Neuroscience*, 5, 341–347.</jrn>
- <jrn>Grossberg, S. (1976). Adaptive pattern classification and universal recoding, II: Feedback, expectations, olfaction, and illusions. *Biological Cybernetics*, 23, 187–202.</jrn>
- <jrn>Heiss, W. D., & Bornschein, H. (1965). Distribution of impulse of continuous activity of single optic nerve fibers: Effects of light, ischemia, strychnine and barbiturate. *Pflügers Archiv für die Gesamte Physiologie des Menschen und der Tiere*, 286, 1–18.</jrn>
- <jrn>Heiss, W. D., & Bornschein, H. (1966). Multimodal interval histograms of the continuous activity of retinal cat neurons. *Kybernetik*, 3, 187–191.</jrn>
- <jrn>Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology*, 160, 106–154.</jrn>
- <jrn>Ishikane, H., Kawana, A., & Tachibana, M. (1999). Short- and long-range synchronous activities in dimming detectors of the frog retina. *Visual Neuroscience*, 16, 1001–1014.</jrn>
- <jrn>Ishikane, H., Gangi, H., Honda, S., & Tachibana, M. (2005). Synchronized retinal oscillations encode essential information for escape behavior in frogs. *Nature Neuroscience*, 8, 1087–1095.</jrn>

- <jrn>Koepsell, K., & Sommer, F. T. (2008). Information transmission in oscillatory neural activity. *Biological Cybernetics*, 99, 403–416.</jrn>
- <jrn>Koepsell, K., Wang, X., Hirsch, J. A., & Sommer, F. T. (2010). Exploring the function of neural oscillations in early sensory systems. *Frontiers in Neuroscience* 4, 53. doi:10.3389/neuro.01.010.2010.</jrn>
- <jrn>Koepsell, K., Wang, X., Vaingankar, V., Wei, Y., Wang, Q., Rathbun, D. L., et al. (2009). Retinal oscillations carry visual information to cortex. *Frontiers in Systems Neuroscience*, 3, 4.</jrn>
- <jrn>Kuffler, S. (1953). Discharge patterns and functional organization of the mammalian retina. *Journal of Neurophysiology*, 16, 37–68.</jrn>
- <jrn>Lakatos, P., Shah, A. S., Knuth, K. H., Ulbert, I., Karmos, G., & Schroeder, C. E. (2005). An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex. *Journal of Neurophysiology*, 94, 1904–1911. doi:10.1152/jn.00263.2005.</jrn>
- <conf>Landecker, W., Brumby, S., Thomure, M., Kenyon, G., Bettencourt, L., & Mitchell, M. (2010). Visualizing classification decisions of hierarchical models of cortex. Paper presented at the Computational and Systems Neuroscience Conference.</conf>
- <jrn>Laufer, M., & Verzeano, M. (1967). Periodic activity in the visual system of the cat. *Vision Research*, 7, 215–229.</jrn>
- <jrn>Markram, H., Lubke, J., Frotscher, M., & Sakmann, B. (1997). Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs. *Science*, 275, 213–215.</jrn>



- <jrn>Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2004). The role of fixational eye movements in visual perception. *Nature Reviews. Neuroscience*, *5*, 229–240.  
doi:10.1038/nrn1348.</jrn>
- <jrn>Mel, B. W., & Fiser, J. (2000). Minimizing binding errors using learned conjunctive features. *Neural Computation*, *12*, 731–762.</jrn>
- <jrn>Milner, P. M. (1974). A model for visual shape recognition. *Psychological Review*, *81*, 521–535.</jrn>
- <jrn>Missal, M., Vogels, R., & Orban, G. (1997). Responses of macaque inferior temporal neurons to overlapping shapes. *Cerebral Cortex*, *7*, 758–767.</jrn>
- <jrn>Nadasdy, Z. (2009). Information encoding and reconstruction from the phase of action potentials. *Frontiers in Systems Neuroscience*, *3*, 6.</jrn>
- <jrn>Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, *9*, 353–383.</jrn>
- <jrn>Neuenschwander, S., & Singer, W. (1996). Long-range synchronization of oscillatory light responses in the cat retina and lateral geniculate nucleus. *Nature*, *379*, 728–732.</jrn>
- <jrn>Ogawa, T., Bishop, P. O., & Levick, W. R. (1966). Temporal characteristics of responses to photic stimulation by single ganglion cells in the unopened eye of the cat. *Journal of Neurophysiology*, *29*, 1–30.</jrn>
- <jrn>Olshausen, B. A., Anderson, C. H., & Van Essen, D. C. (1993). A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information. *Journal of Neuroscience*, *13*, 4700–4719.</jrn>

- <jrn>Prinzmetal, W. (1981). Principles of feature integration in visual perception. *Attention, Perception & Psychophysics*, 30, 330–340.</jrn>
- <jrn>Reynolds, J. H., & Desimone, R. (1999). The role of neural mechanisms of attention in solving the binding problem. *Neuron*, 24, 19–29, 111–125.</jrn>
- <jrn>Riesenhuber, M., & Poggio, T. (1999a). Are cortical models really bound by the “binding problem”? *Neuron*, 24, 87–93, 111–125.</jrn>
- <jrn>Riesenhuber, M., & Poggio, T. (1999b). Hierarchical models of object recognition in cortex. *Nature Neuroscience*, 2, 1019–1025. doi:10.1038/14819.</jrn>
- <jrn>Rodieck, R. W. (1967). Maintained activity of cat retinal ganglion cells. *Journal of Neurophysiology*, 5, 1043–1071.</jrn>
- <jrn>Roskies, A. L. (1999). The binding problem. *Neuron*, 24, 7–9, 111–125.</jrn>
- <jrn>Rucci, M. (2008). Fixational eye movements, natural image statistics, and fine spatial vision. *Network*, 19, 253–285. doi:10.1080/09548980802520992.</jrn>
- <jrn>Schillen, T., & Koenig, P. (1994). Binding by temporal structure in multiple feature domains of an oscillatory neuronal network. *Biological Cybernetics*, 70, 397–405.</jrn>
- <jrn>Schroeder, C. E., & Lakatos, P. (2009). The gamma oscillation: Master or slave? *Brain Topography*, 22, 24–26. doi:10.1007/s10548-009-0080-y.</jrn>
- <jrn>Serre, T., Oliva, A., & Poggio, T. (2007a). A feedforward architecture accounts for rapid categorization. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 6424–6429. doi:10.1073/pnas.0700622104.</jrn>

- <jrn>Serre, T., Wolf, L., Bileschi, S., Riesenhuber, M., & Poggio, T. (2007b). Robust object recognition with cortex-like mechanisms. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, *29*, 411–426. doi:10.1109/TPAMI.2007.56.</jrn>
- <jrn>Shadlen, M. N., & Movshon, J. A. (1999). Synchrony unbound: A critical evaluation of the temporal binding hypothesis. *Neuron*, *24*, 67–77, 111–125.</jrn>
- <jrn>Sohal, V. S., Zhang, F., Yizhar, O., & Deisseroth, K. (2009). Parvalbumin neurons and gamma rhythms enhance cortical circuit performance. *Nature*, *459*, 698–702. doi:10.1038/nature07991.</jrn>
- <jrn>Sompolinsky, H., Golomb, D., & Kleinfeld, D. (1991). Cooperative dynamics in visual processing. *Physical Review A*, *43*, 6990–7011.</jrn>
- <jrn>Sporns, O., Tonioni, G., & Edelman, G. (1991). Modeling perceptual grouping in figure-ground segregation by means of active reentrant connections. *Proceedings of the National Academy of Sciences of the United States of America*, *88*, 129–133.</jrn>
- <jrn>Steinberg, R. H. (1966). Oscillatory activity in the optic tract of cat and light adaptation. *Journal of Neurophysiology*, *29*, 139–156.</jrn>
- <jrn>Tiesinga, P., Fellous, J. M., & Sejnowski, T. J. (2008). Regulation of spike timing in visual cortical circuits. *Nature Reviews. Neuroscience*, *9*, 97–107.</jrn>
- <jrn>Tiesinga, P., & Sejnowski, T. J. (2009). Cortical enlightenment: Are attentional gamma oscillations driven by ING or PING? *Neuron*, *63*, 727–732. doi:10.1016/j.neuron.2009.09.009.</jrn>

- <jrn>Tovee, M. J., & Rolls, E. T. (1992). Oscillatory activity is not evident in the primate temporal visual cortex with static stimuli. *Neuroreport*, 3, 369–372.</jrn>
- <jrn>Treisman, A. (1999). Solutions to the binding problem: Review progress through controversy summary and convergence. *Neuron*, 24, 105–110.</jrn>
- <jrn>Treisman, A., & Schmidt, H. (1982). Illusory conjunctions in the perception of objects. *Cognitive Psychology*, 14, 107–141.</jrn>
- <jrn>Ursino, M., Magosso, E., La Cara, G. E., & Cuppini, C. (2006). Object segmentation and recovery via neural oscillators implementing the similarity and prior knowledge gestalt rules. *Bio Systems*, 85, 201–218.</jrn>
- <edb>von der Malsburg, C. (1981). *The correlation theory of brain function*. MPI Biophysical Chemistry, Internal Report 81-2. Reprinted in: E. Domany, J. L. van Hemmen, & K. Schulten (Eds.), *Models of Neural Networks II*. (1985) Berlin: Springer, 95-106.</edb>
- <jrn>von der Malsburg, C., & Buhmann, J. (1992). Sensory segmentation with coupled neural oscillators. *Biological Cybernetics*, 67, 233–242.</jrn>
- <jrn>Wang, D., & Terman, D. (1997). Image segmentation based on oscillatory correlation. *Neural Computation*, 9, 805–836.</jrn>
- <jrn>Wang, X., Wei, Y., Vaingankar, V., Wang, Q., Koepsell, K., Sommer, F. T., et al. (2007). Feedforward excitation and inhibition evoke dual modes of firing in the cat's visual thalamus during naturalistic viewing. *Neuron*, 55, 465–478.</jrn>

- <jrn>Whittington, M. A., Traub, R. D., & Jeffreys, J. G. R. (1995). Synchronized oscillations in interneuron networks driven by metabotropic glutamate receptor activation. *Nature*, 373, 612–615.</jrn>
- <jrn>Whittington, M. A., Traub, R. D., Kopell, N., Ermentrout, B., & Buhl, E. H. (2000). Inhibition-based rhythms: Experimental and mathematical observations on network dynamics. *International Journal of Psychophysiology*, 38, 315–336.</jrn>
- <jrn>Wickelgren, W. A. (1969). Context-sensitive coding, associative memory, and serial order in (speech) behavior. *Psychological Review*, 76, 1–39.</jrn>
- <edb>Wiskott, L., & von der Malsburg, C. (1996). Face recognition by dynamic link matching. In J. Sirosh, R. Miikkulainen, & Y. Choe (Eds.), *Lateral interactions in the cortex: Structure and function*. Hypertextbook: <http://www.cs.utexas.edu/users/nn/web-pubs/htmlbook96/> Austin: University of Texas.</edb>
- <jrn>Wolfe, J. M., & Cave, K. R. (1999). The psychophysical evidence for a binding problem in human vision. *Neuron*, 24, 11–17, 111–125.</jrn>
- <jrn>Womelsdorf, T., Fries, P., Mitra, P. P., & Desimone, R. (2006). Gamma-band synchronization in visual cortex predicts speed of change detection. *Nature*, 439, 733–736. doi:10.1038/nature04258.</jrn>
- <jrn>Yao, H., & Dan, Y. (2001). Stimulus timing-dependent plasticity in cortical processing of orientation. *Neuron*, 32, 315–323.</jrn>
- <jrn>Young, M. P., Tanaka, K., & Yamane, S. (1992). On oscillating neuronal responses in the visual cortex of the monkey. *Journal of Neurophysiology*, 67, 1464–1474.</jrn>

<jrn>Zayachkivska, O., Gzhegotsky, M., & Coenen, A. (2011). Impact on electroencephalography of Adolf Beck, a prominent Polish scientist and founder of the Lviv School of Physiology. *International Journal of Psychology*, 85, 3-6.</jrn>

### Figure 89.1

Multiplexed information (Inf.) in the lateral geniculate nucleus. (A) Event times aligned to stimulus onset displayed as averaged spike rate (red curve) and rasters for spikes (red) and excitatory postsynaptic potentials (EPSPs) (blue) for 20 trials of a movie clip; spike rasters were smoothed with a Gaussian window (2 ms) before averaging. (B) Responses corrected for small variation in latency (< 10 ms) by aligning the phase of the periodicity in the ongoing (retinal) activity that preceded stimulus onset; conventions as in A. (C) Top, power spectrum of thalamic spike trains decomposed into signal (solid line) and noise (dashed line). Bottom, estimate for spectral information rate, taken from the area under the curve, is 12.7 bit/s; the mean spike rate of 29 spikes/s yields a value of 0.4 bit/spike. (D) Power spectrum (top) of dejittered spike train decomposed into signal (solid line) and noise (dashed line); spectral information rate (bottom). Dejittering increased the total information from 0.4 bit/spike (C) to 1.2 bit/spike (Koepsell et al., 2009). The movie stimulus was presented with 19–50 frames/s on a monitor with a high refresh rate (140 Hz). The neural response did not lock to the frame update or monitor refresh. Reprinted from Koepsell et al. (2010).