Response synchronization in the visual cortex Ad Aertsen and Martin Arndt

Ruhr-Universität, Bochum, Germany

Recently, the classic idea of a 'relational' code in the brain received new impetus from the observation of stimulus-dependent synchronizations in the visual cortex. Work over the past two years has focused on documenting the functional dependencies of such synchronizations. We review and classify the experimental findings with respect to separate spatial and temporal schemes. Thus, we distinguish between different signal classes (spikes, continuous signals), and different types of time-locking to the stimulus. These various classes of synchronization phenomena are discussed with regard to their properties, the underlying mechanisms and their possible relevance for visual processing.

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Introduction

Ever since the time of Sherrington [1] and Hebb [2], neurobiologists have pursued the idea that neurons do not act in isolation, but rather that they form into assemblies to organize perception and action, and to perform the various computational tasks involved (see also [3] for an early formulation of this concept). Over the years, a number of different, somewhat conflicting definitions of 'neural assembly' have been proposed, phrased in terms of anatomy, of shared function, of shared stimulus response, etc. (for a review see [4]). One operational definition for neuron cell assembly has been particularly influential: 'temporal coherence' defined on the basis of near-simultaneity or some other specific timing relation in the firing of the participating neurons. This definition has been elaborated in the concept of the 'synfire chain' [5,6]: the synaptic influence of multiple neurons converging onto others in the cortical network is much stronger if they fire in (near-) coincidence. Thus, synchronized firing is, in fact, directly available to the brain as a potential neural code [7,8]. It has been speculated [9,10] that this code might serve as a mechanism for perceptual integration by 'feature binding': features of a particular object in a composite scene (e.g., in vision or audition) are functionally grouped by virtue of the correlated firing of the associated neurons.

Synchrony of firing in the visual cortex was classically studied by cross-correlation analysis of simultaneously recorded multiple neuron spike trains [11–15]. Following Moore *et al.* [16], peaks and troughs in the cross-correlograms, after comparison with appropriate control measurements [17], are characterized on the basis of parameters describing the shape (symmetry, width

and sign) and delay, and the dependence of these descriptors on stimulus features. The interest in firing synchrony recently received new impetus from reports on stimulus-dependent oscillatory synchronizations in the visual cortex [18-20]. Briefly, extracellularly recorded population activity - local field potentials (LFP) and multi-unit activity (MUA) — in the primary visual cortex of the anaesthetized cat showed oscillatory spindles with frequencies between 35 and 85 Hz upon presentation of moving bar and grating stimuli. In an earlier report [21], synchronized oscillatory responses had been observed in subdural EEG-recordings from the visual cortex of the awake monkey. In contrast to the well-known visual evoked potentials (VEP), these rhythmic events are not time-locked to the stimulus and, hence, not visible after stimulus-triggered signal averaging. Moreover, oscillatory spindles recorded from different electrodes were found to synchronize, depending on the coherence in orientation and direction of movement of the light bar stimuli. Thus, these findings triggered a still continuing debate on the potential role of synchronous brain activity in establishing a coherent percept by 'feature binding'. In order to review the experimental evidence, we develop a classification scheme of synchronization phenomena, emphasizing their different levels of space-time resolution.

Timing, correlation and synchronization

Synchronization on different spatial scales

On closer inspection, the various reports on synchronous activity in the visual cortex pertain to neural activities at

Abbreviations

ACF--auto-correlation function; ACH--auto-correlation histogram; CCF--cross-correlation function; CCH--cross-correlation histogram; EEG--electroencephalogram; IT--inferior temporal cortex; LFP--local field potential; MT---medial temporal area; MUA---multi-unit activity; PSTH--post-stimulus time histogram; RF---receptive field; VEP---visual evoked potential.

widely different levels of spatial resolution, ranging from single neuron spike trains up to EEG recordings. The accompanying differences in signal characteristics, and hence in signal processing techniques, lead to characteristic differences in the nomenclature and interpretation of the temporal coherence phenomena found. Thus, these various differences provide a first means of classifying these coherence phenomena, as summarized in Table 1.

At the lower end of the scale, single and multiple neuron spike trains present examples of discrete signals. They are classically treated as stochastic point processes; computational tools for analysis are usually based on averaging techniques. The internal time structure is evaluated by auto-correlation histograms (ACH) [22], the timing relation with respect to the stimulus is measured by the post-stimulus time histogram (PSTH) [23]. The timing relation between spike trains from different sources is analysed by cross-correlation histograms (CCH) [17], the dependence of joint firing op stimulus timing by the Joint-PSTH [24] or, for more than two neurons at a time, by 'gravitational clustering' [25,26] or related methods [15]. Population signals (such as LFP and EEG), on the other hand, are classically treated as continuous signals, using tools from systems theory such as spectral analysis, auto- and cross-correlation functions (ACF, CCF) and coherence function [27]; the relation to stimulus events is studied by stimulus-locked signal averaging - a typical result being the VEP.

Related to this distinction between discrete and continuous signals is the issue of 'signal generators'. Discrete spike signals represent the output activity of neurons, whereas continuous population signals with a frequency content below some 100 Hz are usually associated with dendritic potentials, i.e. the input signals to the neurons [28]. The transitional category of non-separated MUA is evaluated according to either one of the two signal classes — that is, as population spike activity [18] or as population rate activity [20] — depending on whether the discrete or the continuous aspects are emphasized. Often, the shift in spatial resolution from single neuron to population level is accompanied by a change in terminology for the associated temporal coherence phenomena: the terms shift from 'timing' to 'coincidence' and 'correlation', and on to 'synchronization'. Similarly, the conceptual interpretation shifts from the atomistic view of the single neuron as a 'cardinal cell' [29], to the notion of the 'functional group' or cell assembly [2,9,10,30] and from there to the global dynamic state of the brain (or large parts of it) in relation to behavioral context [31].

Synchronization with different degrees of stimulus coupling

A second classification of visual response synchronizations is based on the degree of 'time-locking' to the stimulus (cf Table 2). Those events that re-occur in a time-locked fashion upon repeated presentation of a stimulus are called 'stimulus-locked', those that alter their frequency of occurrence in relation to the stimulus but without such precise timing-locking are called 'stimulus-related'. In practical terms, the degree to which these events show up after stimulus-triggered signal averaging (PSTH, VEP) determines into which category they are included. Thus, those events which do not survive trial averaging of the signal waveform are by definition classified as stimulus-related.

This emphasis on reproducibility with respect to stimulus time creates a methodological problem with the class of stimulus-related synchronization events. The reason is that the definition given above is essentially a negative one. Clearly this implies that another criterion is needed to detect instances of stimulus-related synchronization in the first place. Marked features (e.g., damped oscillatory waveforms) in time- or trial-averaged cross-corre-

Signal characteristics	Single neuron spike activity	Multiple neuron spike activity	Population spike activity	Population rate activity	Local field potential	EEG
Signal type	Discrete	Discrete	Discrete	Continuous	Continuous	Continuous
Resolution	Time resolution	Time resolution	Time resolution	Frequency	Frequency	Frequency
	< 1 ms	< 1 ms	< 1 ms	1–10 kHz	1 100 Hz	1 40 Hz
Phenomenon	'Timing'	'Correlation'	'Correlation'	'Synchronization'	'Synchronization'	'Synchronization'
History	Gerstein, Kiang 1960 [23]	Perkel <i>et al.</i> 1967 [17]	Gray, Singer 1989 [18]	Eckhorn <i>et al.</i> 1988 [20]	Eckhorn <i>et al.</i> 1988 [20] Gray, Singer 1989 [18]	Freeman, van Dijk 1987 [21] Bullock, McClune 1989 [27]
Evaluation	PSTH, ACH	CCH, Joint PSTH, 'gravit. clustering'	ACH, CCH	ACF, CCF, spectra	ACF, CCF, spectra	Coherence function, spectra
Stimulus	Light bar	Light bar	Light bar, grating	Light bar, grating	Light bar, grating	Grating, checkerboard
Parameters	RF-tuning, cell type, ocular dominance	RF-tuning, -overlap, cell type, ocular dominance	RF-tuning, -overlap, cell types, stimulus velocity, short bars vs. long bar	RF-tuning, -overlap, cell type, ocular dominance, stimulus velocity	RF-tuning, -overlap, cell type, ocular dominance, stimulus velocity	Spatial and temporal frequency; contrast
Suggested relevance for	Neural coding; 'cardinal cell'	Neural coding: cell assemblies	Feature linking, bridge to cognition	Feature linking, bridge to cognition	Feature linking, bridge to cognition	Brain state in relation to behavioral context

lations can be used to indicate the presence (but not necessarily the shape) of stimulus-related synchronizations. Other methods, however, are needed to isolate the individual occurrences and to determine their particular properties (latency, duration, frequency content, etc.). Typically, some conspicuous feature in the time course of the signal under observation [32] or in the sliding cross-correlogram [33••] is used in a templatelike fashion to define and detect the occurrence of an instance of synchronization on a single trial basis. Evidently, this procedure implies a considerable degree of subjective judgement and/or model dependence. For instance, the emphasis on oscillatory events as instances of stimulus-related synchronization is at least partly explained by their eye-catching quality; other arguments come from the EEG literature, with its traditional interest in 'rhythmic activities' (e.g., [28,34]). The question remains, though, whether other instances of stimulusrelated synchronization, possibly with a less periodic or otherwise striking time structure, may have escaped attention, with the danger of incompleteness and/or bias in the functional interpretation of stimulus-related synchronization phenomena (see also the methodological critique in [35••]). In this context we note the existence of a considerable body of recent literature, concerned with the definition, and detection of spatio-temporal activity patterns, not necessarily periodic, in single and multiple neuron activity, and their surprisingly high frequency of occurrence in relation to stimulus and behavioral events [36,37,38•].

A distinction between stimulus-locked and stimulus-related forms of synchronization is also made in crosscorrelation studies of simultaneously recorded multiple spike trains. Synchronization, defined on the basis of departures from baseline firing in time-averaged crosscorrelograms, is separated into a stimulus-locked contribution and a residual component, the latter presumably mediated by network effects. Those instances in which synchronization can be fully explained by stimulus time-locking of the individual responses alone are called 'stimulus-locked'; those in which other sources of synchronization have to be invoked are usually called 'neural coordination' or 'functional coupling'. The degree of stimulus-locked synchronization is typically measured by the correlation of stimulus-locked individual averages ('shift' or 'shuffle predictor' [17], 'PST-predictor' [39]). The amount of residual correlation, possibly after appropriate normalization, measures the degree of neuronal coordination [24]. Clearly, this distinction is somewhat different from the one made above. Cross-correlograms present a time-averaged measure of time-delay between firings of different sources; hence, they cannot specify when the instances constituting the correlation occurred. Thus, it is conceivable that the above defined stimulus-locked synchronizations are accompanied by some stimulus-related contribution in the cross-correlation sense, and vice versa. In spite of these differences, though, we will treat residual correlations as equivalent to stimulus-related synchronizations, bearing in mind the possibility that these classes do not fully overlap.

An intermediate position is taken by cross-correlation analysis using the Joint-PSTH and gravitational clustering. These measures, using stimulus-locked trial averaging rather than time averaging, retain the full resolution of the correlation phenomena along the time axis. Thus, residual correlations measured by these methods present a time-resolved net result of stimulus-triggered averaging. At first sight this would seem to favour their inclusion among the stimulus-locked synchronizations. Nevertheless, and mainly for reasons of consistency, we also classify such residual correlations as signifying instances of stimulus-related synchronizations.

At this point, and not without a certain sense of embarrassment, we note that we have carefully avoided to provide a precise and operational definition of the notion of 'synchronization'. At least at this point the need for a single more precise definition becomes rather pressing. Instead, we have encountered a number of different definitions and associated measurement protocols, each one applicable to a different class of neural signals. This, evidently, makes it hard to compare results across signal classes. Unfortunately, the neuroscience literature is of little avail here, although the term is, in fact, widely used, as testified by the reference list. Perhaps the situation is best illustrated by a quotation from Ted Bullock: "Synchrony would appear to be a major variable, one about which we understand little and for which there is no accepted measure of quantification" (from [40]). Or, even more drastically, in Fowler's Dictionary of Modern English Usage (Oxford University Press, 1965): "synchronize is not a word that we need regret the existence of, since there is useful work that it can do better than any other (e.g., synchronized clocks, gears, television records); but it is a word that we may fairly desire to see as seldom as we may, one of the learned terms that make a passage in which they are not the best possible words stodgy and repellent".

In summary, we conclude that there is a distinct need for more precise and unified measures of synchronization. Such measures should be able to deal with all different levels of spatio-temporal resolution (from spikes to continuous signals), give an adequate description of phase relationships, including the case of multiple frequencies or aperiodic signals, and must be applicable both in single and in multiple trial conditions.

Response synchronization in the visual cortex

Table 2 summarizes the various types of stimulus synchronizations observed in visual cortex, classified according to both the spatial and the temporal schemes developed above, and with an emphasis on the results from the past year.

The notion of stimulus-locked synchronization forms the underlying model for most, if not all, single neuron experiments. In these experiments it is (at least implicitly) assumed that all structure in the time course of visual responses can be attributed to direct stimu-

Table 2. Stimulus dependent synchronizations in the visual cortex with different degrees of stimulus locking.				
Synchronization characteristics	Stimulus-locked synchronization	Stimulus-related synchronization		
Spike	Single neuron: Reid <i>et al.</i> 1992, [45•] Oram, Perrett 1992 [46•] Multi-neuron: Křuger, Becker 1992 [48,49•] Gerstein, Gochin 1992 [50•] Shaw <i>et al.</i> 1993 [51•]	Pair correlation: Aertsen et al. 1989 [24] Nelson et al. 1992 [57••] Population correlation: MUA in cat: Gray, Singer 1989 [18] Eckhorn et al. 1988 [20]		
Measure	Population correlation: MUA in cat: Eckhorn, Schanze 1991 [32] Neuron pairs: shift-predictor, PSTH-predictor	Gray <i>et al.</i> 1992 [33••] Neuron pairs: CCH-PSTH predictor, Joint PSTH		
Generators	Neuron groups: spatially weighted sum of activities (trial average) Stimulus input to feedforward network	Neuron groups: 'gravitational clustering', spatially weighted sum of activities (single trial) Lateral, feedback network		
Dendritic potential	Population correlation:	(Quasi-)Periodic		
Denomic potential	VEP: cat: Eckhorn, Schanze 1990 [32] VEP: Creutzfeldt 1983 [54]	cat: Gray, Singer 1989 [18]; Eckhorn et al. 1988 [20] Gray et al. 1992 [33••] Ghose, Freeman 1922 [77••] monkey: Freeman, van Dijk 1987 [21] Kreiter, Singer 1992 [70•] Eckhorn et al. 1993 [71••]; Young et al. 1992 [35••] membrane potential: Jagadeesh et al. 1992 [78•] Bringuier et al. 1992 [79•] FEG: monkey: Freeman, van Dijk 1987 [21]		
Measure	Neuron groups: spatially weighted sum of activities (trial average)	Neuron groups: spatially weighted sum of activities (single trial)		
Generators Time structure	Stimulus input to feedforward network Transient	Lateral, feedback network (Quasi-)Periodic		

lus effects, and that possible synchronizations among neurons can be reduced to synchronization of the individual firing processes to the stimulus itself. We refer to this level of response synchronization as 'rate coherence' [41•]. Thus, at the level of single neuron spike trains, the class of stimulus-locked synchronizations is particularly concerned with the dynamic coding of stimulus features in the time course of firing rate profiles (e.g., [42-44,45•,46•]). Recently, several multineuron studies in the visual cortex have expanded this approach to incorporate ensemble coding schemes, all based on some form of trial-averaged, dynamic measure of stimulus-evoked activity in groups of neurons [47,48,49•–51•]. In the domain of dendritic signals, the occurrence of stimulus-locked synchronizations is well documented along the entire spatial range, from current source density (CSD)-measurements (reviewed in [52]) via LFPs [32] up to the VEP in the EEG (reviews in [53,54]). The importance of timing aspects in the VEP is reflected in the differential dependence of individual components in the VEP waveform on stimulus properties like contrast and spatial frequency.

Most of the recent studies on synchronizations in visual cortex responses fall into the second class, the stimulusrelated synchronizations. At the level of multiple single-

neuron spike trains we have the classical cross-correlation studies already mentioned in the introduction. More recent reports focus on the relation between correlated firing and receptive field properties [55,56•] and on the appearance of distinct levels of timing precision in correlated firing (at roughly 5, 50 and 500 ms in the cat [57••] and similarly at about 5 and 50 ms in the monkey [58]). Dynamic correlations revealed by the Joint-PSTH and by gravitational clustering analysis [15,24,59] demonstrated that synchronizations are clearly dependent on stimulus features. Moreover, they may overlap in time with, but follow an altogether different time course than, the stimuluslocked components, with time constants of modulation as low as tens of milliseconds. This type of synchronization, referred to as 'event coherence' [41•], has also been observed in the inferotemporal cortex [60], as well as in stimulus- and behavior-related responses in the frontal cortex [61•] of awake, behaving monkeys. Similar dynamic correlation studies in population activity are not known to us, but in our opinion they should be potentially quite rewarding.

At the level of population signals, the initial reports on oscillatory synchronizations in the cat primary visual cortex were followed by a series of papers in the last few years, describing these phenomena in more detail (for excellent reviews see [62••,63••]). Typically (different authors give slightly different numbers), the duration of spindles, either in single-electrode LFPs [32] or in correlated population spike activity from dual electrodes [33••], varies between 50 and 900 ms; their latency with respect to stimulus onset is well above 100 ms [32]. Spindle frequencies vary between 35 and 80 Hz, thus occupying the range referred to in the EEG literature as the high-beta [34] or gamma [64] range. Synchronizations were found to occur within a single area, across different areas (A17-A18-A19 [20,65], A17-posterior medial lateral suprasylvian sulcus (PMLS) [66]) and across hemispheres (A17(left)-A17(right) [67]), provided that the recorded cell groups were activated by coherent stimuli. Delays between oscillatory spindles from different electrodes within A17 range between -3 and +3 ms, with a mean value at about 0 ms [33...]. This distribution gradually becomes broader when the recording sites are in different areas and, even more so, when sites in different hemispheres are compared [67]. The mean delay, however, remains at about 0 ms, which is interesting in view of the increasing conduction length. Other properties that have been investigated are the dependence on spatial separation of recording sites and on angular difference of preferred orientation [19], and the dependence on stimulus properties such as binocularity [20], orientation, velocity [68] and alignment of movement with two light bar stimuli [69].

All these results on oscillatory synchronizations have been obtained from anaesthetized cats. The obvious and important questions as to whether such synchronizations are also observed in other species and, even more crucially in view of their functional relevance, in awake behaving preparations, are only now starting to be addressed. First reports on the monkey are somewhat contradictory: whereas an earlier report (MS Livingstone, Soc Neurosci Abstr 1991, 17:176) confirmed the presence of oscillatory synchronizations in V1 of the anaesthetized monkey, a recent study [35...] reports that such phenomena are found neither in V1, nor in the medial temporal area (MT) or the inferior temporal cortex (IT). After the early observations on oscillatory synchronizations in the fast EEG of the awake, behaving monkey [21], synchronized oscillatory spindles have recently been reported from area MT [70•]. In a very recent study [71••], strong oscillatory synchronizations were observed in the primary visual cortex, with stimulus-specificities comparable to, and amplitudes and frequencies even considerably higher than, those previously reported in both cat and monkey. Experiments in IT, however, showed no [72•], or hardly any [35...], such evidence when static stimuli were used.

Outlook and open issues

The recent observations on stimulus-induced synchronizations among groups of neurons in the visual cortex have created a great deal of excitement in the neuroscience community. Particularly the proposal that such synchronizations present instances of a 'relational' code, providing a mechanism for perceptual coherence by feature linking, has stirred a still continuing debate. For one thing, the emergence of dynamic time structures in neural activity clearly provided a fruitful ground to apply concepts from the field of nonlinear dynamics to brain theory. Thus, these synchronizations were virtually embraced by theoreticians, leading to a remarkable outpour of papers dealing with the generation of synchronized oscillations in various kinds of neural net work models and their usage for implementing cognitive functions. The salient feature of most of these models (the review of which is clearly beyond the scope of this paper) is the self-organization taking place in networks of coupled nonlinear oscillators.

In spite of the considerable progress made, a number of important issues, experimental as well as theoretical, remain to be resolved. We have already referred to the crucial question of whether visual synchronizations are also observed in awake behaving preparations and noted that first reports are clearly contradictory, and further experimental evidence is urgently needed. Also the question as to whether such synchronizations take place within and across other sensory modalities is still very much open. Although first reports on fast oscillatory activity in the somatosensory [73] and the sensorimotor [74•] cortex indeed seem to suggest that oscillatory synchronizations may be a more widespread phenomenon in the neocortex, they have not yet been observed in other modalities, and the relation to stimulus and behavior is far from being settled. Another important question concerns the generating mechanism for the visual synchronizations both purely intra-cortical [63••,75] and thalamo-cortical [76] interactions have been proposed. Again, experimental evidence is far from conclusive. Whereas some reports [16,32] explicitly mention the absence of oscillations in the lateral geniculate nucleus, others [77••] report strong oscillations in that same region. Recent in vivo whole-cell patch recordings from neurons in cat area 17 [78•], and intracellular recordings in kitten area 17 [79•], suggest that oscillatory responses are generated largely by rhythmic synaptic input. Thus, the generator issue is also still very much open. In summary, at the present stage, the experimental evidence, particularly from awake behaving preparations, although highly promising and intriguing, does not yet allow a definitive decision on the functional role of synchronized activity in visual processing.

In addition to these issues, there is the fundamental problem of the so-called 'read-out'. If synchronizations are to provide a mechanism for feature linking, the question emerges of how the brain utilizes such synchronizations to organize perception and action. On the basis of anatomical [80] and physiological considerations, it has been proposed that the cortical 'hardware' is optimally suited to detect, process, and conduct coincident firing in so-called 'synfire reverberations' [6,38•]. Thus, it can be envisaged that waves of synchronous activity travel through the cortical network while dynamically binding coherent subgroups of neurons in various sensory and motor areas [81]. It is still largely unknown, however, how these synchronizations would interact with internal processes involved in learning, memory and intention. Finally, and perhaps as a somewhat superfluous warning against a too single-minded view, we are probably well advised to keep in mind that quite different utilizations of (a)synchrony of neural activity can also be envisaged (e.g., [82•]).

Conclusion

One of the outstanding features of the study of neural synchronizations is that it attempts to build a bridge between brain activity at very different levels of spatial and temporal resolution (see Tables 1 and 2). Thus, it caused a shift in emphasis from descriptions in terms of 'rate coding' (mostly based on single neuron studies) to those that can be characterized as 'coherence coding'. While rate coding seems particularly suited to characterize the flow of information in feedforward networks, coherence coding is a natural candidate in the context of lateral and feedback networks. Clearly both aspects of neural activity are present in the cortex, as is witnessed by the abundance of both stimulus-locked and stimulus-related synchronization phenomena (see Table 2). Hence, the unification of both rate and coherence aspects into a single scheme for coding and computation in the brain would appear to be a great challenge.

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Reviews the general concepts of timing, synchrony and oscillations in the mammalian brain, with special emphasis on the appearance of repeated spatio-temporal patterns of spike activity ('synfire reverberations') in cortical neural networks.

- PALM, G, AERTSEN AMHJ, GERSTEIN GL: On the Significance of Correlations Among Neuronal Spike Trains. *Biol Cybern* 1988, 59:1-11.
- BULLOCK TH: New Descriptors for the Activity of Brain Cell Assemblics: Requirements and Opportunities. In Nonlinear Dynamics and Neuronal Networks Edited by Schuster HG. Weinheim: VCH Verlag; 1991:257–263.
- NEVEN H, AERTSEN A: Rate Coherence and Event Coherence
 in the Visual Cortex: a Neuronal Model of Object Recog-
- nition. Biol Cybern 1992, 67:309–322.

In this model study, the authors emphasize the functional significance of different levels of temporal acuity in synchronous activity in the visual cortex: 'rate coherence' and 'event coherence'.

- RICHMOND BJ, OPTICAN I.M: Temporal Encoding of Two-Dimensional Patterns by Single Units in Primate Inferior Temporal Cortex. II. Quantification of Response Waveform. J Neurophysiol 1987, 57:147-161.
- THORPE SJ, IMBERT M: Biological Constraints on Connectionist Models. In *Connectionism in Perspective*. Edited by Pfeifer R, Schreter Z, Fogelman-Soulié F. Amsterdam: Elsevier, 1989:63–92.
- DINSE HR, KRÜGER K, BEST J: A Temporal Structure of Cortical Information Processing. Conc Neurosci 1990, 1:199–238.
- 45. REID RC, VICTOR JD, SHAPLEY RM: Broadband Temporal Stimuli Decrease the Integration Time of Neurons in Cat Striate Cortex. Vis Neurosci 1992, 9:39–45.

Using a systems theoretical approach, the authors show that with increasing temporal bandwidth of visual stimuli, cortical neurons alter their response dynamics such that the speed of cortical processing becomes faster, presumably due to a dynamic nonlinearity of cortical origin.

 ORAM MW, PERRETT DI: Time Course of Neural Responses
 Discriminating Different Views of the Face and Head. J Neurophysiol 1992, 68:70–84.

On the basis of a quantitative study of the response dynamics and discriminative power of neurons in the superior temporal sulcus responsive to static head views, the authors argue that the rapid emergence of discrimination (within the first 5 ms after response onset) suggests a coding scheme based on the simultaneous arrival of the first spikes from multiple input neurons.

- 47. VOGELS R: Population Coding of Stimulus Orientation by Striate Cortical Cells. *Biol Cybern* 1990, 64:25–31.
- KRÜGER J, BECKER JD: Recognizing the Visual Stimulus from Neuronal Discharges. Trends Neurosci 1991, 14:282–286.
- KRÜGER J, BECKER JD: Is Spike Frequency the Critical Factor
 in Recognising the Visual Stimuli? In *Information Processing* in the Cortex: Experiments and Theory. Edited by Aertsen A, Braitenberg V. Berlin: Springer; 1992:161–165.

Evaluating how visual stimuli could be most reliably recognized on the basis of spike trains recorded simultaneously with 30 micro-electrodes in the monkey striate cortex (see also [42]), the authors conclude that the neuronal signal content is segregated into 'meaning', which is carried by temporal structure of spike trains, and 'importance', which is carried by spike frequencies.

 GERSTEIN GL, GOCHIN PM: Neuronal Population Coding and the Elephant. In *Information Processing in the Cortex: Experiments and Theory*. Edited by Aertsen A, Braitenberg V. Berlin: Springer; 1992:139–160.

This paper reviews different population coding schemes. The authors demonstrate that some neurons add 'useful' information in recordings from the infero-temporal cortex of the behaving monkey, whereas others add 'noise' and, hence, degrade the identification. Possible ways in which the brain might select the neurons whose activity is to be used in each particular case are discussed.

 SHAW GL, KRÜGER J, SILVERMAN DJ, AERTSEN AMHJ, AIPLE F,
 LIU HC: Rhythmic and Patterned Neuronal Firing in Visual Cortex. Neurol Res 1993, 15:46-50.

Analysis of trial-averaged activity in multi-electrode recordings in the visual cortex of the anaesthetized monkey provides evidence for synchronous, rhythmic patterns of activity; these patterns are dependent on cortical layer and on visual stimulus, last for 70–100 ms, and have a spatio-temporal structure which cannot be factorized into separate spatial and temporal components.

- MITZDORF U: Current Source Density Method and Application in Cat Cerebral Cortex: Investigation of Evoked Potentials and EEG Phenomena. *Physiol Rev* 1985, 65:37–100.
- 53. BASAR E: EEG-Dynamics and Evoked Potentials in Sensory and Cognitive Processing by the Brain. In Dynamics of Sensory and Cognitive Processing by the Brain. Edited by Basar E. Berlin: Springer, 1988;30–55.
- 54. CREUTZFELDT OD: Cortex Cerebri. Berlin: Springer; 1983.

- SCHWARZ C, BOIZ J: Functional Specificity of a Long-Range Horizontal Connection in Cat Visual Cortex: a Cross-Correlation Study. J Neurosci 1991, 11:2995–3007.
- 56. LIU Z, GASKA JP, JACOBSON LD, POLLEN DA: Interneuronal In-
- teraction Between Members of Quadrature Phase and Anti-Phase Pairs in the Cat's Visual Cortex. Vision Res 1992, 32:1193–1198.

Cross-correlation study of interactions among simultaneously recorded, adjacent simple cells in the visual cortex of the cat. On the basis of the type of interactions found and the phase-response to drifting sinewave gratings (quadrature phase or anti-phase), the authors propose a model in which each of four possible types of simple cell receptive field profiles is derived independently from the weighted sum of geniculate afferent excitation and intracortical inhibition.

- 57. NELSON JI, SALIN PA, MUNK MHJ, ARZI M, BULLIER J: Spatial
 - and Temporal Coherence in Cortico-Cortical Connections: a Cross-Correlation Study in Areas 17 and 18 in the Cat. Vis Neurosci 1992, 9:21–37.

Elaborate cross-correlation study of interactions between neurons and neuron groups in Areas 17 and 18 of the cat. Special emphasis is given to the temporal dispersion of the central peaks in the crosscorrelograms; these come in three, nonoverlapping classes of widths (modal widths 3, 30 and 400 ms), and may occur singly or in combination. This temporal acuity correlates with the amount of receptive field overlap and/or similarity of receptive field properties. Three different mechanisms for each of the types of temporal coherence are proposed, all sharing the involvement of common input of cortical origin, but differing in the degree of spatial distribution across one or both hemispheres.

- KRÜGER J, MAYER M: Two Types of Neuronal Synchrony in Monkey Striate Cortex. *Biol Cybern* 1990, 64:135–140.
- AERTSEN AMHJ, GERSTEIN GL: Dynamic Aspects of Neuronal Cooperativity: Fast Stimulus-Locked Modulations of 'Effective Connectivity'. In *Neuronal Cooperativity*. Edited by Krüger J. Berlin: Springer; 1991:52–67.
- GOCHIN PM, MILLER ER, GROSS CG, GERSTEIN GL: Functional Interaction among Neurons in Inferior Temporal Cortex of the Awake Macaque. *Exp Brain Res* 1991, 84:505–516.
- VAADIA E, AERTSEN A: Coding and Computation in the Cortex: Single-Neuron Activity and Cooperative Phenomena. In Information Processing in the Cortex: Experiments and Theory. Edited by Aertsen A, Braitenberg V. Berlin: Springer; 1992:81–121.

Review of dynamic response properties of single and multi-neuron spike activity from different cortical areas in anaesthetized and in awake, behaving monkeys, with the emphasis on 'relational' codes, expressed in correlated firing in pairs and in groups of simultaneously recorded neurons.

- ENGEL AK, KÖNIG P, KREITER AK, SCHILLEN TB, SINGER W:
 Temporal Coding in the Visual Cortex: New Vistas on
- Temporal Coding in the Visual Cortex: New Vistas on Integration in the Nervous System. Trends Neurosci 1992, 15:218–226.

Provides an excellent overview of recent findings in the authors' laboratories on oscillatory synchronizations in various parts of the visual cortex, and a discussion of their possible role in binding distributed neuronal activities by a temporal code, presumably subserving scene segmentation and figure-ground segregation.

 ECKHORN R: Principles of Global Visual Processing of Local
 Features can be Investigated with Parallel Single-Cell- and Group-Recordings from the Visual Cortex. In *Information* Processing in the Cortex: Experiments and Theory. Edited by

Aertsen A, Braitenberg V. Berlin: Springer; 1992:385–420. Careful overview of the various properties of stimulus-related synchronizations in the visual cortex of the anaesthetized cat, as observed in the author's laboratory. A distinction is made between stimulus-locked nonoscillatory synchronizations, supporting crude 'instantaneous percepts', and stimulus-induced oscillatory synchronizations, supposedly serving more complex percepts that require interative interactions among different processing levels and memory.

- BRESSLER SL, FREEMAN WJ: Frequency Analysis of Olfactory System EEG in Cat, Rabbit and Rat. Electroencephalogr Clin Neurophysiol 1980, 5:19–24.
- 65. KRUSE W, ECKHORN R, BAUER R: Stimulus-Induced Synchronization Among Three Visual Cortical Areas of the Cat. *Perception* 1990, 19:377.
- 66. ENGEL AK, KREITER AK, KÖNIG P, SINGER W: Synchronization of Oscillatory Neuronal Responses Between Striate and Extrastriate Visual Cortical Areas of the Cat. Proc Natl Acad Sci USA 1991, 88:6048–6052.
- ENGEL AK, KREITER AK, KONIG P, SINGER W: Interhemispheric Synchronization of Oscillatory Responses in Cat Visual Cortex. Science 1991, 252:1177–1179.
- GRAY CM, ENGEL AK, KÖNIG P, SINGER W: Stimulus-Dependent Neuronal Oscillations in Cat Visual Cortex: Receptive Field Properties and Feature Dependence. Eur J Neurosci 1990, 2:607–619.
- ENGEL AK, KÖNIG P, SINGER W: Direct Physiological Evidence for Scene Segmentation by Temporal Coding. Proc Natl Acad Sci USA 1991, 88:9136–9140.
- KREITER AK, SINGER W: Oscillatory Neuronal Responses in the Visual Cortex of the Awake Macaque Monkey. Eur J Neurosci 1992, 4:369–375.

The first report on oscillatory synchronizations in extra-striate areas of the visual cortex in the awake monkey. The authors report that such oscillatory episodes resemble those described earlier in the cat visual cortex, but tend to be shorter and show more variability of oscillation frequencies.

 ECKHORN R, FRIEN A, BAUER R, WOELBERN T, KEHR H: High
 Frequency (60-90) Oscillations in Primary Visual Cortex of Awake Monkey. *Neuroreport* 1993, 4:243–246.

In this very recent study, the authors report strong oscillatory synchronizations in the primary visual cortex of the awake monkey. The dominant frequencies (70-80 Hz) are considerably higher than those previously reported in both cat and monkey. Stimulus-specificities of the oscillations are comparable to and amplitudes even higher (by a factor of about three) than those in cats.

 TOVEE MJ, ROLLS ET: Oscillatory Activity is Not Evident in the Primate Temporal Visual Cortex with Static Stimuli. *Neuroreport* 1992, 3:369–372.

The authors report that they found no evidence for oscillations in the activity of face-selective neurons in the temporal visual cortex of the awake monkey upon presentation of static visual stimuli (faces). They suggest that for the recognition and processing of static objects, other methods than temporal binding by oscillations are used.

- AHISSAR E, VAADIA E: Oscillatory Activity of Single Units in a Somatosensory Cortex of an Awake Monkey and their Possible Role in Texture Analysis. Proc Natl Acad Sci USA 1990, 87:8935–8939.
- MURTHY VN, FETZ EE: Coherent 25- to 35-Hz Oscillations
 in the Sensorimotor Cortex of Awake Behaving Monkeys. Proc Natl Acad Sci USA 1992, 89:5670–5674.

The first report on synchronous (25–35 Hz) oscillations in local field potentials and unit activity in the motor cortex of the awake, behaving monkey. Oscillatory episodes occur in a variety of shapes, and preferentially during demanding sensorimotor tasks, requiring fine finger movements and focused attention.

- GRAY CM, ENGEL AK, KÖNIG P, SINGER W: Temporal Properties of Synchronous Oscillatory Neuronal Interactions in Cat Striate Cortex. In Nonlinear Dynamics and Neuronal Networks. Edited by Schuster HG. Weinheim: VCH Verlag; 1991:27–56.
- STERIADE M, CURRÓ DOSSI R, PARÉ D, OAKSON G: Fast Oscillations (20-40Hz) in Thalamocortical Systems and their Potentiation by Mesopontine Cholinergic Nuclei in the Cat. Proc Natl Acad Sci USA 1991, 88:4396–4400.
- GHOSE GM, FREEMAN RD: Oscillatory Discharge in the Visual
 System: Does it Have a Functional Role? *J Neurophysiol* 1992, 68:1558–1574.

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On the basis of an elaborate study of the properties of oscillatory responses from neurons in the visual cortex and the lateral geniculate nucleus of anaesthetized, paralyzed cats and kittens, the authors conclude that the oscillations seen in the visual cortex arise from spontaneous oscillations of a subpopulation of retinal ganglion cells and, hence, may be "an epiphenomenon of no obvious functional significance for the visual system".

 JAGADEESH B, GRAY CM, FERSTER D: Visually Evoked Oscillations of Membrane Potential in Cells of Cat Visual Cortex. Science 1992, 257:552–554.

In vivo whole cell patch recordings from cells in cat Area 17 upon presentation of moving light bar stimuli reveal strong oscillations of membrane potential around 40 Hz that show similar response properties to visual stimulation as extracellularly recorded action potentials. Such oscillations are presumably produced by corresponding oscillations in the excitatory synaptic input (see also [79•]).

79. BRINGUIER V, FREGNAC Y, DEBANNE D, SHULZ D, BARANYI A:
 Synaptic Origin of Rhythmic Visually Evoked Activity in

Kitten Area 17 Neurones. *Neuroreport* 1992, 3:1065–1068. *In vivo* intracellular and extracellular recordings from cells in kitten area 17 upon presentation of moving light bar stimuli reveal oscillations of membrane potential and rhythmic firing (frequency range in both cases mostly 7–20 Hz). The stimulus dependence of these oscillations suggests that they are generated largely by rhythmic synaptic input (see also [78•]).

- 80. BRAITENBERG V, SCHUZ A: Anatomy of the Cortex. Statistics and Geometry. Berlin: Springer; 1991.
- 81. BIENENSTOCK E: Notes on the Growth of a 'Composition Machine'. In *Contributions to Interdisciplinary Worksbop on Compositionality in Cognition and Neural Models*. Asnières sur Oise (Fr): Abbaye de Royaumont Publ; 1991:1–19.
- BARLOW HB: The Biological Role of Neocortex. In *Information Processing in the Cortex: Experiments and Theory*. Edited by Aertsen A, Braitenberg V. Berlin: Springer; 1992:53–80.

In this interesting conceptual paper, the author argues that an important task of the neocortex is to signal the novelty or unexpectedness of features and compound events in the sensory input and, hence, to categorize the input in such a way that the representational elements occur, as nearly as possible, independently in the normal, probabilistically known environment. Especially relevant for a discussion on 'relational' codes, the author proposes a dual scheme of neural plasticity, characterized by Hebbian correlation of firing due to feedforward connections and anti-Hebbian de-correlation, carried by lateral connections.

A Aertsen and M Arndt, Institut für Neuroinformatik, Universitätsstrasse 150, Ruhr Universität, D-44780 Bochum, Germany.