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6. AUTHOR(S)

Dr Christof Koch

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)

Division of Biology, 216-76
California Institute of Technology
1201 E. California Blvd
Pasadena CA 91125

8. PERFORMING ORGANIZATION REPORT NUMBER

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9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)

Dr John F. Tangney
AFOSR/NL
Building 410
Bolling AFB DC 20332-6448

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Over the last three years, we have carried out a number of projects under this grant, relating to the gating and processing of information in the mammalian visual pathway. Specifically, they have involved 1.) a detailed computational investigation of the early visual system of the cat using both analytical as well as numerical tools, 2.) a study of the dynamic properties of 2-D networks of coupled oscillatory neurons and 3.) the outline of a first neurobiological theory of visual awareness.

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Controlling the Flow of Visual Information through the Lateral Geniculate Nucleus: From Single Cells to Neural Networks

AFOSR-89-0029

Final Report

11/1/1988 - 10/31/1991

Over the last three years, we have carried out a number of projects under this grant, relating to the gating and processing of information in the mammalian visual pathway. Specifically, they have involved 1.) a detailed computational investigation of the early visual system of the cat using both analytical as well as numerical tools, 2.) a study of the dynamic properties of 2-D networks of coupled oscillatory neurons and 3.) the outline of a first neurobiological theory of visual awareness. The research was carried out by myself in collaboration with three post-doctoral fellows in my laboratory, Drs. Dan Kammen, Ernst Niebur and Florentin Wörgötter, as well as with three outside collaborators, Prof. John Kulli from the Department of Anesthesiology at the Medical School of the University of Rochester, Dr. Francis Crick at the Salk Institute in La Jolla and Prof. Heinz Schuster from the Department of Physics at the University of Kiel in Germany.

Modeling the early visual system of the cat

In our long-term effort to understand the early visual system of mammals, we constructed a simulator of a 5° by 5° patch of the visual field in the adult cat, by simulating the underlying neurons in the retina, lateral geniculate nucleus and layer IV of the primary visual cortex (Wehmeier et al., 1989; Wörgötter and Koch, 1991). The current model includes over 15,000 neurons and 4,000,000 synapses. The simulator was implemented on workstations and, when the execution time became prohibitively long, on the Connection Machine CM-2. The parallel structure of the early visual system proved to be ideally suited for the implementation on this massively parallel machine. Our approach enabled us to test several ideas about how feature extraction in the first stages of the visual system is accomplished. The three main results are as follows: 1.) A feed forward excitatory bias from LGN to V1 as postulated by Hubel and Wiesel (1962) is neither sufficient nor robust enough to explain the observed orientation tuning of area 17 simple cells. 2.) We investigated a number of different intra-cortical inhibitory schemes superimposed onto the Hubel and Wiesel excitatory bias. The most robust scheme and the one in agreement with both anatomy and physiology is a local inhibition (iso-orientation inhibition) in addition to a homogeneous inhibition extending over 500 μm (circular inhibition; every cortical cell receives inhibition from cells on an annulus with this radius). 3.) Spontaneous direction selectivity emerges from our mixed excitatory-inhibitory wiring scheme, although we did not specifically include asymmetric inhibitory connections. We showed that this is caused by inherent asymmetries due to the mapping of periodic orientation columns onto the 2-D cortical surface (Wörgötter et al, 1992).

We further investigated this last point using analytical methods. The effects we observed in our large-scale simulations result from the *interaction* between intracortical interactions and the underlying column structure which is generated by geniculate afferents. In order to gain a deeper understanding of these phenomena, we stripped the

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cortical cells of all their spatio-temporal properties with the exception of their orientation selectivity and arranged them according to simple column structures. For straight orientation columns we could then compute analytically the sharpening of the orientation selectivity which results from the proposed intracortical interaction scheme. This proved the effectiveness of the proposed circular inhibition scheme. Although straight orientation columns are an oversimplification, the results hold for more realistic artificial systems and also for experimentally observed cortical column structures (Niebur and Wörgötter, 1990a,b).

Temporal Dynamics of Interacting Neuronal Populations

We have been greatly intrigued by the experimental findings of 30-70 Hz, stimulus-induced, semi-synchronous neuronal oscillations in the visual cortex of cats. Particularly noteworthy is the fact that neurons up to 10 mm away can oscillate synchronously, with no detectable phase-shift, if stimulated by a single object in coherent motion. Given the great relevance we attach to synchronously firing neuronal populations (see Crick and Koch, 1990 and below), we investigated the ability of various networks of oscillating neurons to rapidly phase-lock to each other. We first explored the phase coupling in two "extreme" types of networks: nearest-neighbor coupling and global feedback where every cell communicates with every other cell through a central "comparator" node (Kammen, Holmes and Koch, 1990).

This model led directly to studies of more realistic two-dimensional networks: we used a CM-2 Connection Machine to simulate a 128 by 128 grid of 16,384 cells under a variety of stimulation patterns (Niebur, Kammen & Koch, 1991). To explore phase locking between extended or spatially separated groups of cells, we stimulated the network with a series of "bars" that receive similar input. To simulate biologically observed connection schemes, we first connected each cell to all of its neighbors within a given distance by a synapse whose strength is a Gaussian function of the distance between the cells. We then modified the Gaussian scheme by deleting nearly 99% of the connections, but setting the remaining 1% to equal weight, and discovered that locking and phase coherence was dramatically improved (Niebur et al 1991b). This always involved large parts of the system and therefore it is a plausible mechanism for long-range, complete synchronization. We showed analytically and numerically that the development of long-range synchronicity is a general property of dynamical systems consisting of sparsely connected oscillators (Niebur et al, 1991a). On the other hand, much of the local information is destroyed by this process and therefore tasks like figure-ground segregation (which have been put forward as a possible function of these oscillations) seem to require relatively localized connections, as the Gaussian connectivity scheme provides. Our results suggest that long-range synchronization of neural activity, as is observed in the neurophysiological recordings, is likely to be subserved by pathways of quite spare yet long-range connections. Recent studies of cortical microcircuitry indicate that while the majority of connections are locally dense, or Gaussian, there does exist a small population of pyramidal cells with long axons that make contacts on cells up to 3 mm away. Our simulation results therefore find a role for both kinds of connections.

Transmission of information in the cortex is subject to considerable time delays (from a minimum of about 1 *ms* to many *ms*) between the time an action potential is generated in the sending cell and the time it has an effect on the receiving cell. Although this delay, which is due to the finite propagation velocity along nerve processes and to the finite transmission time across chemical synapses, is usually significantly smaller than the period of the 40 Hz oscillations, it is certainly not negligible and we set out to explore the consequences of small delays on coupled oscillations in cortical systems. We used again

systems of 16,384 oscillators simulated on the Connection Machine CM-2, this time interacting by nearest neighbor connections. We found two surprising results: 1) even if the delays are small compared to the average period of the oscillators, the average frequency of the system is lowered considerably in the case of strong interactions (which is the case we are interested in), and 2) for larger delays, the system has numerous metastable states with higher frequencies besides the one stable state with low frequency. We then developed an analytical model of the system and verified that both effects can be understood in this model (Niebur, Schuster & Kammen 1991, 1992).

While the 30-70 Hz oscillations have been unambiguously established in cat cortex, their existence is more controversial in the cortex of the awake and behaving macaque monkey. Thus, it is all the more rewarding that we have been recently able to show that in a cortical network based on the canonical microcircuit of Douglas and Martin, strong "burst" synchronization can occur without oscillating neurons (Koch and Schuster, 1992; Schuster and Koch, 1992). The network consists of all-to-all excitatory coupled binary neurons with global inhibition. We prove rigorously that for random input signals, the output of the network consists of synchronized bursts with apparently random intermissions of noisy activity. Our results imply that synchronous bursts can be generated by a simple neuronal architecture which amplifies incoming coincident signals. This synchronization process is accompanied by dampened oscillations which, by themselves do not play any constructive role in this and can therefore be considered to be an epiphenomenon.

The neuronal basis of visual awareness

We published several papers (Crick and Koch, 1990, 1991; Koch and Crick, 1991) that outline a testable, neurobiological theory of consciousness. In particular, we suggest that visual awareness is a favorable form of consciousness to study neurobiologically. We propose that it takes two forms: a very fast form, linked to iconic memory, that may be difficult to study; plus a somewhat slower one involving visual attention and short-term memory. In the slower form an attentional mechanism transiently binds together all those neurons whose activity relates to the relevant features of a single visual object. The neuronal correlate of binding is temporal synchrony of firing; i.e. all neurons that code for different attributes of the same object fire synchronously. This synchronous firing may involve oscillatory neuronal activity in the 40-70 Hz range. The synchronous firing then activates a transient short-term (working) memory (for a short and succinct summary of this see Koch and Crick, 1991).

Future Research

We are pursuing these ideas at several levels. In a joint collaboration with Prof. Bill Newsome at Stanford University Medical School, we are analyzing the temporal dynamics of single and multi-unit recordings from extrastriate visual cortex in the awake and behaving macaque monkey using various statistical techniques. The aim is to relate the fine structure of temporal firing (e.g. 40 Hz oscillator activity, bursting, synchronized activity) to the known and measured behavior of the monkey (Bair, Koch, Newsome and Britten, 1992).
Our models of geniculate and visual cortex are becoming more refined. In collaboration with Drs. Kevan Martin and Rodney Douglas from Oxford University (R.D. spends 3 months each year in our laboratory at Caltech), we are elaborating on our earlier detailed models of cat cortex, by using more realistic single cells models and the more detailed knowledge of cortical mircocircuit that is now available. Again, one aim here is to study

and understand in more detail the onset and development of temporal correlation among neurons (Suarez, Douglas and Koch, 1992).

To what extent is the temporal structure of neuronal firing involved in attentional gating in higher cortical areas? We are pursuing this issue by constructing a detailed model of the cortical and subcortical structures underlying selective visual attention in primates (pulvinar, colliculus, V1, V2, V4, infero-temporal cortex, parietal cortex, etc.) and replicating the classical experiments of Moran and Desimone (1985). The performance of such a firmly neuronal based model must also, however, be in agreement with the extensive psychophysical literature on the effects of attention (e.g. "serial" versus "parallel" search; effortless segregation of certain textures and patterns; see the work by Julesz, Treisman, and Posner).

Thus, the three strands of the research funded by AFOSR under this grant are coming together in our ongoing and future efforts to understand at the neurobiological level how attentional gating of visual information occurs in the visual pathways of monkeys and humans and, ultimately, how perception and awareness is expressed at the level of neuronal firing. This, of course, is the principal topic of our current research proposal.

Publications

The following is a list of all papers and book chapters, explicitly acknowledging support from AFOSR, which appeared over the last two years or are still in press. Abstracts are not cited. This list includes 12 publications in refereed journals as well as 14 chapters in edited books and conference proceedings.

Refereed Journals

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Koch, C. and Crick, F. (1991) "Understanding awareness at the neuronal level," Behavioral and Brain Sciences 14: 683-684.

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