Active Sensing – Closing Multiple Loops*

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In this contribution, it is argued that the prevailing view of the sensory system as an intricate, but passive processor of external information does not capture the full complexity of brain performance. Instead, we try to reinforce a notion that sees the brain as a system embedded within the environment and actively exploring it. We will attempt to emphasize the bidirectional interaction between brain and environment at all levels of processing and at different scales of the system description. This modified approach to the understanding of the brain has profound consequences for experimental investigations, starting with the experimental design and extending into data analysis and interpretation.

Introduction

Looking for a description of the visual system in one of the most widely distributed (and excellent) textbooks on the neurosciences (Kandel *et al.*, 1991) yields a typical sequence of chapters starting with phototransduction, information processing in the retina, the lateral geniculate nucleus, primary visual cortex and then a flood of higher cortical areas. Such a sequence seems to be a useful introduction to the subject; however, the consecutive alignment of areas has several additional implications.

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* This paper was written as a contribution to the workshop on "Natural Organisms, Artificial Organisms, and Their Brains" in Bielefeld (Germany) at the Zentrum für interdisziplinäre Forschung (ZiF) on March 8–12, 1998, in order to encourage fruitful interactions and lively discussions. We are well aware that the truth is more often than not found between the extreme viewpoints. Still, for the sake of clarity and the intended purpose of this paper we describe an extreme view to emphasize aspects that might have been neglected in current research. Furthermore, for the same reasons and the sake of brevity, we do not delve into technical details, which might be worth consideration, but try to keep an informal style. The only apology for that negligence is our hope, that the group report, summarizing the resultant discussions, will give a more balanced view and deal with a detailed evaluation of all arguments when necessary.

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First, the sequence of brain structures is often associated with a one way street – feed forward type – of interactions. For example, the neuronal activity observed in the lateral geniculate nucleus is dominated by the retinal afferents and not by cortical activity. In turn, neurons in the lateral geniculate nucleus dominate the activity in primary visual cortex, but have no influence on the activity of ganglion cells in the retina. Thus, the sequence of brain structures mentioned is usually mapped on a hierarchy, where each level decisively influences subsequent but not preceding levels; i.e., it is a clear-cut example of feed forward processing. Furthermore, the interaction of the brain with the environment appears as one big loop that starts in the distal sensory system, takes the route through the central sensory systems, and finally converges onto the motor areas to generate the muscle activity involved in the appropriate behavior. Moreover, this introduction neglects the multitude of visual pathways originating in the retina, therefore giving the impression that the elements described are sufficient for visual processing.

Second, this view implies that the information that is contained in the external stimuli is passively processed by the brain. As the input stage, e.g., the retinal image, dominates the dynamics at later stages, it decisively shapes the distribution of activity in higher subcortical and cortical areas. This in turn means that the later stages of the visual image "represent" the input stimulus like an internal

copy of the outside world. Many investigators – including the authors – address the structure and properties of these representations, such as the groups of neurons involved, their specific properties and connections, the faithfulness of the representation, and so on. These investigations treat the sensory systems as machines designed to build faithful internal representations of the external environment. Only in recent years, research has started on the active processes of the brain involved in, e.g., decision-making and attention.

In our contribution, we want to argue that these two specific aspects of the commonly held view prohibit to capture the full complexity of processes in the brain at the system level. We will try to compile some arguments why the brain should be understood as a system embedded within the environment with bidirectional interactions at multiple levels and, furthermore, actively exploring it. However, we do not want to build a man of straw, the better to burn, but we will first compile several good reasons for the wide acceptance of this view of neuronal processing, and then give these reasons a second thought.

Ten Good Reasons for the Classical View

(1) The purpose of feedback projections is rather elusive

The existence of feedback connections within the sensory systems has been known for a long time. Often, they do outnumber the feed forward projections by a large margin. This puzzling fact has prompted many experiments and some subtle effects have been found (e.g. addressing cortico-thalamic feedback see Murphy and Sillito, (1987); Gulyas et al., 1990; McClurkin et al., 1994; Funke et al., 1996). Furthermore, in a comparative study of the effects of physiological effects of feed forward vs. feedback projections, the former were found to exert a larger influence as expected from the anatomically defined projection strength, whereas the latter had a smaller influence compared to the expectations based on anatomy (Vanduffel et al., 1997). Thus, the general purpose of these feedback connections has remained elusive for many years, and no generally accepted theory of their function has been put forward (Koch, 1987; Mumford, 1991).

(2) The eyes act like cameras, not like flashlights

The transduction process in the retina, converting external stimuli into the universal language of the brain, action potentials, is very complex and unidirectional (Jacobs, 1996). Thus, already this crucial first step in the processing hierarchy is "feed forward".

(3) The complexity of receptive fields increases in the hierarchy

Response properties of neurons in the visual pathway are characterized by "receptive fields" (Hubel and Wiesel, 1962). They can be understood like complex filters and allow, knowing the external stimulus, to predict the mean firing activity of the respective neuron. The complexity of receptive fields increases along the visual pathway, suggesting that the more complex receptive fields are build by integrating afferent (feed forward) activity from neurons with simpler receptive fields (Ferster, 1986; Ferster et al., 1996; Hubel, 1996). Again, this leaves no obvious function for the intrinsic and feedback connections.

(4) Response latencies increase within the hierarchy

Neurons in the visual system do not respond instantaneously to the presentation of a visual stimulus, but time in the order of several dozens of milliseconds passes, before the activity of neurons with suitable receptive fields is affected. This latency increases for neurons higher up in the hierarchy (Maunsell and Gibson, 1992; Munk et al., 1995; Nowak et al., 1995). Thus, it seems that neurons at later stages are activated too late to influence response properties of neurons in earlier stages, once again arguing against feedback contributions.

(5) Feed forward projections are more specific than feedback projections

Within several cortical areas, histochemical visualization of cytochrome-oxidase activity labels several different compartments (Wong-Riley, 1989). The response properties of neurons are more similar within one type of compartment and differ between the compartments (Hubel and Livingstone, 1987). Moreover, feed forward connections seem to be more specific with respect to axonal terminal fields in these subdivisions than the feedback pro-

jections (Livingstone and Hubel, 1987; Roe and Ts'o, 1995; Salin and Bullier, 1995). As it is plausible that the more specific wiring serves a more specific purpose, feed forward connections will dominate the dynamics for the processing of stimuli.

(6) Top-down equals slow-down?

If feedback connections are involved in the generation of highly specific response properties of neurons in the highest levels of the hierarchy of visual areas, more synapses have to be traversed before those relevant neurons are appropriately activated. In this respect, the occurrence of specific responses in temporal cortex after very short latencies puts severe constraints onto any theory involving feedback projections (Oram and Perrett, 1992, 1994).

(7) Building faithful representations of the external world

Understanding the properties of neurons in the visual system in terms of a representation of the outside world has been highly successful. The concept of a receptive field does not only predict the activity of a neuron in response to the external stimulus, but allows as well to draw conclusions about the external stimulus, knowing the neuronal activation and its receptive field properties (e.g. Lehky and Sejnowski, 1990). Thus, as most of the variance of neuronal properties can be explained by the external stimulus, this leaves little room for internal dynamics and top-down processing. It can even be argued that the faithful representation of the external world, without unnecessary distortions, is a primary goal of the visual system.

(8) Objectivism

Communication in the sciences requires a common base, fostering the objectivistic viewpoint and, by the same token, the predefined objective existence of the outside world. Competitive constructivist ideas have been widely discussed, but have had limited impact on the design and conduct of experiments in the neurosciences (Engel and König, 1993).

(9) The computer metaphor

Paying tribute to the astonishing complexity of the brain and the amazing performance of animals, the brain has been compared to the, under certain assumptions, most powerful computing device possible, the turing machine. As everyday computers are viewed as an instantiation of such a theoretical device – with a few practical limitations – the comparison is shortened to the computer metaphor: Is the brain a computer? As typical computers are not sensing or acting in the world, but relate symbolic input to symbolic output, the aspect that the brain is situated within a body is easy to forget. As a consequence, the performance of the brain is reduced to "just" computing and extracting information from external stimuli. There is no need to deal with the internal life of the brain and a possible influence of internal states onto early sensory processing via top-down interactions.

(10) Never change a winning team

Last but not least, the classical view has been highly successful. We started out citing a well known and very good text book. A large part of the knowledge available in the Neurosciences today is related in one way or another to the classical view and has tremendous explanatory power. So, why change a winning team?

What Can Feedback/Top-Down Interactions Be Good for?

Given the reasoning above, it is easy to discard the significance of top-down interactions by feedback projections. However, those connections exist, and their number is large. Therefore, we like to give the arguments compiled above a second thought and show that they do not stick as precisely as it appears.

(1) The effect of feedback projections on the mean firing activity

The effect of feedback projections has been intensively studied in several sensory systems. In the auditory thalamus of bats, recent work indicates that the frequency tuning of neurons (the equivalent of the receptive field) is subject to cortical influence (Zhang et al., 1997). Although comparable evidence is still lacking in the visual system, it

seems that even fundamental properties like frequency tuning or receptive fields of neurons at the level of the thalamus can be influenced by later stages.

(2) The effect of feedback projections on the temporal structure of neuronal activity

Early investigations of the function of the corticothalamic projection concentrated on effects on the mean firing activity. The rising interest in the dynamics of neuronal activity (König and Engel, 1995) led to new experimental designs that investigated the effect of feedback connections onto the temporal structure of neuronal activity. With respect to the corticothalamic projection, an influence on the precise timing and the synchronization of different neurons at the thalamic level has been demonstrated (Sillito et al., 1994; Funke et al., 1996; Neuenschwander and Singer, 1996). These experiments suggest that the qualitative effect of feed forward and feedback projections is different. While the former primarily influences the activity level of neurons, the latter acts on the temporal structure of activity. Thus, concentrating on any one kind of effect does only yield a unidirectional interaction between different levels, which does not describe the dynamics of the system.

(3) Complex properties of receptive fields of neurons in early visual areas

In recent years, a surge of investigations into non-classical receptive fields has revealed a multitude of effects, e.g., responses of neurons to subjective contours (von der Heydt et al., 1984). Specific responses to such stimuli can already be observed in the primary visual cortex, making a strong argument that they are not constructed by feed forward connections (Grosof et al., 1993). Furthermore, in theoretical investigations "reentrant" feedback connections can mediate invariant responses on the level of early visual areas (Finkel and Edelman, 1989). Thus, the dominance of the feed forward projections is partly due to the concentration onto the "classical receptive field", and as soon as more general stimuli are investigated, the function of feedback projections is readily observable.

(4) Ears act like microphones and like loudspeakers

As we have described for the retina, sensory transduction seems to be a passive and feed-forward process. However, for other sensory modalities, transduction at the level of the sensory epithelia is not a unidirectional process. In the auditory system, the discovery of the Kemp-echo and, subsequently, of spontaneous oto-acoustic emissions has initiated an active field of research (de Boer, 1980; Zurek, 1981; Zwicker and Schloth, 1984; van Dijk and Wit, 1987; Kemp et al., 1990). This has lead to the insight that, in the inner ear, not only a transduction from mechanical oscillations to electrical signals occurs, but that the reverse process takes place as well and is of great importance for the function of the cochlea (Hudspeth, 1997). In non-mammalian vertebrates, centrifugal efferents to the retina innervate association amacrines and modulate the retinal response (Uchiyama and Barlow, 1993; Woodson et al., 1995; Clarke et al., 1996). Thus, even at the very first stages of sensory processing, bidirectional interactions are observed.

(5) An asymmetry in the experimental setup

There are several constraints to most experimental paradigms that favor the analysis of feed forward interactions. First, it is much easier to manipulate external stimuli as compared to manipulations of the internal dynamics of the system itself. Second, communication in the sciences requires precise definitions of experimental procedures, e.g., stimulation parameters. Third, most approaches attempt to isolate specific aspects or steps in a network where the complexity of processing might indeed be reduced to feed forward interactions.

Thus, experimental design has introduced a bias to observe changes in neuronal dynamics due to variations of external stimuli. Breaking down a network to approachable units does not allow to study network dynamics such as those introduced by feedback interactions. The necessity to define objective stimulus criteria has led most researchers to disregard internal states, as feedback influences on all stages of processing would not allow to characterize the stimulus precisely. Moreover, the internal state of the system is usually far too com-

plex to be controlled at all. As most early experiments have worked on anesthetized animals, the variability of neuronal responses induced by different internal states could be neglected; however, this does not lead to an appropriate description of a behaving animal.

(6) A selective view of the world or: there is more to vision than the geniculocortical pathway.

The sampling of external stimuli by the visual system is rather incomplete. For example, the spatial acuity of the retina is high only at the central two degrees and drops off dramatically with increasing eccentricity (Perry and Cowey, 1985). To construct the apparently complete image of the environment, a complex interplay with several subcortical systems dedicated to eye positioning is required. It is well known that a major structure for the control of eye movements is the midbrain superior colliculus, that receives a strong retinal projection. Bidirectional interactions between the superior colliculus and the cortex are of great importance, as the decision where to direct one's gaze (and visual attention) is elementary for survival and depends on both visual stimuli and the internal state of the system (Stein et al., 1995). Moreover, the superior colliculus projects to the pulvinar, the largest (!) thalamic nucleus in humans, that itself gives rise to widespread cortical projections (Cowey and Stoerig, 1993; Levitt et al., 1995; Romanski et al., 1997). Interactions of the colliculo-pulvino-cortical and the geniculo-cortical pathway have been demonstrated on various levels; well-known examples are blindsight (Cowey and Stoerig, 1995; Weiskrantz, 1996) and paradoxical functional facilitations like, e.g., the Sprague effect (Sprague, 1991; Kapur, 1996). These complex and still poorly understood phenomena strongly argue against a one-way flow of information along the geniculo-cortical pathway. Comparative studies corroborate the importance of the non-geniculate projections to the telencephalon: In many vertebrates, the contribution of the geniculocortical system to visual processing is rather weak compared to the colliculo-pulvino-cortical projection (Hodos and Karten, 1974; Kertzmann and Hodos, 1984; Engelage and Bischof, 1993). As the visual capacities of many of these vertebrates often rival those of primates, the contribution of these systems should not be underestimated.

(7) Coactivation of large parts of the visual system

Although there is a general trend of increasing response latencies along the hierarchy of the visual system, a detailed examination reveals a more complicated picture. First, latencies differ tremendously between different subsystems, even within the geniculo-cortical pathway. In particular, responses of neurons in the magnocellular pathway are more than 10 ms shorter than those of neurons in the parvocellular pathway at comparable levels (Munk et al., 1995). Thus, afferent signals via the magnocellular pathway relayed in V2 might reach neurons of the parvocellular pathway in V1 before the thalamic feed forward input. Furthermore, the spread of response latencies within one population of neurons is large compared to the differences in latency of the fastest responding neurons in different areas (Dinse and Krüger, 1994). Thus, for most of the time between stimulus presentation and response of the subject, neurons in the visual system are simultaneously active. In addition, the whole issue of latencies along the visual pathway is rendered less significant if we consider the continuity of visual processing in a behaving animal. The visual system is usually engaged in continuous analysis of the environment, leading to permanent activation of areas higher up in the hierarchy and, thus, to a "dynamic equilibrium" between feed forward and feedback interactions.

(8) Latencies are not identical to relative timing

Latency measurements investigate the temporal relation of neuronal activity with respect to an external stimulus. This does not allow conclusions regarding the relative timing of activity of different neurons within the visual pathway. Indeed, simultaneous recordings in several areas on different levels of the hierarchy of the visual system found precisely correlated activity of neurons without phaselag (Engel et al., 1991; Frien et al., 1994). Thus, measurements on a millisecond timescale do not support the view that neurons at lower levels of the hierarchy fire prior to the neurons at subsequent levels.

(9) Speedup by top-down interactions

In many studies of detection or categorization by neuronal networks, the set of input stimuli

tested is rather limited. The network under investigation can therefore be very much specialized for the task at hand and display only a limited set of flexibility. Actually, in many experiments on awake behaving animals, stereotyped responses after many weeks and month of training are investigated. This experimental paradigm is highly artificial and may introduce inadvertent effects like, e.g., priming. In the psychological literature, a large abundance of priming effects like cross-modal and semantic priming has been reported (Tulving and Schacter, 1990; Ochsner *et al.*, 1994). Priming effects are supposed to exert a top-down influence via feedback connections. Thus, the observed extremely short reaction times in highly trained tasks might not constrain the available time for top-down interactions, but actually be a consequence of the feedback projections.

(10) Information is in the eye of the beholder

In recent years an information theoretical approach to the processing of stimuli has become fashionable. The concept of information, though, requires the complete set of allowed signals (i.e., stimuli or objects) to be predefined. However, the situation for a behaving animal in its natural environment is much more complex. It has to define its own relevant set of stimuli, ranging from neutral objects over food and mates to predators. There is no such thing as an invariant "information content" in a stimulus; rather, the relevance of a stimulus is defined by complex interactions between internal determinants of the organism, including its life history, and the physical characteristics of a stimulus. Thus, the categorization of input stimuli performed by the nervous system is actually dependent on the – changing – needs of the animal (Orban *et al.*, 1996).

In a more general context, the notion of brains as information processing devices turns out to be misleading. Brains are not primarily designed to give faithful representations of the environment, but to ensure survival of their bearers and their genes. In many systems, this does indeed lead to a faithful representation of the environment, but this is not necessarily so. To accomplish survival, a multitude of neuronal mechanisms and designs has evolved that may be far away from processing "objective" parameters of the world.

Conclusions

In conclusion, we think that it is worthwhile to consider the effects of feedback interactions and internal states for the processing of sensory evoked excitation. The analysis of feed forward processing in brains has tremendous explanatory power for many systems and has now opened up the field for research on the more complex interactions. For many systems, the classical approach might still be a sufficient level of description. However, to capture and understand the full complexity of brain performance, organisms should not be regarded as information processing devices, but rather as actively exploring subjects that adapt the neuronal analysis of their environment according to their needs and their life history. Feedback interactions are one mechanism that aids in achieving this adequate processing.

Neglecting the close interaction of the animal with its environment would neglect essential aspects of their fascinating behavior and amazing performance (Chiel and Beer, 1997). Taken together, we think that it is not a question of changing a winning team – it is rather a question to start a successful team on a new ball game.

Chiel H. J. and Beer R. D. (1997), The brain has a body: adaptive behavior emerges from interactions of nervous system, body and environment. Trends Neurosci. **20**, 553–557.

Clarke G. H. Gyger M. and Catsicas S. (1996), A centrifugally controlled circuit in the avian retina and its possible role in visual attention switching. Vis. Neurosci. **13**, 1043 -1048.

Cowey A. and Stoerig P. (1993), The neurobiology of blindsight. Trends Neurosci. **14**, 140–145.

Cowey A. and Stoerig P. (1995), Blindsight in monkeys. Nature **373**, 247–249.

de Boer E. (1980), Nonlinear interactions and the 'Kemp echo'. Hear. Res. **2**, 519–526.

Dinse H. R. and Krüger K. (1994), The timing of processing along the visual pathway in the cat. Neuroreport **5**, 893–897.

Engel A. K., Kreiter A. K., König P. and Singer W. (1991), Synchronization of oscillatory neuronal responses between striate and extrastriate visual cortical areas of the cat. Proc. Natl. Acad. Sci. USA **88**, 6048–6052.

Engel A. K. and König P. (1993), Paradigm shifts in neurobiology: towards a new theory of perception. In: Philosophy and the Cognitive Sciences (R. Casati and G. White, eds.). Wittgenstein-Gesellschaft, Kirchberg, pp. 131–138.

Engelage H. and Bischof H. J. (1993), Anatomy of the avian tectofugal pathway. In: Vision, Brain and Behavior in Birds (H. P. Zeigler and H. J. Bischof, eds.). MIT Press, pp. 136–154.

Ferster D. (1986), Orientation selectivity of synaptic potentials in neurons of cat primary visual cortex. J. Neurosci **6**, 1284–1301.

Ferster D., Chung S. and Wheat H. (1996), Orientation selectivity of thalamic input to simple cells of cat visual cortex. Nature **380**, 249–252.

Finkel L. H. and Edelman G. M. (1989), Integration of distributed cortical systems by reentry: a computer simulation of interactive functionally segregated visual areas. J. Neurosci. **9**, 3188–3208.

Frien A., Eckhorn R., Bauer R., Woelbern T. and Kehr H. (1994), Stimulus-Specific fast oscillations at zero phase between visual areas V1 and V2 of awake monkey. Neuroreport **5**, 2273–2277.

Funke K., Nelle E., Li B. and Wörgötter F. (1996), Corticofugal feedback improves the timing of retino-geniculate signal transmission. Neuroreport **7**, 2130–2134.

Grosof D. H., Shapley R. M. and Hawken M. J. (1993), Macaque V1 neurons can signal 'illusory' contours. Nature **365**, 550–552.

Gulyas B., Lagae L., Eysel U. T. and Orban G. A. (1990), Corticofugal feedback influences the responses of geniculate neurons to moving stimuli. Exp. Brain Res. **79**, 441–446.

Hodos W. and Karten H. J. (1974), Visual intensity and pattern discrimination deficits after lesions of the optic lobe in pigeons. Brain Behav. Evol. **9**, 165–194.

Hubel D. H. (1996), A big step along the visual pathway. Nature **380**, 197–198.

Hubel D. H. and Livingstone M. S. (1987), Segregation of form, color, and stereopsis in primate area 18. J. Neurosci. **7**, 3378–3415.

Hubel D. H. and Wiesel T. N. (1962), Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. J. Physiol. **160**, 106–154.

Hudspeth A. (1997), Mechanical amplification of stimuli by hair cells. Curr. Opin. Neurobiol. **7**, 480–486.

Jacobs G. H. (1996), Primate photopigments and primate color vision. Proc. Natl. Acad. Sci. U S A **93**, 577–581.

Kandel E. R., Schwartz J. H. and Jessell T. M. (1991), Principles of Neural Science. Third Edition. Appleton & Lange, Norwalk, Connecticut.

Kapur N. (1996), Paradoxical functional facilitation in brain-behaviour research. A critical review. Brain **119**, 1775–1790.

Kemp D. T., Ryan S. and Bray P. (1990), A guide to the effective use of otoacoustic emissions. Ear Hear. **11**, 93–105.

Kertzman C. and Hodos W. (1984), Near field acuity after visual system lesions in pigeons. I: Thalamus. Behav. Brain Res. **13**, 1–14.

Koch C. (1987), The action of the corticofugal pathway on sensory thalamic muclei: a hypothesis. Neuroscience **23**, 399–406.

König P. and Engel A. K. (1994), Kommentar zur Relevanz von konnektionistischen Modellen in der Computational Neuroscience. In: Künstliche neuronale Netze: Eine Bestandsaufnahme (K. Möller , G. Paaß, Hrsg). KI 4/1994: 44–46.

König, P. and Engel A. K. (1995), Correlated firing in sensorimotor systems. Curr. Opin. Neurobiol. **5**, 511–519.

Lehky S. R. and Sejnowski T. J. (1990), Neural model of stereoacuity and depth interpolation based on a distributed representation of stereo disparity. J. Neurosci. **10**, 2281–2299.

Levitt J. B., Yoshioka, T. and Lund J. S. (1995), Connections between the pulvinar complex and cytochrome oxidase-defined compartments in visual area V2 of macaque monkey. Exp. Brain Res. **104**, 419–430.

Livingstone M. S. and Hubel D. H. (1987), Connections between layer 4B of area 17 and the thick cytochrome oxidase stripes of area 18 in the squirrel monkey. J. Neurosci. **7**, 3371–3377.

Maunsell J. H. R. and Gibson J. R. (1992), Visual response latencies in striate cortex of the macaque monkey. J. Neurophysiol. **68**, 1332–1344.

McClurkin J. W., Optican L. M. and Richmond B. J. (1994), Cortical feedback increases visual information transmitted by monkey parvocellular lateral geniculate nucleus neurons. Visual Neurosci. **11**, 601–617.

Mumford D. (1991), On the computational architecture of the neocortex. I. The role of the thalamo-cortical loop. Biol. Cybern. **65**, 135–145.

Munk M. H. J., Nowak L. G., Girard P., Chounlamountri N. and Bullier J. (1995), Visual latencies in cytochrome oxidase bands of macaque area V2. Proc. Natl. Acad. Sci. USA **92**, 988–992.

Murphy P. C. and Sillito A. M. (1987), Corticofugal feedback influences the generation of length tuning in the visual pathway. Nature **329**, 727–729.

Neuenschwander S. and Singer W. (1996), Long-range synchronization of oscillatory light responses in the cat retina and lateral geniculate nucleus. Nature **379**, 728–733.

Nowak L. G., Munk M. H. J., Girard P. and Bullier J. (1995), Visual latencies in areas V1 and V2 of the macaque monkey. Visual Neurosci. **12**, 371–384.

Ochsner K. N., Chiu C. Y. and Schacter D. L. (1994), Varieties of priming. Curr. Opin. Neurobiol. **4**, 189–194.

Oram M. W. and Perrett D. I. (1992), Time course of neural responses discriminating different views of the face and head. J. Neurophysiol. **68**, 70–84.

Oram M. W. and Perrett D. I. (1994), Modeling visual recognition from neurobiological constraints. Neural Networks **7**, 945–972.

Orban G. A., Dupont P., Vogels R., De Bruyn B., Bormans G. and Mortelmans L. (1996), Task dependency of visual processing in the human visual system. Behav. Brain Res. **76**, 215–223.

Perry V. H. and Cowey A. (1985), The ganglion cell and cone distributions in the monkey's retina: implications for central magnification factors. Vision Res. **25**, 1795–1810.

Raiguel S. E., Lagae L., Gulyás B. and Orban G. A. (1989), Response latencies of visual cell in macaque areas V1, V2 and V5. Brain Res. **493**, 155–159.

Roe A. W. and Ts'o D. Y. (1995), Visual topography in primate V2: multiple representation across functional stripes. J. Neurosci. **15**, 3689–3715.

Romanski L. M., Giguere M., Bates J. F. and Goldman-Rakic P. S. (1997), Topographic organization of medial pulvinar connections with the prefrontal cortex in the rhesus monkey. J. Comp. Neurol. **379**, 313–332.

Salin P.-A. and Bullier J. (1995), Corticocortical connections in the visual system: structure and function. Physiol. Rev. **75**, 107–154.

Sillito A. M., Jones H. E., Gerstein G. L. and West D. C. (1994), Feature-linked synchronization of thalamic relay cell firing induced by feedback from the visual cortex. Nature **369**, 479–482.

Sprague J. M. (1991), The role of the superior colliculus in facilitating visual attention and form perception. Proc. Natl. Acad. Sci. USA **88**, 1286–1290.

Stein B. E., Wallace M. T. and Meredith M. A. (1995), Neural mechanisms mediating attention and orientation to multisensory cues. In: Cognitive Neurosciences (Gazzaniga, M. S., ed.). MIT Press, Cambridge, MA, pp. 683–702.

Tulving E. and Schacter D. L. (1990), Priming and human memory systems. Science **247**, 301–306.

Uchiyama H. and Barlow R. B. (1994), Centrifugal inputs enhance responses of retinal ganglion cells in the japanese quail without changing their spatial coding properties. Vision Res. **34**, 2189-2194.

van Dijk P. and Wit H. P. (1987), The occurrence of click-evoked oto-acoustic emissions ("Kemp echoes") in normal-hearing ears. Scand. Audiol. **16**, 62–64.

Vanduffel W., Payne B. R., Lomber S. G. and Orban G. A. (1997), Functional impact of cerebral connections. Proc. Natl. Acad. Sci. USA **94**, 7617–7620.

von der Heydt R., Peterhans E. and Baumgartner G. (1984), Illusory contours and cortical neuron responses. Science **224**, 1260–1262.

Weiskrantz J. (1996), Blindsight revisited. Curr. Opin. Neurobiol. **6**, 215–220.

Wong-Riley, M. T. (1989) Cytochrome oxidase: an endogenous metabolic marker for neuronal activity. Trends Neurosci **12**, 94–101.

Woodson W., Shimizu T., Wild J. M., Schimke J., Cox K. and Karten H. J. (1995), Centrifugal projections upon the retina: an anterograde tracing study in the pigeon *(Columba livia)*. J. Comp. Neurol. **362**, 489 -509.

Zhang Y., Suga N. and Yan J. (1997), Corticofugal modulation of frequency processing in bat auditory system. Nature **387**, 900–903.

Zurek P. M. (1981), Spontaneous narrowband acoustic signals emitted by human ears. J. Acoust. Soc. Am. **69**, 514–523.

Zwicker E. and Schloth E. (1984), Interrelation of different oto-acoustic emissions. J. Acoust. Soc. Am. **75**, 1148–1154.