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Time, Assemblies, and Consciousness[*]

Abstract

Cognitive functions like perception, memory, language and consciousness are based on highly parallel and distributed information-processing by the brain. One of the major unresolved questions is how information can be integrated and how coherent representational states can be established in the distributed neuronal systems subserving these functions. It has been suggested that this so-called binding problem may be solved in the temporal domain. The hypothesis is that synchronization of neuronal discharges can serve for the integration of distributed neurons into cell assemblies, and that this process may underlie the selection of perceptually and behaviourally relevant information. As this paper intends to show, this temporal binding hypothesis has implications for the search for the neural correlate of consciousness. A number of recent experimental results, mainly obtained in the visual system, support the notion of temporal binding. In particular, experiments on the neural mechanisms of binocular rivalry suggest that synchronization among cortical neurons may be one of the necessary conditions for the buildup of perceptual states and the awareness of sensory stimuli.

Introduction

This paper intends to contribute to the ongoing debate about the neural correlate(s) of consciousness from the viewpoint of a particular experimental approach: the study of distributed neuronal processing and of dynamic interactions that implement specific bindings in neural network architectures. The now-classical notion of binding and the search for potential binding mechanisms has received increasing attention during

the past decade. First introduced in the psychological discourse, the issue of binding has now advanced into the focus of research also in other disciplines within cognitive science, such as neural network modelling, the philosophy of mind and cognitive neuroscience.

In all these domains, the problem has been identified that encoding and retrieval of information in neuronal networks requires some sort of binding mechanism that allows the expression of specific relationships between elementary processors. This binding problem arises for several reasons: first, information processing underlying cognitive functions is typically distributed across many network elements and, thus, one needs to identify those neurons or network nodes that currently participate in the same cognitive process. Second, perception of and action in a complex environment usually require the parallel processing of information related to different objects or events that have to be kept apart to allow sensory segmentation and goal-directed behaviour. Thus, for example, neuronal activity pertaining to a particular object needs to be distinguished from unrelated information in order to avoid confusion and erroneous conjunctions (von der Malsburg, 1981). Third, it has been claimed that specific yet flexible binding is required within distributed activation patterns to allow the generation of syntactic structures and to account for the systematicity and productivity of cognitive processes (Fodor and Pylyshyn, 1988). Fourth, many cognitive functions imply the context-dependent selection of relevant information from a richer set of available data. It has been suggested that appropriate binding may be a prerequisite for the selection and further joint processing of subsets of information (Singer et al., 1997). These arguments suggest that cognitive functions require the implementation of binding mechanisms in the distributed networks subserving these functions.

In what follows, I want to focus on the idea that some kind of binding mechanism may also be critical for the establishment of conscious mental states. In recent years, several authors have emphasized a close link between binding and consciousness, following the intuition that consciousness requires some kind of integration, or coherence, of mental contents. Damasio (1990) has suggested that conscious recall of memory contents requires the binding of distributed information stored in spatially separate cortical areas. In various publications, Crick and Koch have discussed the idea that binding may be intimately related to the neural mechanisms of sensory awareness (Crick and Koch, 1990). According to their view, only appropriately-bound neuronal activity can enter short-term memory and, hence, become available for access to phenomenal consciousness. Llinás and coworkers (1994) have proposed that arousal and awareness require the binding of sensory information, which is imple-

mented by interactions between specific and nonspecific thalamocortical loops. Recently, Metzinger (1995) has extended this discussion by speculating that binding mechanisms might account not only for low-level properties of phenomenal consciousness like the holistic character of perceptual objects, but also for the formation of a phenomenal self-model and its embedding in a global world-model.

In the context of the present paper, discussion of the consciousness issue will be restricted to one particular aspect, namely, sensory awareness. With many authors, I share the view that sensory awareness is one of those facets of consciousness that is (probably) most easily accessible, both in terms of experimental quantification and theoretical explanation (Crick and Koch, 1990). Furthermore, there can be little doubt that we have this basic form of phenomenal consciousness in common with many other species (presumably at least with most other higher mammals). Thus, it is conceivable that research on animals can contribute substantially to explaining this aspect of consciousness, which may not hold for many higher-order features of consciousness, that require, for instance, a language system or an elaborated self-model.

There seems to be wide agreement that awareness as the basic form of phenomenal consciousness has the following prerequisites (Crick and Koch, 1990): first, generating sensory awareness seems to involve some form of attention mechanism, i.e., a mechanism that selects relevant information and enhances its impact on subsequent processing stages. Second, awareness presumably requires working memory, which allows the short-term storage of episodic contents. Third, awareness seems to presuppose the capacity for structured representation, i.e., the ability to achieve coherence in the contents of mental states and to establish specific relationships between representational items. The basic assumption made in the following is that all three capacities are, on the one hand, closely related to each other and, on the other hand, strongly dependent on binding mechanisms implemented in sensory systems. As one particular candidate for the latter, I will discuss dynamic binding by the transient and precise synchronization of neuronal discharges (Engel et al., 1997; Singer et al., 1997). As I will argue, there is now empirical evidence suggesting that temporal binding may be crucial for generating functionally efficacious representational states and for the selection of perceptually or behaviourally relevant information.

The concept of temporal binding

The concept of dynamic binding by the synchronization of neuronal discharges has been developed mainly in the context of perceptual processing. One source of inspiration for this model has come from the insight that perception, like most other cognitive functions, is based on highly parallel information-processing carried out by numerous brain areas. A paradigmatic case is provided by visual processing, which shows a highly distributed organization. In monkeys, anatomical and physiological studies have led to the identification of more than 30 distinct visual areas in the cortex (Felleman and Van Essen, 1991). This parcellation is assumed to reflect some kind of functional specialization, since neurons in each of these visual areas are, at least to some degree, selective for characteristic subsets of object features. Thus, for instance, some areas contain cells responding to the colour of objects, while others primarily process information about the form of an object or its direction of motion in the visual field. As a consequence of this functional specialization, any object present in the field of view will activate neurons in many cortical areas simultaneously. The highly complex organization of visual processing naturally raises the question of how distributed neuronal responses can be integrated, which seems necessary to enable the brain to represent and store information about the external world in a useful way.

It has been suggested that the binding problem arising in distributed sensory networks may be solved by a mechanism that exploits the temporal aspects of neuronal activity (von der Malsburg, 1981; for review, see Engel et al., 1997; Singer et al., 1997). The prediction is that neurons that respond to the same sensory object might fire their action potentials in temporal synchrony (with a precision in the millisecond range). However, no such synchronization should occur between cells that are activated by different objects appearing in sensory space (Fig. 1). Such a temporal integration mechanism would provide an elegant solution to the binding problem since, on the one hand, the synchrony would selectively tag the responses of neurons that code for the same object and, on the other hand, demarcate their responses from those of neurons activated by other objects. This highly selective temporal structure would allow the establishment of a distinct representational pattern (a so-called assembly) for each object and, thus, would enable the visual system to achieve figure-ground segregation. On the other hand, such a temporal binding mechanism could also serve to establish relationships between neuronal responses over large distances and, thus, solve the problems imposed by the anatomical segregation of specialized processing areas.
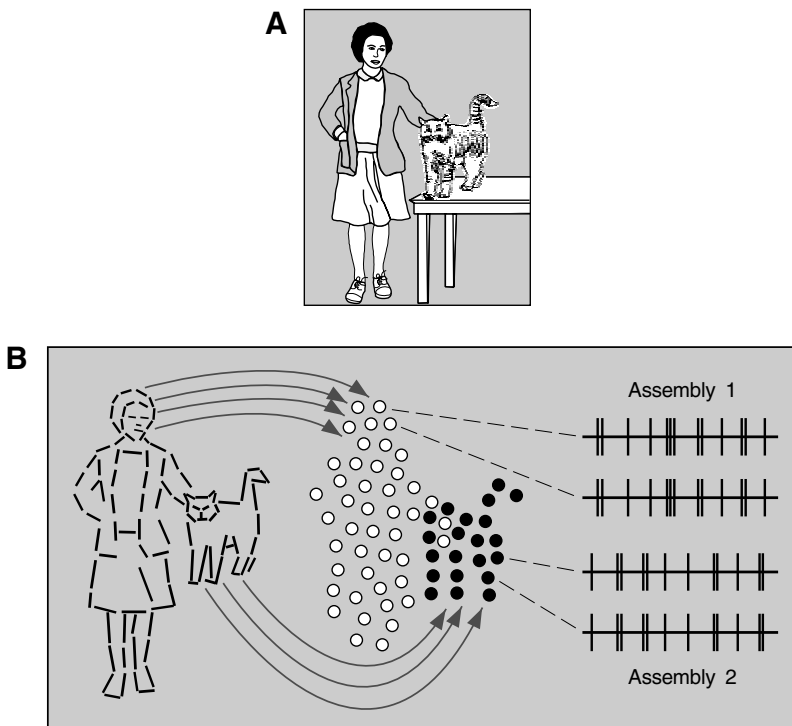
Fig. 1: Establishment of coherent representational states by temporal binding. (A) Example of a visual scene. (B) The model assumes that objects are represented in the visual cortex by assemblies of synchronously firing neurons. In this example, the lady and her cat would each be represented by one such assembly (indicated by open and filled symbols, respectively). These assemblies comprise neurons that detect specific features of visual objects (such as the orientation of contour segments) within their receptive fields (left). The relationship between the features can then be encoded by the temporal correlation among these neurons (right). The model assumes that neurons that are part of the same assembly fire in synchrony whereas no consistent temporal relation is found between cells belonging to different object representations.

This strategy of temporal binding exhibits a number of crucial advantages. First, it preserves the general advantages of distributed coding schemes such as robustness against loss of network elements and richness of representations that contain explicit information about object features and do not only signal the presence of the object (like a small set of cardinal cells would do). Second, this strategy enhances processing speed,

because binding can, in principle, occur using the very first spikes of a response (Singer et al., 1997). Third, temporal binding alleviates superposition problems that occur in conventional distributed systems that operate solely on the basis of average firing rates (von der Malsburg, 1981). The reason is that using synchrony as an additional coding dimension allows the dissociation of the binding code from the feature code (object features being signalled by firing rates). This allows the coactivation of multiple assemblies without confusion, because the temporal relationship between neuronal discharges permits the unambiguous distinction of subsets of functionally related responses. Fourth, temporal binding provides an efficient mechanism for the selection of assemblies for further processing (Singer et al., 1997), because precisely synchronized spikes constitute highly salient events that can be detected by coincidence-sensitive neurons in other brain areas (König et al., 1996).

It should be noted at this point that, although the temporal binding model has mainly been elaborated with respect to the visual modality, it can be generalized, because binding problems similar to those described here for vision have to be coped with by other systems as well. Obviously, the problem of perceptual integration merely exemplifies a much more general problem of integration that always occurs in neuronal networks operating on the basis of coarse coding and distributed representation. Since information processing in other sensory modalities and in the motor system is also highly parallel, the needs to organize and bind distributed responses are similar to those encountered in the visual system. Furthermore, information must be flexibly coordinated both across sensory modalities and between sensory and motor processes to allow adaptive behaviour of the organism. The hypothesis pursued here therefore predicts that temporal binding mechanisms should exist not only in the visual system, but in other cortical systems as well, and, moreover, that synchrony should occur between different systems.

In the present context, the most spectacular extension of the concept of temporal binding has been its application to the issue of consciousness by Crick and Koch. As already mentioned, they have argued for a close relationship between binding and sensory awareness (Crick and Koch, 1990). Beyond that, they were the first to suggest that it could be a temporal binding mechanism of the kind discussed here that is required for the establishment of awareness. Inspired by the finding that visual stimuli can elicit synchronized oscillatory activity in the visual cortex (Eckhorn et al., 1988; Gray et al., 1989), they proposed that an attention mechanism induces synchronous oscillations in selected neuronal populations and that this temporal structure would facilitate transfer of the encoded information to working memory. The provocative

scent of this hypothesis comes from the authors' implicit assumption that these are not merely necessary, but indeed sufficient conditions for the occurrence of awareness. At the time it was published, Crick and Kochs speculative proposal was not supported by experimental evidence. In the present contribution, I will discuss more recent results that suggest that temporal binding may indeed be a prerequisite for the access of information to phenomenal consciousness. However, although largely in line with the Crick and Koch hypothesis, the present data do not seem to support the conclusion that the synchronization of assemblies would constitute a sufficient condition for the production of awareness.

Physiological evidence for the functional relevance of temporal binding

By now, the synchronization phenomena predicted by the temporal binding hypothesis are well documented for a wide variety of neural systems. It is well established that neurons in both cortical and subcortical centers can synchronize their discharges with a precision in the millisecond range (for review, see Engel et al., 1997; Singer et al., 1997). This has been demonstrated in particular for the visual system, but similar observations have been made for the other sensory systems, for the motor system, and for cortical association areas. In the following, we will focus on experimental data suggesting that the observed synchrony does indeed serve the binding and selection of functionally related responses. This data has been obtained mainly in experiments on cats and monkeys, but presumably the results can be generalized to the human brain, where recent EEG and MEG studies have provided evidence for similar synchronization phenomena.

For the case of the visual system, the temporal binding model predicts a synchronization of spatially separate cells within individual visual areas to account for the integration of perceptual information across different locations in the visual field. In addition, synchrony should occur across large distances in the cortex to allow for binding between visual areas involved in the analysis of different object features. According to the temporal binding model, this would be required for the full representation of objects. Both predictions have been confirmed experimentally. In cats and monkeys (both in the anesthetized and awake preparation), synchrony has been observed within striate and extrastriate visual areas (e.g. Eckhorn et al., 1988; Gray et al., 1989; Kreiter and Singer, 1996). Moreover, it has been shown that response synchronization can extend well beyond the borders of a single visual area. Thus, for instance, correlated firing has

been observed between neurons located in different cerebral hemispheres (Engel et al., 1991a). In terms of the temporal binding hypothesis, this result is important, because interhemispheric synchrony is required to bind the features of objects extending across the midline of the visual field. In addition, temporal correlations have been studied for neurons located in different areas of the same hemisphere. Finally, recent evidence shows that synchronous firing is not confined to the cortex, but occurs also in subcortical visual structures such as the retina, the lateral geniculate nucleus and the superior colliculus (Neuenschwander and Singer, 1996; Brecht et al., 1998).

Studies in non-visual sensory modalities and in the motor system provide evidence for very similar synchronization phenomena. Synchronization is well known to occur in the olfactory system of various vertebrate and invertebrate species, where these phenomena have been related to the processing of odor information (Laurent, 1996). Moreover, in both the auditory (deCharms and Merzenich, 1996) and the somatosensory cortex (Murthy and Fetz, 1992), precise neuronal synchronization has been observed. Furthermore, neuronal interactions with a precision in the millisecond range have been described in the hippocampus (Buzsáki and Chrobak, 1995) and in the frontal cortex (Vaadia et al., 1995). Finally, similar evidence is available for the motor system, where neural synchronization has been discovered during both the preparation and the execution of movements (Murthy and Fetz, 1992).

Although the temporal binding model offers an attractive conceptual scheme for understanding the binding and selection of distributed neuronal responses, definitive evidence that the brain actually uses synchronization in exactly this way has not yet been obtained. However, a number of findings strongly suggest that the synchrony is indeed functionally relevant. One important result supporting the temporal binding model is that neuronal synchronization in the visual system depends on the stimulus configuration (Fig. 2). It was demonstrated that spatially separate cells show strong synchronization only if they respond to the same visual object. However, if responding to two independent stimuli, the cells fire in a less correlated manner or even without any fixed temporal relationship (Gray et al., 1989; Engel et al., 1991b; Kreiter and Singer, 1996). The experiments demonstrate that Gestalt criteria such as continuity or coherent motion, which have psychophysically been shown to support perceptual grouping, are important for the establishment of synchrony among neurons in the visual cortex. These data strongly support the hypothesis that correlated firing provides a dynamic mechanism which permits binding and response selection in a flexible manner.
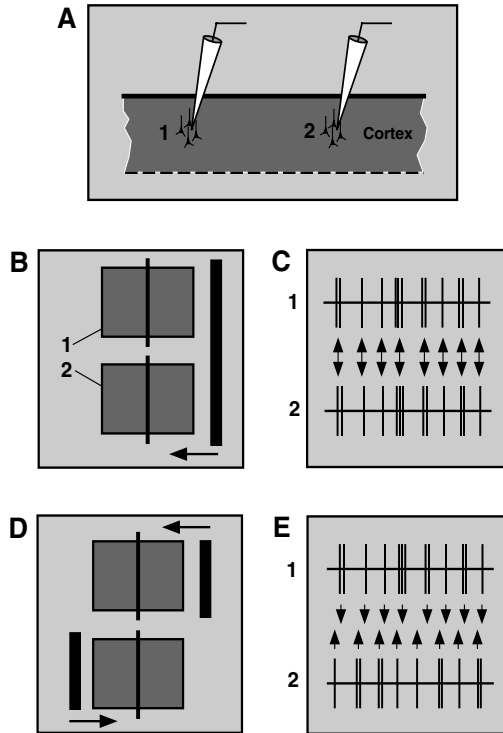
Fig. 2: Synchrony in visual cortex is dependent on the configuration of visual stimuli. (A) Typically, activity of spatially separate cell groups (1, 2) is recorded with two microelectrodes. The neurons can then be activated using different stimulus paradigms. (B, C) If a single coherent object is moved across the receptive fields (1, 2), the cells at the two recording sites are synchronously active (arrows in C). (D, E) Activation of the same neurons with two different objects moving in opposite directions does not induce synchrony (cf. offset of arrowheads in E).

Additional evidence that neuronal synchronization is indeed function-ally relevant and related to the animal's perception is provided by experi-ments on cats with convergent squint (Roelfsema et al., 1994). Subjects with this type of strabismus often use only one eye for active fixation. The non-fixating eye then develops a syndrome of perceptual deficits called strabismic amblyopia. Symptoms of strabismic amblyopia include a reduced acuity of the affected eye, temporal instability and spatial distor-tions of the visual image, and the so-called crowding phenomenon, i.e., discrimination of details is worse if other contours are nearby. Clearly, at
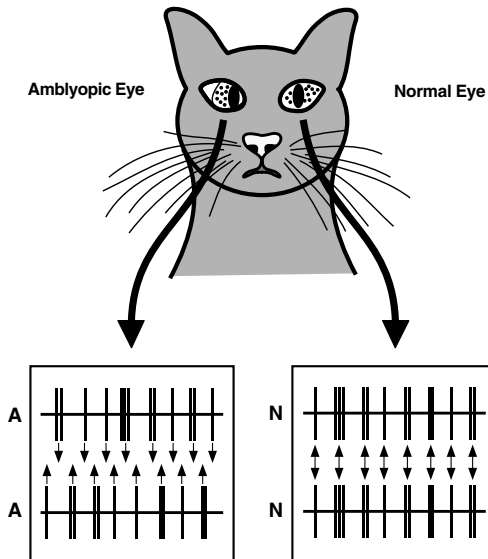
Fig. 3: Neuronal synchronization in the primary visual cortex of animals with strabismic ambylopia. Experiments were performed on cats with a convergent squint (in this case an inward deviation of the animal's right eye). The deviating eye develops a specific perceptual deficit denoted as strabismic amblyopia. The lower panel illustrates the temporal correlation between neurons driven by the amblyopic eye ("A", left) and the normal eye ("N", right), respectively. Temporal correlation is strong if both recording sites are driven by the normal eye (arrows). Synchronization is, however, much weaker or absent between cells dominated by the amblyopic eye (A).

least some of these deficits indicate a reduced capacity to integrate visual information and an impairment of the mechanisms responsible for feature binding. The results of the correlation study by Roelfsema et al. (1994) indicate that these perceptual deficits may be due to a disturbance of intracortical interactions. Thus, clear differences were observed in the synchronization of cells driven by the normal and the amblyopic eye, respectively (Fig. 3). In the primary visual cortex, responses of neurons activated through the amblyopic eye showed a much weaker correlation than the discharges of neurons driven by the normal eye. Surprisingly, however, in terms of average firing rates, the responses of neurons driven by the normal and amblyopic eye were indistinguishable. These results indicate that strabismic amblyopia is accompanied by a selective impairment of intracortical interactions that synchronize neurons responding to coherent stimuli. As mentioned above, most of the problems in amblyopic vision

result from an improper segregation of features and from the formation of false conjunctions. Therefore, the fact that the only measurable abnormality correlating with the perceptual deficit was the reduced synchronicity is in good agreement with the hypothesis that synchronization is employed for feature binding and serves to disambiguate distributed response patterns.

Evidence for a functional role of neural synchrony is also provided by recent studies of sensorimotor interactions. Synchronization between sensory and motor assemblies has been investigated in a recent study on awake behaving cats that were trained to perform a visuomotor coordination task (Roelfsema et al., 1997). In these animals, neural activity was recorded with electrodes chronically implanted in various areas of the visual, parietal and motor cortex. The results of this study show that synchronization of neural responses occurs not only within the visual system, but also between visual and parietal areas as well as between the parietal and motor cortex. Importantly, the interareal interactions changed dramatically in different behavioural situations. Precise neuronal synchronization between sensory and motor areas occurred specifically in those task epochs in which the animal had to process visual information attentively to direct the required motor response. The observations of this study suggest that synchrony may indeed be relevant for visuomotor coordination and may serve the linkage of sensory and motor aspects of behaviour. The specificity of such interactions might allow, for instance, the selective channeling of sensory information to different motor programs that are concurrently executed. Similar conclusions are suggested by recent studies in monkeys, where synchronization between sensory and motor cortical areas has also been reported (Murthy and Fetz, 1992).

Another example of the potential relevance of synchrony for sensorimotor transformations is provided by the interaction of cortical assemblies with subcortical integrative structures such as the superior colliculus. Recent experiments in the cat show that neurons in visual cortical areas can synchronize, via the corticotectal pathway, with cells in the superficial layers of the colliculus (Brecht et al., 1998). These studies have revealed the occurrence of precise temporal relationships between cortical and collicular neurons. Moreover, it was shown that corticotectal interactions are strongly dependent on the temporal coherence of cortical activity. This finding is consistent with the idea that the temporal organization of activity patterns determines the efficiency of the output of the visual cortex. More recent experiments have directly tested the role of synchrony for the selection of targets during the animal's orienting responses, which are mediated by the superior colliculus (Brecht et al., 1997). These experiments investigated how electrically evoked saccadic eye movements were

affected by varying the temporal relation between microstimulation trains applied at two different sites in the colliculus. Synchronous activation of two collicular sites led to vector averaging, i.e., to movements along a vector corresponding to the mean of the saccades evoked by stimulating the two sites individually. In contrast, asynchronous stimulation (10ms or 5ms offset between the pulses of the two stimulation trains) led to vector summation, i.e., in this case, the saccades had the same direction as those evoked by synchronous pulse trains, but showed approximately double amplitude. These data show that vector averaging in the colliculus is restricted to synchronously active cells, whereas small temporal phase-shifts lead to a radically different motor strategy. This strongly suggests that synchrony in the millisecond range is an important determinant for the motor output in sensorimotor loops that read the temporally encoded information from sensory assemblies.

Binding and phenomenal consciousness: experiments on binocular rivalry

The experimental data discussed in the preceding section clearly argues for the importance of synchrony in the establishment of coherent sensory representations and for sensorimotor integration. Recent evidence indicates that these synchronization phenomena may also be relevant for the build-up of phenomenal states and the selection of visual information for access to awareness. This is suggested by experiments in which we recorded neuronal responses from the visual cortex of strabismic cats under conditions of binocular rivalry (Fries et al., 1997). Binocular rivalry is a particularly interesting case of dynamic response selection that occurs when the images in the two eyes are incongruent and cannot be fused into a coherent percept. In this case, only signals from one of the two eyes are selected and perceived, whereas those from the other eye are suppressed. In normal subjects, perception alternates between the stimuli presented to left and right eye, respectively. The important point is that this shift in perceptual dominance can occur without any change in the physical stimulus. Obviously, this experimental situation is particularly revealing for the issue at stake, because neuronal responses to a given stimulus can be studied either with or without being accompanied by awareness (Crick and Koch, 1990) and, thus, there is a chance of revealing the mechanisms leading to the selection of perceptual information.

Previous studies have examined the hypothesis that response selection in binocular rivalry is achieved by a modulation of firing rate. In these experiments, a number of different visual cortical areas were recorded in

awake monkeys experiencing binocular rivalry. With respect to early processing stages (visual areas V1, V2, V4, MT), the results were not conclusive (Logothetis and Schall, 1989; Leopold and Logothetis, 1996). The fraction of neurons that decreased their firing rates upon suppression of the stimulus to which they responded was about the same as the fraction of cells that increased their discharge rate, and, altogether, response amplitudes changed in less than 50% of the neurons when eye dominance switched. A clear and positive correlation between firing rate and perception was found only in the inferotemporal cortex, i.e. at a relatively late stage of visual processing (Sheinberg and Logothetis, 1997).

In our study (Fries et al., 1997), we have investigated the hypothesis that response selection in early visual areas might be achieved by modulation of the synchronicity rather than the rate of discharges. These measurements were performed in awake cats with wire electrodes chronically implanted in areas 17 and 18. The animals were subjected to dichoptic visual stimulation, i.e., patterns moving in different directions were simultaneously presented to the left and the right eye. Perceptual dominance for a given set of stimuli was inferred from the direction of eye movements induced by the drifting gratings (the so-called optokinetic nystagmus), which were recorded by periorbital electrodes (during correlation measurements, however, precautions were taken to minimize eye movements; for details, see Fries et al., 1997). As a baseline, neuronal responses were also recorded under monocular stimulation conditions. The results obtained with this experimental approach show that visual cortical neurons driven by the dominant and the suppressed eye, respectively, differ neither in the strength nor in the synchronicity of their response to monocular visual stimulation. They show, however, striking differences with respect to their synchronization behaviour when exposed to the rivalry condition (Fig. 4). Neurons representing the stimulus that wins in rivalry and is perceived increase their synchrony, whereas cells processing the suppressed visual pattern decrease their temporal correlation. However, no differences were noted under the rivalry condition for the discharge rates of cells responding to the dominant and the suppressed eye, respectively.

These results show that, in areas 17 and 18 of awake, strabismic cats, dynamic selection and the suppression of sensory signals are associated with modifications of the synchrony rather than the rate of neuronal discharges. This suggests that, at an early level of visual processing, it is the degree of synchronicity rather than the amplitude of responses that determines which of the input signals will be processed further and then support perception and oculomotor responses. Changes in synchronicity at early stages of processing are bound to result in changes of discharge rate
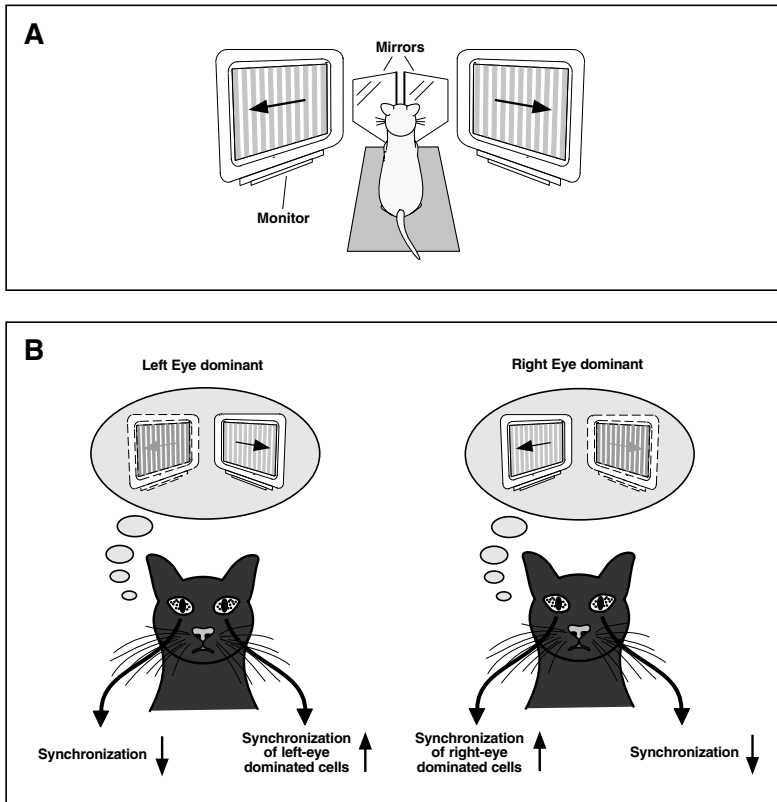
Fig. 4: Neuronal synchronization under binocular rivalry. (A) To induce binocular rivalry, two mirrors are mounted in front of the animal's head such that the eyes are viewing different stimuli. (B) Under this condition, animals as well as humans alternate between two perceptual states. In certain episodes (left), the pattern presented to the left eye will dominate perception, while the information conveyed by the right eye is suppressed and excluded from perception. In other instances (right), the opposite effect may occur, leading to perceptual dominance of the pattern presented to the right eye. As indicated in the bottom panel, synchrony will increase between neurons that represent the perceived stimulus, while it decreases between cells responding to the suppressed pattern. Thus, for instance, during dominance of the left eye (bottom left), neurons driven by this eye will increase their temporal correlation, but correlation becomes weaker for cells driven by the right eye.

at later stages. Thus, the rate changes observed with perceptual rivalry in higher cortical areas (Sheinberg and Logothetis, 1997) could be secondary to modifications of neuronal synchronization at lower levels of processing. In the present context, the important conclusion from these experiments is that only strongly synchronized neuronal responses can contribute to awareness and conscious phenomenal states. The data suggest that the activation of feature-detecting cells is, as such, not sufficient to grant access of the encoded information to consciousness (note that the cells representing the suppressed stimulus still respond well). Rather, to be functionally effective and to be selected for perception, neurons have to be strongly synchronized and bound into assemblies. In this respect, the data support the proposal by Crick and Koch (1990) that neuronal synchronization may be a necessary condition for the occurrence of awareness. Admittedly, this conclusion rests on the assumption that sensory awareness of the stimulus correlates well with the oculomotor behaviour that we have used as an indirect measure of the cats perceptual state. However, this correspondence has been well established in humans, where a nearly perfect correlation has been found between the direction of the pursuit phase of the optokinetic nystagmus and the perceived direction of motion (Fox et al., 1975), meaning that, in the rivalry situation, it is impossible to track one of the patterns with the eyes but consciously perceive the other.

Conclusions

In this paper, I have discussed the concept of temporal binding and its application to the issue of sensory processing and perceptual awareness. The basic assumption is that synchrony is introduced as an additional coding dimension which complements the conventional rate code. While the latter serves the coarse coding of representational contents, the former may permit the dynamic expression of specific relations within a network. In this way, the combination of two different coding strategies could allow the multiplexing of different types of information within the same activity patterns and, thus, could enhance the representational power of distributed systems. As discussed above, the available data suggest that a temporal binding mechanism may indeed exist in the brain. Rather than being a futile epiphenomenon of network connectivity, precise synchronization of neuronal discharges seems to be functionally relevant for the binding of distributed responses in a wide variety of neural systems. In sensory systems, temporal binding may serve perceptual grouping and, thus, constitute an important prerequisite for scene segmentation and object recognition. Moreover, temporal binding may be

involved in sensorimotor integration, i.e., in establishing selective links between sensory and motor aspects of behaviour.

The crucial advantage of temporal binding is that it could permit the rapid and reliable selection of perceptually or behaviorally relevant information. Because precisely synchronized discharges have a high impact on the respective postsynaptic cells, the information tagged by such a temporal label could be rapidly and preferentially relayed to other processing centers (Singer et al., 1997). As proposed here, such a process of response selection, which is based on temporal correlation among subsets of activated neurons, may be an integral part of the mechanisms responsible for perceptual awareness. As shown by the experiments on binocular rivalry, the selection of visual information for perception is associated with an enhanced synchronization of the respective neuronal populations. Therefore, temporal binding may indeed be a necessary condition for the occurrence of awareness and the establishment of conscious phenomenal states.

Thus, studying the dynamics of neuronal interactions may be particularly rewarding in the search for the neural correlates of consciousness. The important point of the results presented here is that, at least in early stages of sensory processing, the degree of synchronicity predicts reliably whether neural activity will contribute to conscious experience or not. Therefore, experiments designed to investigate neuronal synchronization may help to identify the selection mechanisms that are required for phenomenal consciousness. At this point, we have deliberately restricted our discussion to the issue of awareness, because it seems that, based on the present data, one can hardly argue for a relevance of binding mechanisms for other forms of consciousness. However, it has been speculated that temporal binding may also account for higher-order properties of phenomenal consciousness (Metzinger, 1995) – an exciting possibility that clearly awaits further research.

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