Solutions for the Binding Problem*

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Visual cortical neurons are broadly tuned to one or a few feature dimensions, like color and motion. This is advantageous because broadly tuned neurons can contribute to the representation of many visual scenes. However, if there are multiple objects in a visual scene, the cortex is at risk to combine features of different objects as if they belong to a single object. The term "binding problem" was introduced to refer to the difficulties that may occur in sorting out those responses that are evoked by a single perceptual object. The present article reviews proposals suggesting that the binding problem is solved by labelling an assembly of neurons that is responsive to a single perceptual obejct. Evidence is reviewed in favor of two possible assembly-labels: rate enhancement due to visual attention and neuronal synchrony. Assembly-labels should be spread through the cortical network to all neurons that have to participate in an assembly. The present article tries to shed light on the mechanisms that subserve such a selective spread of assembly labels. Moreover, it is suggested that assembly labels may fulfill an equivalent role in the motor system, since binding problems can also occur during the generation of useful patterns of motor activity.

Introduction

The past 2 decades of research on the cerebral cortex have revealed an organizational complexity that was largely unforeseen. The various cortical regions have been subdivided in ever-smaller compartments, each of which is characterized by distinct response properties and connections to other brain structures. In the monkey visual cortex, for example, more than 30 distinct visual areas have been classified (Felleman and Van Essen, 1991; Zeki, 1993), and areas are equally numerous in other brain regions like the somatosensory, auditory and motor cortex (Jeannerod *et al.*, 1995; Kalaska and Crammond, 1992). The parcellation of the visual cortex reflects some kind of functional specialization since neurons in each of the visual areas are, at least to some degree, selective for a characteristic subset of stimulus features. This functional subdivision has far reaching consequences for the nature of representations in the visual cortex.

Some areas, for example, are dedicated to the analysis of motion, others are dedicated to the analysis of colour and again others to the analysis of visual shape. A single visual stimulus always possesses features that are represented in different areas and, therefore, activates cells in many areas of the visual cortex. The hypothesis that the representation of the different visual aspects of everyday objects is distributed over many distinct subdivisions of the visual cortex can be traced back to Hebb (1949), who called the group of neurons that respond to the various features of an object an assembly. Now we should wonder what the advantage is of such a distributed representation. Why is it that the visual cortex disentangles the information present at the retina into largely different aspects of the visual world?

One advantage of representation with assemblies of cells is an economical use of neurons. The characterization of a visual stimulus by summing up its properties along the various feature dimensions requires a relatively low number of neurons. For each feature dimension a group of neurons, or module (or visual area) may be set aside that is able to encode any possible value that an object make take on this dimension. Objects, then, are

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represented as unique patterns of activation over all these modules. This representational strategy requires a low number of cells since neurons that exhibit selectivity for a particular feature may participate in the representation of all visual stimuli that contain this feature. For example, cells that are selective for the colour red can join, at different times, a great number of different assemblies, like assemblies representing red apples, representing red streetlights, or any other category of red objects. An elegant property of such a distributed representation is that similar objects, which differ in only a few feature domains, evoke representational states that are more similar than objects that differ in more respects. Furthermore, objects that have never been encountered may be easily accommodated as new patterns of activation over the existing modules. These considerations imply that the assembly code is an economic and flexible representational strategy.

Having summed up some of the virtues of an assembly code, and having mentioned evidence for distributed representation in the visual cortex, the reader might wonder if there are still viable theories around that compete with the assembly theory of visual representation. Contemporary representational theories share the view that lower visual areas use a distributed code, which is not surprising in the light of the compelling physiological evidence. However, there are theories that abandon the assembly code for higher visual areas. This is related to a disadvantage of the assembly representation that will play a central role in this chapter.

Any typical and realistic visual scene contains more than a single object, and when multiple objects are presented to the visual system, distributed representations suffer from a binding problem. Neurons that respond to one of the objects are, in principle, indistinguishable from neurons that respond to another object. These responses signal a set of visual features that are present in the image, but information about which feature belongs to which object may be lost (Fig. 1). This problem, which von der Malsburg (1981) called the superposition catastrophe, calls for a mechanism that keeps track of those responses that are evoked by a single object, and distinguishes them from responses evoked by different objects. It is in their strategies for overcoming the superposition catastrophe that contemporary theories of visual representation differ. These theories benefit from a long tradition of psychophysical research that was started in the beginning of our century by the Gestalt psychologists. In their study of perceptual grouping by the visual system the Gestalt psychologists were able to show that the visual system is quite effective in recovering image regions belonging to a single object (Köhler, 1930; Rock and Palmer, 1990; Wertheimer, 1923). They found, for example, that image components with a similar shape or colour, that are close, and that are moving in the same direction are likely to be grouped together. Further Gestalt rules include collinearity and connectedness; image elements that are collinear or connected through a path in the image are likely to belong to the same visual object. These rules of perceptual grouping should still guide the search for neuronal mechanisms that are capable of sorting out responses that originate from the same image component, and thus allow a disambiguation of the assembly code.

One possibility for removing ambiguities from the assembly representation is to equip the cortical network with binding units, neurons that are selective for conjunctions of features from different domains (Fig. 1C). These neurons should fire if a combination of features, for example movement to the right and the shape of an apple, are combined in a single object, but not if these features belong to different image components. Physiological evidence favouring binding units comes from two recent physiological studies. Rao *et al.* (1997) recorded from neurons in the prefrontal cortex of awake monkeys and found cells that were selective for conjunctions of shapes and locations. Similarly, Oram and Perrett (1996) demonstrated the existence of cells in area STP that are selective for conjunctions of shape and direction of motion (like in Fig. 1C). Importantly, these neurons did not only signal the simultaneous presence of a particular motion and shape, but also required that these two features were combined in a single object. At a later point in this chapter mechanisms will be discussed with which such selectivity can be achieved. For now it suffices to remark that a simple convergence from neurons selective for a particular shape and a particular direction of motion does not suffice. This would not enforce the constraint that both features originate from the same visual object.

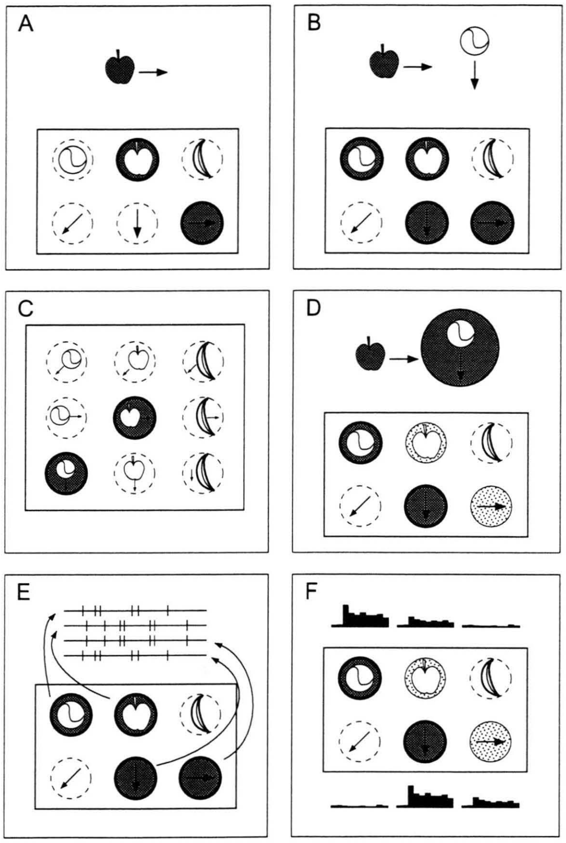

Fig. 1. Solutions for the binding problem. (**A**) A network consisting of 6 feature detectors: 3 detectors of form and 3 detectors of motion (bottom). If a single object is presented (top) the representation is unambiguous. The object is represented by the activity of a neuron selective for its shape and another neuron selective for the direction of motion (thick shaded circles). (**B**) However, if several objects are presented (top) an ambiguity occurs: the actual conjunctions of features cannot be inferred from the pattern of active cells (bottom). (**C**) Resolution of ambiguities by "cardinal cells". These are single neurons with selectivity for a conjunction of features. (**D**) Solution to the binding problem by focal attention. The activity of neurons, which respond to the region of the visual field occupied by the attentional spotlight (shaded area surrounding the ball), is enhanced relative to the activity of neurons responsive to other regions in the visual field. Neurons that respond to features of the apple have a reduced firing rate as indicated by the lighter shading. (**E**) Resolution of ambiguities by temporal coding. Neurons that represent features of the same object fire their action potentials at the same time. (**F**) Solution of the binding problem by object-based attention. A single object is selected by the visual system. This is associated with an enhancement of the responses of neurons representing the respective features. Thus, object-based attention is similar to focal attention (D). However, when objects overlap each other, focal attention cannot solve the binding problem (modified from Roelfsema *et al.*, 1996).

An extreme version of this solution for the binding problem is the cardinal cell hypothesis which proposes the existence of cells that are selective for very specific feature constellations (Barlow, 1972), say a grandmother with a red hat who is entering the dining room with a pot of tea. Cardinal cells are hypothesized to reside in higher visual areas, and are assumed to acquire this high degree of selectivity by a convergence of selectivity from neurons situated in lower visual areas. Unfortunately, the cardinal cell hypothesis, while resolving the binding problem, reintroduces problems that the assembly representation handled very well. In particular, this strategy is very expensive in terms of the number of neurons that would be required for encoding all possible conjunctions of features that readily outnumber the cells that are available in the entire brain. Furthermore, with this type of representation the ability to represent particular feature constellations is not necessarily associated with the potential for representing different combinations of the same features. Clearly, that what is needed should preserve the virtues of the assembly representation, while avoiding the superposition catastrophe and the unrealistic cell numbers required by the cardinal cell hypothesis. It will be suggested that conjunction detectors comprise an important, but intermediate step in the general solution of the binding problem.

An alternative and popular solution for the binding problem, that is consistent with a distributed representation, uses a focus of attention (Fig. 1D) for demarcating a region of the visual field from which responses are selected for further processing (Crick, 1984; Treisman and Gelade, 1980). Neurons that respond to features that are contained in the focus of attention are usually suggested to have an enhanced firing rate relative to neurons that respond to other regions of the visual field. It has been shown that the responses of neurons in various regions of the visual cortex are indeed enhanced when monkeys pay attention to a visual stimulus (reviewed in Maunsell, 1995; Newsome, 1996; Posner and Dehaene, 1994; Wise and Desimone, 1988). When the focus of attention is positioned accurately, and the inclusion of more than a single object is avoided, the binding problem may be circumvented. However, positioning the window exactly around the object of interest is necessary, and may be a difficult problem in itself, in particular when its outline is erratic and different objects are in close proximity. In these situations, the segmentation of the image into the constituent objects and background is a prerequisite for the appropriate positioning of the attentional focus, and not its result. Further limitations may result from restricting the window to a single contiguous image region at a time. This causes severe problems when objects are partially occluded by others, since responses from non-contiguous parts of the visual field may need to be integrated into a coherent percept. Difficulties also arise in the representation of relations between different objects, since the superposition catastrophe looms as soon as more than a single object is included in the window of attention.

A third option for solving the binding problem is possible when the cortical network has a tag at its disposal in order to label a subset of cortical neurons. This label should be spread among the assembly of neurons that respond to features of the same object, a process that I call 'tag-spreading'. Two possible tags will be discussed: the synchrony of neuronal discharges and enhanced firing rates. The synchronization label was proposed by Abeles (1982) and von der Malsburg (1981, 1986) and, in a preliminary form, also by Milner (1974). These authors pointed out that ambiguities might be removed from a distributed representation by using the precise timing of action potentials as a label. The hypothesis was put forward that neurons that respond to the various features of a single image component should synchronize their discharges on a fine temporal scale, whereas neurons that respond to different image components should not fire in synchrony. This disambiguating strategy allows multiple assemblies to become active at the same time (Fig. 1E). A further advantage is that the integration of responses from non-contiguous image regions is not prohibited.

An enhanced firing rate is the second candidate tag will be considered for labelling the assembly of cells responding to features of a particular object. As was discussed above, many authors have suggested that focal attention is associated with an enhanced firing rate of visual cortical neurons. However, when objects overlap each other it may be impossible to restrict the attentional focus to a single object. Psychophysical evidence (e.g. Duncan, 1984) indicates, however, that visual attention is quite capable of selecting one of two overlapping objects. An implementation of object-based attention in the visual cortex will be proposed, using enhanced firing rates in order to label the object that is currently selected by the visual system (Fig. 1F). Moreover, it will be suggested that the spread of an enhanced firing rate is computationally similar to the spread of the synchrony label, and that both can rely on a similar architecture of corticocortical connections.

Experimental Evidence for Assembly Forming Tags

In this section evidence will be reviewed for the hypothesis that labels may indicate the assembly membership of cortical neurons. First, evidence in favour of enhanced firing rates as an assembly-forming label will be discussed. Then I will turn to evidence favouring neuronal synchrony as a label.

Enhanced firing rates as a label for assembly membership

Treisman and co-workers (Treisman, 1996; Treisman and Gelade, 1980; Treisman and Gormican, 1988; Treisman and Schmidt, 1982) have proposed a now classical theory on how the visual brain might solve the binding problem. Their 'feature integration theory' suggests that when the visual system is confronted with multiple objects, attention is directed serially to the various objects. Visual features from unattended objects are floating freely; they are not incorporated into coherent percepts. However, as soon as attention is focused on a region of the visual field, the features that are present within this region are assembled. Typically, the attentive focus is proposed to be a circular region in the visual field. When more then a single object is included in the attentional focus, feature migrations may occur: illusory conjunctions of features are perceived which are not present in the visual image (Treisman and Schmidt, 1982). For example, when a red square and a yellow triangle are both present in the attentional focus, the perceiver may report to see a red triangle.

A large amount of data indicates that when visual attention is directed to a visual object, responses of neurons encoding its various features are enhanced relative to the responses to unattended objects. Response enhancement to attended objects occurs, for example, in area V4 of the visual cortex, an area that is presumably involved in the analysis of visual shape and colour (Boch and Fischer, 1983; Connor *et al.*, 1996; Luck *et al.*, 1997; Moran and Desimone, 1985; Motter, 1993, 1994). It also occurs in area MT which is believed to be devoted to motion analysis (Treue and Maunsell, 1996), and in other areas of the parietal cortex (e.g. Bushnell *et al.*, 1981). These data suggest a physiological solution to the binding problem: in order to integrate features which belong to one of the objects in the visual field, the responses of neurons selective for the respective features, which are distributed over many visual areas, may be enhanced simultaneously. It remains unclear, however, how the selectivity of response enhancement is achieved. Of all responses, only those evoked by a single visual object should be enhanced at a particular point in time. This problem is particularly difficult when objects overlap each other (Duncan, 1984) so that attentional enhancement cannot be solely based on spatial factors. In these cases, the distribution of visual attention should be determined by Gestalt criteria, like coherence of motion or similarity of colour, that allow the visual system to recover the regions occupied by the attended object. It has been shown that visual attention indeed has a tendency to spread from attended image regions to image elements that related to these regions by various perceptual grouping criteria (Baylis and Driver, 1992; Kramer and Jacobson, 1991). Moreover, feature migrations which give rise to illusory conjunctions are more likely to occur within a region that is coherent according to the Gestalt criteria than between different image regions (Baylis *et al.*, 1992; Prinzmetal, 1981). Neuropsychological evidence supports the hypothesis that attention spreads within image regions defined by perceptual grouping criteria. There are patients with a lesion in the parietal cortex who typically perceive only one of a number of simultaneously presented visual objects (cf. Farah *et al.*, 1993; Humphreys *et al.*, 1994). The interference between simultaneously presented image components is called extinction and is often taken as evidence for a disturbance in directing visual attention. When the perceived and non-perceived image components are incorporated in the same perceptual group, however, extinction can sometimes be prevented (Farah *et al.*, 1993; Humphreys and Riddoch, 1993). This suggests that attention spreads according to perceptual grouping criteria from image components that receive attention to those that are normally suppressed, thus preventing the latter from being ignored.

There is physiological evidence showing that the Gestalt laws of perceptual grouping determine the spread of an enhanced firing rate among cortical neurons. When a region of the visual image differs from the rest in orientation or movement direction, it stands out as a coherent figure against a background. In the psychophysical literature this phenomenon is usually called texture segregation (e.g. Beck, 1966; Julesz, 1984; Olson and Attneave, 1970). Lamme (1995) found that the responses of neurons in the primary visual cortex to image elements that belong to such a figure are stronger than responses to image elements that belong to the background. In his experiment there was no difference in the content of the classical receptive field between the condition in which the neurons responded to the figure and the condition in which they responded to the background. Thus, response enhancement to a figure represents an influence from outside the classical receptive field of neurons in area V1. Importantly, response enhancement occurs throughout the region occupied by the figure but is completely absent in the rest of the image, even at locations close to the figure. Thus, the label of an enhanced firing rate spreads among neurons with a similar tuning to orientation or direction of motion but not across borders where the orientation or movement direction of image elements changes abruptly. Thus, the Gestalt rule that regions with similar features should be grouped together into a coherent percept appears to be reflected by a selective spread of an enhanced firing rate. Other grouping criteria, like similarity of colour or depth (Zipser *et al.*, 1996) and collinearity of image elements (Kapadia *et al.*, 1995) are associated with similar changes in the firing rate of neurons in area V1. Preliminary data from a recent study (Roelfsema *et al.*, 1997a) directly addressed the issue of whether object-based attention is associated with an enhanced firing rate of cortical neurons. It was found that responses of neurons in area V1 to the various regions occupied by an attended object were enhanced relative to responses evoked by an unattended object.

Neuronal synchronization as a label for assembly membership

However, there are also a few disadvantages associated with the use of different activity levels as a label for neuronal assemblies. First, an enhanced activity level does not allow for the simultaneous representation of multiple objects. When multiple objects are selected by object-based attention, it is again impossible to decide which of the enhanced responses are evoked by one object and which by the others, and therefore, illusory conjunctions may occur (Treisman and Schmidt, 1982). Second, this tag may be confounded with the extent to which the stimulus matches the feature preferences of the neurons. Any visual stimulus will be suboptimal for a large population of visual cortical neurons and will therefore evoke a wide spectrum of activity levels in different cells. These variations in activity levels might be indistinguishable from the assembly tag. Let us therefore now turn to neuronal synchrony, the other candidate tag for labelling neuronal assemblies. The hypothesis is that neurons that respond to the various features of a single image component synchronize their discharges on a fine temporal scale, whereas neurons that respond to different image components do not fire in synchrony. An advantage of this solution is that multiple assemblies may become active at the same time (Fig. 1E). Moreover, the temporal structure in a train of action potentials is largely independent of firing rate.

Several studies have demonstrated that spatially separate cells in the primary visual cortex of cats and monkeys synchronize their spike trains on a millisecond time scale (for review, see Engel *et al.*, 1992a; Singer and Gray, 1995). Fig. 2B illustrates the interaction between two cell groups in the primary visual cortex of the anaesthetised cat. A single moving light bar activated neurons at both recording sides (Fig. 2A). The center peak in the crosscorrelation function indicates that the neurons synchronized their responses with a precision of a few milliseconds. However, when the two cell groups responded to two different light bars moving in opposite directions the interaction between them was drastically different. The respective crosscorrelation function was flat which indicates that the neurons fired without any fixed temporal relationship (Fig. 2C,D). These data illustrate the rather general finding that neurons in the visual cortex of cats and monkeys only show strong synchronization if they respond to features of the same visual stimulus. If neurons respond to different stimuli, synchronization between them is weaker or completely absent (Engel *et al.*, 1991a;

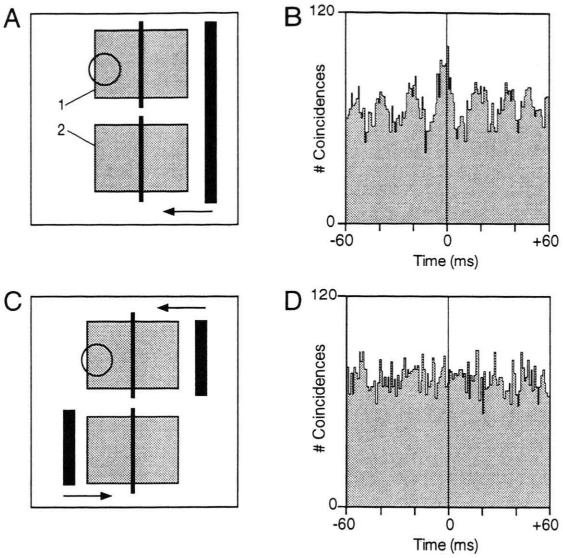

Fig. 2. Influence of stimulus coherence on neuronal synchronization in the visual cortex. In this experiment, multiunit activity was recorded from two sites separated by 7 mm in area 17 of the visual cortex of an anaesthetized cat. (**A**), (**C**) Receptive fields of neurons at the two recording sites which were tuned to vertical orientations. In (A) neurons were activated with a single moving light bar, and in (C) with two smaller bars that were moving in opposite directions. (**B**), (**D**) Cross-correlation functions for these stimulus conditions. Clear synchronization was observed between responses to the single moving light bar (B). Note the prominent center peak in the crosscorrelation function, indicative of synchronization with a precision of a few milliseconds. Synchronization was disrupted, however, when the stimulus consisted of smaller light bars that moved in opposite directions (D) (modified from Engel *et al.*, 1992a).

Freiwald *et al.*, 1995; Gray *et al.*, 1989; Kreiter and Singer, 1996, Livingstone, 1996). These observations provide support for the hypothesis that correlated firing could serve as an assembly-forming tag. In addition, they demonstrate that the Gestalt criteria of continuity and coherent motion determine the strength of synchrony among visual cortical neurons. Notably, the differences in synchronization behaviour between conditions represent an influence from outside the classical receptive field of the neurons.

Further experiments in anaesthetised cats have revealed that synchronization among the responses of cortical neurons can well extend beyond the borders of a single visual area (Eckhorn *et al.*, 1988; Engel *et al.*, 1991b; Nelson *et al.*, 1992). For example, neurons in the primary visual cortex have been found to synchronize their responses with those of cells in area PMLS (posterior medial lateral suprasylvian sulcus) if neurons in both areas were activated with the same light bar (Engel *et al.*, 1991b). Neurons in the primary visual cortex have a high spatial resolution and are sharply tuned to the orientation of a visual stimulus whereas neurons in area PMLS have a low spatial resolution and are primarily selective to the direction of motion. These observations agree with the proposal that synchrony serves to establish relations between the responses evoked by the different features of a single stimulus. Importantly, interareal synchronization is not specific for the lightly anaesthetised state, but also occurs in the awake cat (Roelfsema *et al.*, 1997b) and monkey (Frien *et al.*, 1994).

A number of studies in animals with an abnormal visual system caused by squint provide hints that neuronal synchronization is indeed functionally relevant and related to the animal's perception and behaviour. Misalignment of the eyes during early development has a pronounced influence on a wide range of visual functions (reviewed in von Noorden, 1990). A percentage of squinting animals develop a habit of fixating objects of interest with one of their eyes, while the other eye never participates in fixation. Another outcome of the squint is alternating fixation, a situation in which both eyes are used for fixation but at different times.

Since the pioneering studies of Hubel and Wiesel (1965) it is known that in squinting animals visual cortical neurons lose binocularity, which means that they can be activated through one eye only. Squinting subjects exhibit a striking inability to combine information that arrives simultaneously through the two eyes into a single percept. This deficit is accompanied by a loss of synchronization between neuronal populations activated through different eyes (Fig. 3B) (König *et al.*, 1993; Roelfsema *et al.*, 1994). In contrast, neurons that are activated through the same eye can synchro-

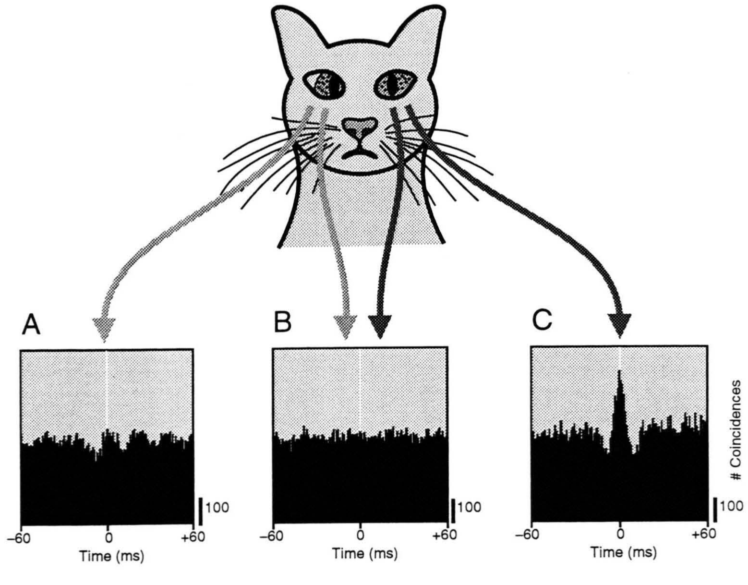

Fig. 3. Neuronal synchronization in the primary visual cortex of cats with strabismic amblyopia. The lower panel shows examples of crosscorrelograms between cells driven by the normal eye, by the amblyopic eye and between cells dominated by different eyes. Temporal correlation is strong if both recording sites are driven by the normal eye (C). Synchronization is, on average, much weaker between cells dominated by the amblyopic eye (A) and is absent in most cases if the recording sites receive their input from different eyes (B) (modified from Roelfsema *et al.*, 1994).

nize their discharges just as in the visual cortex of normal animals. However, the strength of these interactions depends on the eye that is being used for visual fixation. In the first group of squinters, those that always use the same eye for fixation, the non-fixating eye develops a syndrome of perceptual deficits called strabismic amblyopia. Symptoms of strabismic amblyopia include a reduced acuity, and distortions of visual perception (Sireteanu *et al.*, 1993; von Noorden, 1990). Strabismic amblyopia is not associated with a loss of neurons that are activated through the affected eye, and is most surprisingly also not associated with a change in the responsiveness of visual cortical neurons to high spatial frequencies (Blakemore and Vital-Durand, 1992; Chino *et al.*, 1983; Crewther and Crewther, 1990; Freeman and Tsumoto, 1983). Thus, patterns composed of spatial frequencies exceeding the threshold of the amblyopic eye can still evoke responses from visual cortical neurons that are as vigorous as responses evoked through the normal eye. However, it was found that the strength of synchrony is drastically lower among responses evoked through the amblyopic eye than among responses evoked through the normal eye (Fig. 3A,C). Furthermore, the loss of synchrony among responses of neurons activated through the amblyopic eye was most pronounced for high spatial frequencies that the animals had been unable to discriminate during previous behavioural testing (Roelfsema *et al.*, 1994). Taken together, these results indicate that strabismic amblyopia is associated with a selective loss of neuronal synchrony among neurons at the lowest level of the visual cortical hierarchy.

If synchronization is important for binding, feature integration should be impaired for vision through the amblyopic eye. Hess *et al.* (1978) explored the visual distortions that patients with strabismic amblyopia perceive when viewing with their affected eye. They asked amblyopic observers to look with their amblyopic eye at gratings of various spatial frequencies and to make drawings of the distorted percepts. Examples of such drawings are shown in Fig. 4. Apparently, the patients failed to perceive connections among contours that were actually connected, and vice versa, grouped contour segments that did not belong together. These visual distortions were most pronounced for gratings with higher spatial frequencies. Thus, it seems that conditions under which synchronization is disturbed are associated with visual distortions that, at least in part, can be explained by the breakdown of a binding mechanism.

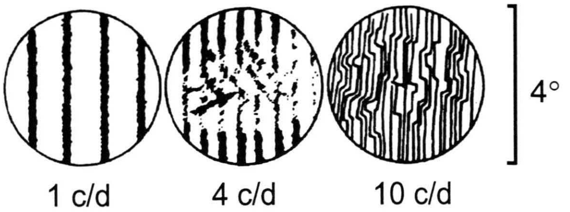

Fig. 4. Spatial distortions of amblyopic vision. Gratings of various spatial frequencies were shown to the amblyopic eye of a patient with strabismic amblyopia. After looking at these patterns, the patient was asked to open the normal eye and to draw his impression of the visual stimulus. Shown in this figure are the drawings of gratings with different spatial frequencies. The scale bar denotes the size of the presented stimuli in degrees of visual angle. Note that with increasing spatial frequency the spatial distortions become more severe. The patient reports on seeing connections between contour segments that are actually disconnected. Conversely, to the amblyopic eye elongated contours appear to be interrupted (reproduced with permission from Hess *et al.*, 1978).

The second group of squinters, those that can use both eyes in an alternating manner, have to suppress the responses of one of their eyes from conscious experience under binocular viewing conditions. Recently, it was shown that the synchronicity among the responses of neurons connected to the suppressed eye decreases under these conditions, whereas the strength of synchrony among the responses of neurons connected to the dominant eye is enhanced (Fries *et al.*, 1997). It seems likely that the increased synchronization among the responses of neurons connected to the dominant eye enhances the saliency of these responses. Neurons that have synchronized their discharges are more likely to activate neurons at higher levels of the visual system since synchrony results in more effective summation of synaptic potentials (Abeles, 1982; Softky and Koch, 1993). This should lead to a competitive advantage of these responses relative to those evoked through the suppressed eye. Thus, the deterioration of synchrony among responses evoked from an amblyopic or suppressed eye may prohibit these responses from reaching conscious experience.

Which is the proper tag, response enhancement or synchrony?

The data reviewed in the foregoing sections indicate that both synchrony and enhanced firing rates may be involved assembly formation. In my opinion, the physiological data that are available at present do not allow a firm rejection of either enhanced firing rates or synchrony as a label for assembly membership. In contrast, it will be argued in the remainder of this article that both labels may have functional significance. Both tags may be manifestations of grouping operations that are performed by the visual cortex, albeit at different temporal and spatial scales. I will suggest that synchrony, which occurs on a fine temporal scale, is useful for short range grouping operations. Enhanced firing rates, which occur on a slower time scale, may be important for grouping operations on a larger spatial scale, i.e. across many synapses. In the next section I wish to address the mechanisms that are responsible for the selectivity of the tag spreading process. Why is it that the spread of an assembly label is confined to the subset of neurons that respond to features of the same visual object?

The Selectivity of Tag-Spreading

In this section I will first discuss the type of connections that cause the spread of assembly labels. Second, I will elaborate on the mechanisms that bring about the spread of a label through the network of connections. Third, I wish to discuss the timescale on which tag- spreading should take place.

The interaction skeleton

Let us first consider the type of connections that are responsible for the spread of a label to neurons that respond to features of the same visual object. With respect to the layout of connections that are essential for spreading enhanced firing rates, no physiological data are presently available, to my knowledge. Clues for synchrony spreading connections, on the other hand, have been obtained in animals with a split callosum, and also in squinting animals. The corpus callosum is the fiber system that links the primary visual cortices of the two hemispheres. In animals with an intact corpus callosum visual cortical neurons in opposite hemispheres can synchronize their discharges, just as neurons within the same hemisphere. However, when the corpus callosum is sectioned, interhemispheric synchrony is abolished, while cells within the same hemisphere still engage in synchrony (Engel *et al.*, 1991c; Munk *et al.*, 1995). Since the corpus callosum is in many respects an extension of the network of interareal connections (e.g. Schmidt *et al.*, 1997a), this is strong evidence that intracortical connections are the carriers of synchrony. Experiments in squinting animals lend supportive evidence for the involvement of corticocortical connections in the spread of synchrony. In animals with a misalignment of the optical axes there is a breakdown of binocularity in the primary visual cortex, as was discussed above. Thus, visual cortical neurons are split between two populations, each of which is driven almost exclusively by one of the two eyes (Hubel and Wiesel, 1965). Löwel and Singer (1992) found that in squinting animals corticocortical connections selectively interconnect neurons that are activated through the same eye. There are almost no connections between neurons that are activated by different eyes. Thus, the absence of corticocortical connections between neurons driven by different eyes in squinters is accompanied by a loss of synchronization among them (König *et al.*, 1993; Roelfsema *et al.*, 1994). Taken together, these data suggest that corticocortical connections are responsible for the spread of the assembly labels.

As was discussed above, the spread of assembly labels should obey the Gestalt rules of perceptual grouping. Therefore, it was proposed that the architecture of corticocortical connections should reflect these perceptual grouping criteria (Singer, 1993). One of the Gestalt rules states that image elements with similar features like colour, texture or movement are likely to be grouped. Many authors have suggested that this grouping criterion can be implemented by interconnecting cell groups with a corresponding feature selectivity (reviewed in Roelfsema *et al.*, 1996). Physiological evidence is in accordance with this proposal. Intracortical connections selectively interconnect neurons with similar orientation or colour selectivity (Gilbert and Wiesel, 1989; Gilbert, 1992; Livingstone and Hubel, 1988; Malach *et al.*, 1993, 1994;

Ts'o and Gilbert, 1988). In addition, connections in the primary visual cortex preferentially interconnect cells with collinear receptive fields (Bosking *et al.*, 1997; Schmidt *et al.*, 1997b). This selectivity is probably related to the perceptual grouping criterion of collinearity.

A further grouping criterion, which illustrates some of the virtues of tag-spreading, is connectedness (Rock and Palmer, 1990). The visual system readily groups image regions together that are connected to one another, as is illustrated in Fig. 5A. The detection of connectedness is demanding, because connectedness is a global image property that cannot be detected by neurons receiving information from a subregion of the image (Minsky and Papert, 1969). If a neuron receives information from a subregion of the visual field, the cell will be unable to distinguish between connected and disconnected image components, since components may be connected outside this subregion. Detection of connectedness would therefore be impossible at the early levels of the visual system, where receptive fields are small, if the only information that neurons convey stems from this restricted receptive field. This, however, appears to be at odds with the fact that connectedness detection is an early, 'preattentive' visual function on which much of the subsequent visual processing depends, at least when one adopts a primarily feedforward view of visual cortical processing (e.g. Rolls and Tovée, 1994).

However, if tag-spreading occurs among neurons that are activated by a retinal image, connectedness detection becomes possible at the early stages of the visual system. Consider the network of Fig. 5C consisting of units that are activated from a particular image location (tile). Units that receive input from adjacent image positions are linked by connections (lines between units), in accordance with the Gestalt criterion of proximity.

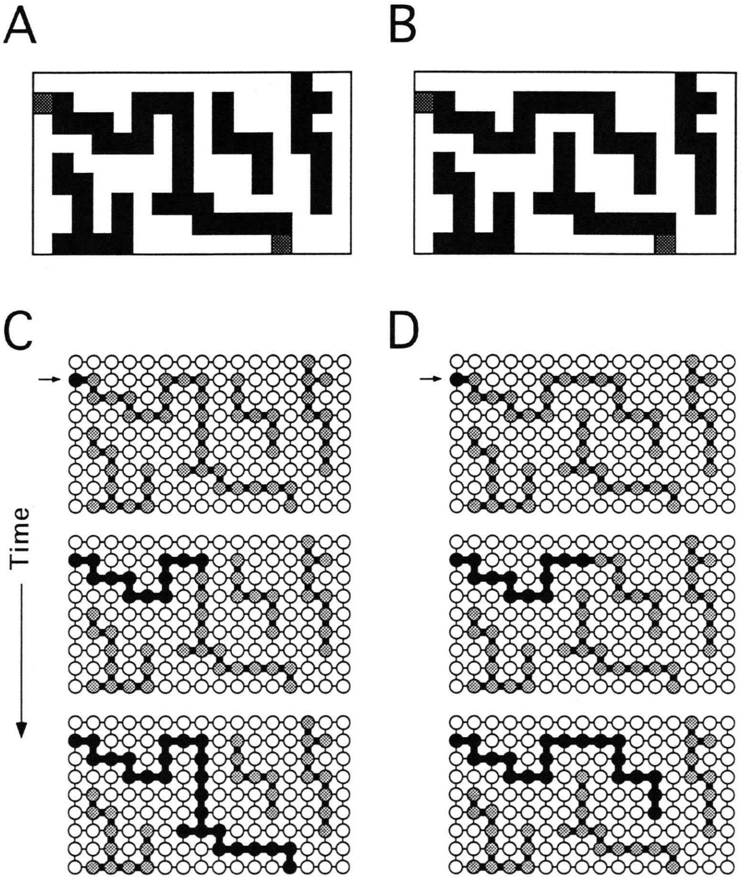

Fig. 5. Connectedness as a grouping criterion. (**A,B**) Subtle and local changes in the visual image may exert a pronounced effect on the process of image segmentation. A change in the position of a singe black tile is the only difference between (A) and (B). This minor change is associated with a large change in the segmentation of the image. In (A) the two grey tiles are connected, but in (B) they are not. (**C,D**) Schematic illustration of the interaction skeleton. Neurons (circles) with adjacent receptive fields are reciprocally coupled (lines). Neurons that are activated by the image have been indicated in grey. The interaction skeleton consists of those connections that link active neurons (thick lines). In order to detect connectedness, a label (black) is spread among activated neurons, starting at the arrow. The label will only propagate to neurons that respond to image locations that are connected to the tile that is indicated by the arrow. Note that, in principle, the tag spreading process could be initiated anywhere in the interaction skeleton. (*D*) A local change (between C and D) in the image results in a global change in the composition of the interaction skeleton, and in an equivalent change in the tag spreading process.

Let us assume that tags can spread through these connections, but that tag-spreading is restricted to those units that are activated by the image. This implies that a connection is only effective if both the pre- and postsynaptic cell are active (thick lines). The subset of connections that are enabled because neurons one both sides of the connection are active will be called the *interaction skeleton* (Fig. 5C). Let us suppose tag-spreading starts at one of the neurons that are activated by the image. It is easy to see that this tag spreads to precisely those neurons that respond to image regions that are connected to this tile. Indeed, if the interaction skeleton connects neuron A to neuron B on the one hand, and neuron B to neuron C on the other, then it is obvious that it also connects neuron A to neuron C. Thus, connectedness within the interaction skeleton is signalled by a transitive process, and accordingly, the tag spreads to precisely those neurons that respond to tiles that are connected through a path in the image.

Importantly, a *local* change in the image (Fig. 5B) results in the activation of different connections which, in turn, results in a *global* change of the tag-spreading process (Fig. 5C,D). The assembly label represents an influence on the units from beyond their classical receptive field. This is advantageous, since cells with restricted receptive fields can express connectedness using this additional signal. Thus, tag-spreading allows for the representation of connectedness at early levels of the visual system. It is remarkable that the visual distortions that occur in amblyopic vision (Fig. 4) suggest a rather selective disturbance of connectedness detection, as was discussed above.

It is straightforward to incorporate other grouping criteria into the interaction skeleton. The assumption that tag-spreading connections link neurons with closely spaced receptive fields, and an approximately similar tuning in one of these feature dimensions suffices. If a visual feature, like disparity, changes gradually within the boundaries of a perceptual object, but changes abruptly across its borders, the interaction skeleton will selectively link neurons that respond to the object. In this situation the interaction skeleton also links neurons with a widely different disparity tuning, through cells with an intermediate disparity tuning. Note that it is the *transitivity* of the tag-spreading process that allows for the integration of local similarities in order to arrive at a meaningful global segmentation of the visual image.

The architecture of tag-spreading connections can also be generalized to account for the formation of assemblies composed of neurons that are tuned to different features. This argument is based on the fact that the firing rate of most cortical neurons is influenced by variations along multiple feature dimensions (Zohary, 1992). For example, the neurons in the primary visual cortex are selective for both the orientation and the location of a contour, and a large proportion of these cells is in addition selective for the colour or movement direction of stimuli (Leventhal *et al.*, 1995). The same holds for cells in other visual areas. Two neurons may therefore both be tuned to particular, shared feature domain and at the same time exhibit tuning to distinct domains. It has been proposed that neurons having a similar selectivity for a shared feature domain should be linked with tag-spreading connections (Roelfsema *et al.*, 1996). Figure 6 illustrates a network that consists of neuronal groups each of which is selective for two feature domains. Neurons in one cluster are selective texture and location, those in the other cluster for shape and location. Thus, location in the visual field is the feature domain that the two clusters have in common, and tag-spreading connections link neurons whose receptive field positions are similar. As a consequence, neurons of the two clusters will join the same assembly if they are coactivated and if their receptive fields are close together (Fig. 6). This will be the case if the preferred shape and texture coincide at the same location, a conjunction suggesting the presence of an object having both the appropriate texture and shape. It is convenient to introduce the concept of *linking dimension* for the feature domain that is shared by neurons that are selective for more one feature dimension. Thus, in Fig. 6 location functions as the linking dimension. It should be noted that information about the association of a particular texture with a particular shape is also implicitly available without tag-spreading, because the respective receptive fields have a common location. Tag-spreading serves to make this information explicit. This is advantageous, since I will suggest that subsequent processes are sensitive to the distribution of assembly labels. The mechanisms responsible for what may be called *label-evalua-*

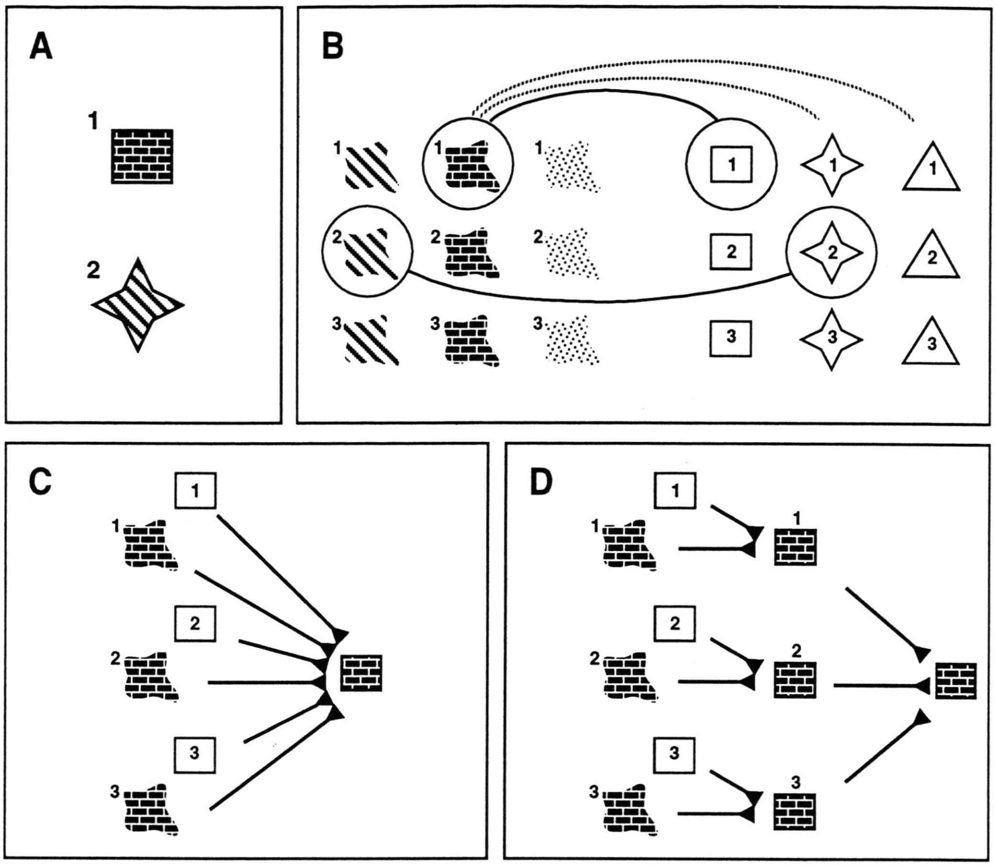

Fig. 6. Computation of translational invariant feature conjunctions. (**A**) Visual image composed of two objects that differ in form, texture, and position. Numbers refer to positions in the visual field. (**B**) Groups of neurons that are simultaneously selective for two feature domains. An icon represents a group of cells with similar feature selectivity. Two clusters of such cell groups are indicated, with selectivity for texture and position in the visual field (left), and for form and visual field position (right), respectively. Groups of neurons that would respond to the image in (A) have been marked with circles. Groups of cells with a corresponding selectivity for the feature domains that they have in common (i.e. similar visual field position) are linked with tag-spreading connections. All connections that contact the cells selective for the "bricks" texture at retinal position 1 have been indicated. For clarity, additional connections are only indicated between those neurons that are activated by the illustrated stimulus configuration (interaction skeleton: uninterrupted lines). Note that in response to this image two assemblies are formed, one for each image component. (**C**) Construction of cells that only respond to a rectangle with a "bricks" texture irrespective of its position in the visual field. A subset of the neurons of (B) are shown. An additional neuron has been indicated that receives synaptic input from all neurons that are selective for the "bricks" texture and all cells that are selective for a rectangle. Let us assume that this cell only responds when its afferents have received the assembly label. Note that in this example only afferents with a selectivity for the same visual field position can belong to the same assembly. This implies that the postsynaptic neuron only responds when the form and texture for which it is selective are located at the same position in the visual field. (**D**) Construction of cells which are selective for the same conjunction of features as in (C) without making use of tag-spreading. In order to assure that the neurons respond only to a conjunction of features that belong to the same image component, a convergence onto cells that are simultaneously selective for texture, shape *and* visual field position is required.

tion are presumably different for the synchrony label and the label of an enhanced firing rate.

With respect to the synchrony label, it has been proposed that cortical cells are particularly sensitive to simultaneously arriving synaptic input and act as 'coincidence detectors' (Abeles, 1982; Bernander *et al.*, 1994; Murthy and Fetz, 1994; Softky and Koch, 1993; but see Shadlen and Newsome, 1994). Synchronization among discharges of converging afferents is likely to enhance the probability that postsynaptic cells are activated. Figure 6C shows how neurons that only respond if their synaptic input is sufficiently synchronous may acquire selectivity for the conjunction of a new combination of features. The neurons that provide input to the postsynaptic cell in Fig. 6C will only exhibit synchronized activity if the texture and the shape to which they respond have the same visual field position. Therefore, a neuron that acts as a coincidence detector may integrate information over a large part of the visual field but need not respond if the texture and the shape for which it is selective belong to different image components.

For the enhanced firing rate label a similar mechanism can be devised. A single straightforward assumption needs to made: the postsynaptic neuron in Fig. 6C should only respond when the input of both afferents is enhanced. This implies that the postsynaptic neurons will only become active if the texture and shape belong to the same object. Thus, both assembly labels can be used to generate translational invariant response properties (Hummel and Biederman, 1992) that are found, for example, in visual areas of the inferotemporal stream (Ito *et al.*, 1995; Kobatake and Tanaka, 1994; Tovee *et al.*, 1994). In these areas neurons have been found that are selective for conjunctions between shapes and textures (Kobatake and Tanaka, 1994; Komatsu and Ideura, 1993). A similar mechanism could explain why neurons in area STP that are selective for conjunctions of shape and direction of motion only respond when both properties are combined in a single object (Oram and Perrett, 1996).

The possibility to generate new tuning characteristics by label-evaluation, as is illustrated in Fig. 6C, is one of the main advantages of tag-spreading. If A, B and C are feature domains, and if conjunctions of the type A_iB_j and B_jC_k have been computed by the network, conjunctions of the type A_iC_k in individual image components, invariant for the value of B, can be generated using B as the linking dimension. In contrast, standard connectionist networks would first need to enumerate all possible combinations $A_iB_jC_k$, and only then can construct cells selective for the presence of A_iC_k in a single image component by having responses of neurons $A_iB_jC_k$ (for all values of j) converging onto a further set of cells A_iC_k (Fig. 6D). This indicates that networks that utilize tag-spreading in order to express conjunctions are more economic with respect to the number of units required for the computation of invariant receptive field properties.

These considerations, however, do not explain the selectivity of tag-spreading among neurons tuned to completely unrelated feature domains. The neuronal groups in the two clusters of Fig. 6 share selectivity for visual field position. Indeed, it is this statistical dependence of firing probabilities that allows for the specificity of the tag-spreading connections. However, since tag-spreading is a transitive process, the label may spread further to neurons that are tuned to completely unrelated aspects of the visual world. This is illustrated in Fig. 7 showing a highly simplified network consisting of 3 modules. In each module neurons are selective for two feature domains. In the left module neurons are tuned to conjunctions between shape and texture. In the middle module neurons are selective to shape and position in the visual field, and in the right module neurons are selective for position in the visual field and movement direction. Neurons with a similar selectivity for a shared feature domain are linked with tag-spreading connections. For example, the neuron selective for a rectangle at position 1 in the visual field is connected to all neurons with their receptive field at position 1 and to all neurons that respond to a rectangle (continuous and stippled curves in Fig. 7B). The interaction skeleton, however, is composed of only those connections that link neurons that are activated by the image (thick lines). Is it easy to see that the interaction skeleton connects only neurons that respond to features that belong to the same object. Note that when the tag spreads through the interaction skeleton conjunctions are encoded that are not represented by dedicated neurons. When the visual image is changed, different cells of the middle cluster are activated, which alters the pattern of effective connections (compare Fig. 7B and D). Thus, local changes in the pattern of activated neurons may lead to global changes in tag-spreading (just as in Fig. 5). It can be seen that the problem of associating cells tuned to different feature domains into assemblies is equivalent to the problem of detecting connectedness within the interaction skeleton.

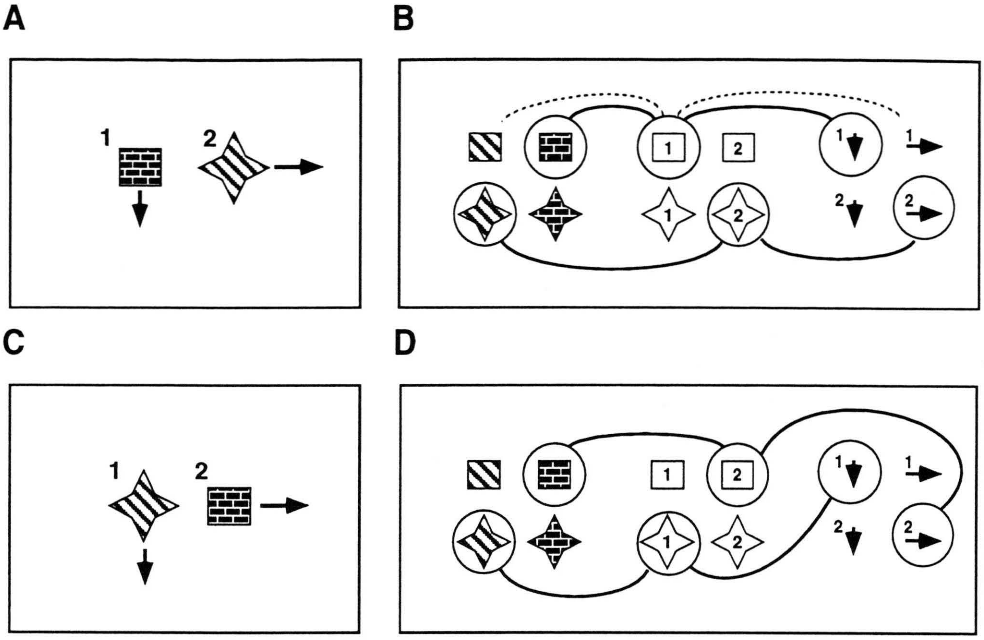

Fig. 7. Tag-spreading among neurons with different feature selectivities. (**A**) Visual image composed of two objects that differ in form, texture, direction of motion, and position in the visual field. (**B**) Three clusters of neurons that are simultaneously selective for two feature domains; form and texture (left), form and position in the visual field (middle), and position in the visual field and direction of motion (right). Circles, groups of neurons that respond to the image in (A). Groups of cells with a corresponding selectivity for the feature domains that they have in common are linked with tag-spreading connections. All connections that contact the cells selective for a square at retinal position 1 are indicated. For clarity, additional connections are only indicated between those neurons that are activated by this stimulus configuration. These connections form the interaction skeleton (uninterrupted lines). Note that in response to this image two assemblies are formed, one for each image component. (**C**) Image composed of the same objects, but at different positions in the visual field and with different direction of motion. (**D**) In the middle cluster different cells are activated by the stimulus configuration of (C) and, thus, a different subset of the connections can exert their effects, again leading to the incorporation of the appropriate neurons into assemblies (modified from Roelfsema *et al.*, 1996).

How Do Assembly Labels Spread through the Interaction Skeleton?

According to the proposal, the distribution of assembly labels is determined by the layout of the interaction skeleton which, in turn, is determined by the subset of activated neurons. Which processes are responsible for the spread of these tags through the interaction skeleton? First, the spread of the synchrony label will be discussed. Then, I will turn to mechanisms subserving the spread of an enhanced firing rate.

Closely located neurons in the visual cortex exhibit a tendency to fire their action potentials at approximately the same (e.g. Gray *et al.*, 1989). This suggests that local cortical circuits are laid out to allow for cooperativity of firing among these local cell groups (see also Somers *et al.*, 1995). Thus, neurons that have reached the firing threshold are likely to activate others that are also close to the threshold rapidly, thus starting a burst of activity (Bush and Douglas, 1991). It seems likely that such bursts, or neuronal avalanches as they may be called, travel some distance along the interaction skeleton. Then they die out, for example because inhibition builds up or because they collide with avalanches that started at other positions. These bursts of activity would provide a mechanism for synchronizing neurons that are connected through the interaction skeleton. The course that an avalanche can take is constrained by the layout of the interaction skeleton. Neurons that are not connected by the interaction skeleton cannot participate in the same avalanche.

One apparent contradiction of this proposal with the experimental data is related to the fact that individual avalanches will always be accompanied by time lags between neurons that are activated successively. At first glance, this seems to be incompatible with the findings on synchronization among cortical neurons that have almost always revealed correlation functions with peaks indicative of close to zero ms time-lag. However, these correlation functions are the average of a large number of episodes in which the cell groups fired at approximately the same time. In individual epochs neurons exhibit a variety of time-lags that change between stimulus presentations and even within a single stimulus presentation (Engel *et al.*, 1990). These variations are probably related to differences in the starting position of avalanches and the path that they take through the interaction skeleton. The time-lag between two neurons averaged over a large number of avalanches may therefore be close to zero ms.

Evidence that supports avalanches as a mechanism for neuronal synchrony has recently been obtained in a study on time-lags that occur in the interactions between neurons in the primary visual cortex. König *et al.* (1995a) studied the dependence of time-lags in the correlation functions between neurons that were activated by visual stimuli matching the feature selectivities of these neurons to varying degrees. Neurons that were optimally activated by a visual stimulus tended to lead in time over cells that were less optimally activated by the stimulus. Thus, by changing the extent to which a visual stimulus matches the preferences of different cell groups, time-lags between them can be changed in a predictable way. Cells that are activated by an optimal visual stimulus are more rapidly depolarized to their firing threshold and thus, are more likely to start a burst than neurons that are stimulated suboptimally. Thus, the data indicate that the average course taken by an avalanche is not invariant, but depends on the visual drive experienced by the neurons that are embedded in the interaction skeleton.

In order to synchronize neurons that are separated by a large number of synapses of the interaction skeleton, an avalanche should have enough time to develop. The width of a peak in the correlation function provides an estimate of the average duration of such avalanches. Many studies have reported widths of approximately 8–10 ms (Fig. 2,3) (cf. Eckhorn *et al.*, 1988; Gray *et al.*, 1989; Ts'o *et al.*, 1986). In such a short time an avalanche cannot, with all likelihood, spread further than 6–8 synapses. Therefore, additional mechanisms may be required to synchronize neurons separated by more synapses, if this is necessary. I will discuss two such mechanisms.

The first mechanism that may bring about synchronization over long distances in the interaction skeleton is an oscillatory firing pattern of the constituent neurons (Engel *et al.*, 1992b). Temporal constraints on the synchronizing interactions are less severe for units engaging in oscillatory activity than they are for stochastically firing cells, because the predictability of the spike trains can be exploited for the spread of synchrony. Even long transmission and synaptic delays are compatible with the generation of synchrony among oscillators (König and Schillen, 1991). Excitatory connections between oscillators cause synchrony if they are fast in comparison to the duration of the oscillatory cycle, or if they are delayed up to the next oscillatory cycle (Gerstner *et al.*, 1993; Sompolinsky *et al.*, 1990; Sporns *et al.*, 1989; Wilson and Bower, 1991). Similarly, inhibitory interactions among oscillators may postpone the firing of post-synaptic neurons up to next oscillatory cycle, as has been demonstrated in neural network models (Bush and Douglas, 1991; Jefferys *et al.*, 1996) and also in hippocampal slices (Cobb *et al.*, 1995; Whittington *et al.*, 1995). Physiological evidence is consistent with a prominent role of oscillatory activity with frequencies in the gamma range (30–80 Hz) in mediating synchronization over large cortical distances. In anaesthetized cats, episodes of oscillatory firing are associated with the appearance of synchrony over large cortical distances, whereas such long-range synchronization does not occur when neurons fire more irregularly (König *et al.*, 1995b). Also in the olfactory bulb and entorhinal cortex synchronization was shown to depend on the occurrence of oscillations in the gamma frequency range (Barrie *et al.*, 1996; Freeman and Skarda, 1985).

The second mechanism, which may help to synchronize neurons that are separated by many synapses, is an increase of the average avalanche duration. Many studies on the interactions among neurons in the visual cortex have focused on synchronization with a precision of a few milliseconds, a time scale that puts a severe restriction on the average burst duration. However, Nelson *et al.* (1992) found that visual cortical neurons synchronize their discharges on a variety of timescales. In their study the widths of peaks in correlation functions among visual cortical neurons could be subdivided in three categories: T-, C- and H-type coupling. T-type coupling (T for tower) was most precise, and associated with an average width (at half height) of peaks in the correlation functions of 3 ms. Peaks indicative of C-type coupling (C for castle) had an average width of 30 ms, and peaks indicative of H-type coupling (H for hill) an average width of 400 ms. The spread of synchrony was found to be larger for H- and C- type coupling than it was for T-type coupling. Thus, these slower types of coupling are associated with a longer avalanche duration and, hence, synchrony may spread over longer distances in the interaction skeleton. The range of possible avalanche durations can be extended even further, since rate changes that covary among neurons on a timescale of even seconds have been found (Amzica and Steriade, 1995; Bach and Krüger, 1986).

There is, however, also a disadvantage associated with long avalanche durations. A new burst of activity should only be initiated after the last avalanche died out. Therefore, long avalanche durations need to be accompanied by a low probability of their initiation. If by chance avalanches simultaneously occur in unconnected regions of the interaction skeleton, the respective neurons are spuriously labelled as if they belong to a single assembly. This should give rise to illusory conjunctions. Thus, when the avalanche duration is too long, the assembly label does not allow for simultaneous representation of different image components. There is a trade-off between the duration of avalanches, the frequency with which they can be initiated, the number of image components that can be represented at the same time and the probability of spurious synchronization. One of the virtues of the synchrony label, the possibility for simultaneous representation of multiple objects on a perceptual timescale, is sacrificed with very long avalanche durations. More prolonged changes in firing rates in a connected compartment of the interaction skeleton are a likely correlate of visual attention. Indeed, neurons that respond to attended image regions tend to have an enhanced firing rate whereas neurons that respond to unattended image regions have a reduced firing rate (Maunsell, 1995; Motter, 1993; Treue and Maunsell, 1996). Therefore, it is plausible that image components encoded by neurons that did not participate in avalanches for a perceptually relevant time-span are temporarily excluded from conscious visual perception, as was discussed above. At these timescales the synchrony label may be similar, if not identical, to the label of enhanced firing rates. The only distinction between the two labels is the timescale on which neurons in unconnected regions of the interaction skeleton may alternate, the timescale for the synchrony label being considerably shorter than the timescale of attentive shifts. Thus, the two labelling mechanisms have a highly similar computational structure, and can rely on the same architecture of intracortical connections.

Dynamic Adjustments of the Spread of Assembly Labels

In the above I have emphasized the benefits of an extensive spread of assembly labels. This permits binding of responses to features of a single object over large distances in the visual field (Fig. 5) and across different feature dimensions (Fig. 7). There is, however, also a disadvantage associated with a large spread. This may result in the participation of neurons that respond to features of different image components in a single assembly. In realistic situations, objects are usually composed of components that are related to each other by numerous grouping criteria. In these cases an extensive spread of assembly labels may cause false conjunctions between the responses evoked by different components of the same object (Fig. 8A,B). However, in case of an intermediate spread the strength of coupling between a pair of neurons will depend on their distance in the interaction skeleton and the strength of the connections between the interposed positions. Thus, in this case, the prevalence of a particular grouping criterion should be reflected by the strength of the respective tag-spreading connections. With a suitable choice of synaptic strengths, it can thus be assured that neurons responding to features of the same image component exhibit a stronger degree of synchrony (or rate covariation) than neurons responding to different but related parts of the image. Thus, gradations in the strength of tag-spreading connections can be used to express hierarchical clustering, or *parsing*, of the visual image (Kaneko, 1990; von der Malsburg, 1981).

The degree to which responses to different image components should segregated perceptually depends on the behavioural context. In the example of Fig. 8C, the task of identifying the small A's requires the segregation of one of the small letters from the background. However, when the large B should be identified responses to the small letters should be integrated into a more global percept. Therefore, it would be advantageous if the degree to which assembly tags will spread would be a dynamic parameter of the cortical network, so that the grain of the resultant grouping process may be adapted to the actual behavioural requirements. Physiological evidence is consistent with a variable spread of synchrony. Recordings from the visual cortex of anaesthetized cats have revealed that the strength of synchronization between neurons in different hemispheres is quite variable over time (König *et al.*, 1995b). As discussed above, episodes of oscillatory firing that were found to be associated with the appearance of synchronization over large cortical distances were intermixed with episodes in which neurons fired more irregularly and long-range synchronization did not occur. Some of the variability observed during anaesthesia is probably due to spontaneous changes in the activity of modulatory systems that influence cortical excitability and the regularity of firing. It was shown recently that in the anaesthetised cat activation of the mecencephalic reticular formation has a pronounced effect on the strength of the interactions between visual cortical neurons (Munk *et al.*, 1996). Electrical stimulation of the reticular formation facilitates oscillatory firing with frequencies in the gamma range (30–80 Hz) and increases the strength of synchrony among spatially separated neurons in the primary visual cortex (Munk *et al.*, 1996; Steriade *et al.*, 1996). Thus, the spread of synchrony is controlled by modulatory systems. Also in awake cats that are engaged in a repetitive behavioural task the extent of synchronizing interactions among cortical cell groups differs between behavioural conditions (Roelfsema *et al.*, 1997b). This is consistent with the proposal that the degree of spread of assembly labels through the interaction skeleton is continuously adapted to the actual behavioural requirements.

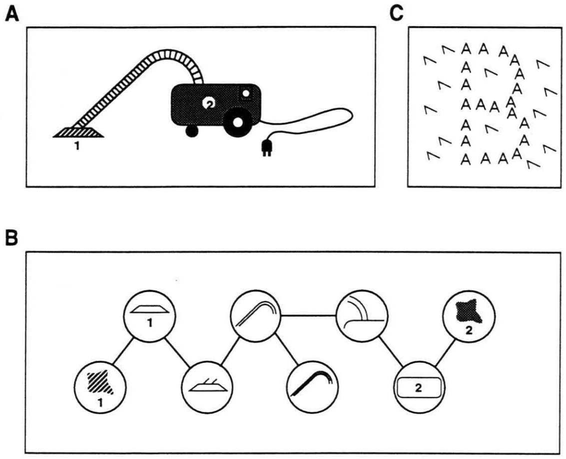

Fig. 8. Limitations of an extensive spread of assembly labels. (**A,C**) Images in which the global shapes are composed of smaller components. In these cases a radical spread of synchronization can be detrimental. (**B**) A subset of the neurons that might be activated by the stimulus in (A). The interaction skeleton includes neurons selective for configurations of the connected geometrical figures. In this example, neurons are indirectly connected to all other responsive cells. If the assembly labels spread through the entire interaction skeleton, neurons selective for the texture of the housing and the cells responding to the form of the head, for example, are incorporated into a single assembly. Thus, illusory conjunctions would occur between the shapes and textures of the respective image components (Modified from Roelfsema *et al.*, 1996).

Role of Assembly Labels in Sensorimotor Coordination

It is necessary that the composition of neuronal assemblies in the visual cortex influences the subsequent selection and execution of behavioural responses. Thus, it would be advantageous, if the motor system could utilize the assembly code in order to avoid erroneous responses that would result if different image components are not segregated appropriately. There is a multitude of parameters that are necessary for specifying a motor act in all its details. The degrees of freedom of the various joints and parameters of movement timing allow an enormous number of different movements that may be performed. Thus, visuomotor coordination entails a transformation from the richness of the visual world into this combinatorial richness of motor activity. Available evidence suggests that many parameters of a movement are extracted from the visual input by independent processes.

Let us, for example, briefly consider the transformations that are required for grasping an object under visual control. Relevant movement parameters that need to be extracted by the visual system include the form and presumed weight of the object and its location with respect to the body. The grip configuration of the hand has to be adapted to the size and shape of the object and is relatively independent of the object's exact location. Conversely, the proximal arm movements that transport the hand to the object depend on the object's position relative to the trunk and are independent of its shape. Thus, the cortical neurons that are related to the implementation of the proximal arm movement and the neurons that implement the hand movement require different types of visual information. Physiological evidence indicates that these cell groups are also anatomically separated to some extent. Proximal and distal arm movements are represented in different subdivisions of the premotor and parietal cortex (Kurata and Tanji, 1986; Rizzolatti *et al.*, 1988, Sakata *et al.*, 1995). Many neurons encoding proximal arm movements to a particular position in the extrapersonal space respond to visual targets at a corresponding location in the visual field (Gentilucci *et al.*, 1988). Such neurons are not easily classified as sensory or motor neurons, because their activity depends on both sensory input and motor planning. The activity of such cells appears to signal the compatibility of a particular proximal arm movement with the location of an object in the peripersonal space.

Similarly, neurons related to a specific kind of hand movement, for instance precision grip, respond before and during the execution of this movement. Many such cells exhibit visual responses to stimuli for which this type of grasping is appropriate (Rizzolatti *et al.*, 1988; Rizzolatti and Gentilucci, 1988, Sakata *et al.*, 1995). This indicates that the different movement components are programmed within parallel processing streams from the visual to the motor cortex (Goodale and Milner, 1992). However, such a modular implementation is susceptible to interference if several features are present simultaneously, as is the case when more than one object is within reach.

In this situation activity related to incompatible movement components is evoked (Schall and Hanes, 1993), like the option to perform a movement of the arm to different regions of the peripersonal space at the same time, which is obviously impossible. Thus, if multiple visual stimuli are present, multiple and contradictory premotor signals are generated within each module. These conflicts are resolved by a competition in which neurons related to the most salient or behaviourally relevant stimulus will eventually win (Schall and Hanes, 1993). In this selection process it is of paramount importance that in different modules movement components related to the same visual object prevail. If a proximal arm movement to one of the objects is selected it should not be combined with preshaping of the hand for a different visual object. Thus, in the presence of multiple objects that can be acted upon, the motor system also suffers from a binding problem. Such interference can be circumvented, however, when neurons with premovement activity related to the same visual object participate in assembly formation. For the present purposes, it will suffice to indicate how the label of an enhanced firing rate can aid in the selection processes. A mechanism that allows synchrony to resolve the binding problem in the motor system has been described previously (Roelfsema *et al.*, 1996).

In Fig. 9 an oversimplified scheme is shown in order to illustrate the effects of assembly formation on processing in areas related to response selection and execution. Two objects are depicted that might be grasped by a monkey. Both objects evoke their own pattern of premovement activity in parallel (Fig. 9B). The first object, a banana, induces neuronal activity that is related to a grasping with the whole hand and an arm movement to its the spatial location (stippled lines). The second object, a leaf, evokes activity related to a precision grip. This is a hand movement in which the index finger and thumb are used for grasping. The leaf also evokes activity related to an arm movement to its spatial location (continuous lines). Neurons related to different movement components evoked by the same object are connected through the interaction skeleton (the mechanisms subserv-

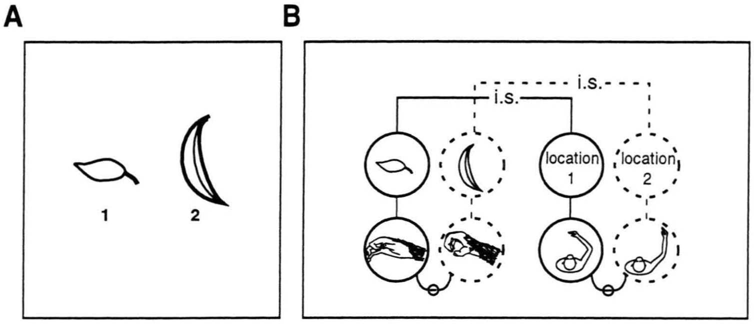

Fig. 9. Assembly formation can affect response selection in the motor cortex. (**A**) Visual image composed of two possible targets for a grasping movement. (**B**) Neurons that are selective for 2 different feature domains evoke premovement activity. Groups of neurons at the left exhibit activity related to hand movements. Activity related to whole-hand prehension is evoked by the shape of the banana, whereas the leaf should be grasped with a precision grip. Groups of neurons at the right are selective for the location of the stimuli in movement space. These cells activate neurons that are related to proximal arm movements toward the position of the leaf (location 1) and the banana (location 2), respectively. Dashed circles, assembly of neurons that is activated by the banana. Solid circles, cell assembly activated by the leaf. Inhibitory connections (−) exist between neurons with activity preceding incompatible movement components. i.s., interaction skeleton that links neurons that respond to features of the same visual object.

ing the selectivity of this linking have been discussed above, see Fig. 7).

Let us assume, for example, that activity in the pathway related to the hand movement has converged to a state in which whole-hand prehension, which is appropriate for the banana, is being planned. This implies that activity of neurons devoted to whole-hand prehension is stronger than activity of neurons related to precision grip. It can be seen that neurons that transport the hand to the location of the banana can benefit, through the interaction skeleton, in *their* competition from this enhanced activity. Therefore, the spread of an enhanced activity level through the interaction skeleton helps to avoid the combination of movement components that are evoked by different objects. This does not imply that these particular cells should always collaborate. An interchange of the position of the two objects, for example, would connect different cell groups through the interaction skeleton (as in Fig. 7) and, therefore, promote cooperative interactions between different cell groups.

Physiological Evidence for Sensorimotor Assemblies

If assembly formation contributes to the selection of movement components evoked by a single object, assembly labels should spread all the way from the visual to the motor cortex. Is there direct evidence for the incorporation of visual and motor cortical neurons into single assemblies?

In monkeys, spatially separate neurons in the motor cortex and frontal cortex can synchronize their discharges on a millisecond time-scale (Kwan *et al.*, 1987; Murthy and Fetz, 1992; Sanes and Donoghue, 1993; Vaadia *et al.*, 1995). Remarkably, there is also evidence that synchronization occurs between cell groups in widely separated areas of the cerebral cortex. In monkeys, synchronization between sensory and motor cortical areas has been reported (Murthy and Fetz, 1992; Bressler *et al.*, 1993). Similar results were obtained in a recent study in awake behaving cats that were trained in a task in which they had to respond to a sudden change of a visual pattern (Roelfsema *et al.*, 1997b). In these cats, local field potentials were recorded with electrodes chronically implanted in various areas of the visual, parietal and motor cortex. Figure 10 shows spatial pattern of synchronization strength among the areas from which recordings were obtained in episodes during which the cats paid attention to the visual stimulus. The data show that synchronization occurs not only among areas of the visual cortex (Engel *et al.*, 1991b; Frien *et al.*, 1994; Nelson *et al.*, 1992), but also between areas of the visual and parietal cor-

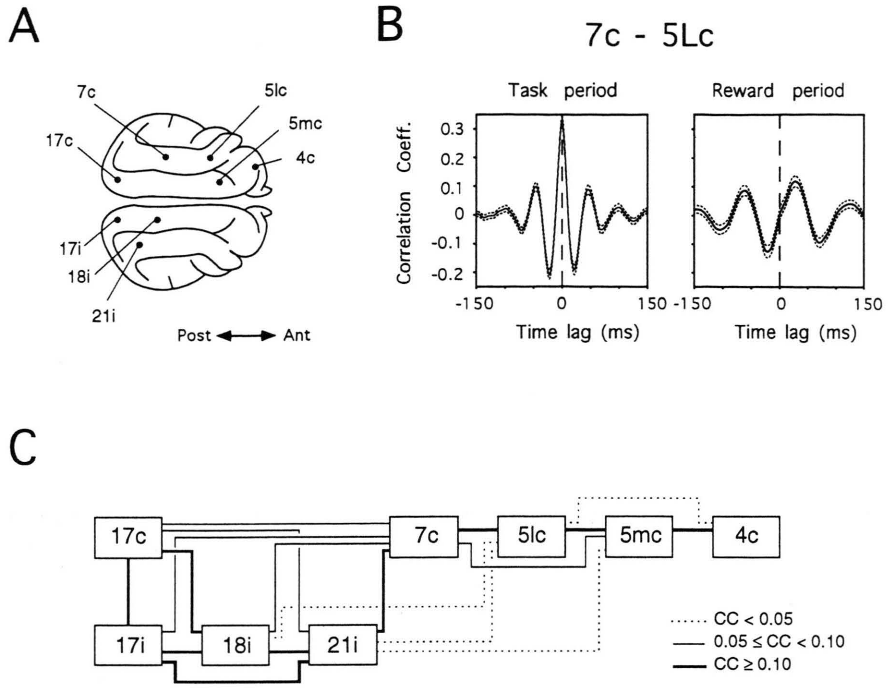

Fig. 10. Synchronization between areas of the visual, parietal and motor cortex in awake behaving cats. The cats were situated unrestrained in a testing box and were trained to press and release a lever in response to visual stimuli. Local field-potentials were recorded with transcortical electrodes chronically implanted in several areas of the visual and parietal cortex as well as in the primary motor cortex. (**A**) Location of the recording sites. Electrodes were implanted in areas 17, 18 and 21 of the visual cortex, in areas 5 and 7 of parietal cortex and in the forepaw representation in area 4 of the motor cortex. c, recording sites contralateral to the forepaw used by the cats. i, recording sites ipsilateral to the forepaw used by the cats. (**B**) Crosscorrelation function between the field potentials recorded in area 7 and area 5 l of the parietal cortex during the task period (left) and during the reward period (right). Stippled lines indicate the 95% confidence intervals. Note the prominent center peak aligned on time 0 during the task period that is indicative of synchrony without time-lag. During the reward epoch, on the other hand, a time lag of more than 15 ms occurred in the interaction between these areas. (**C**) Pattern of synchrony in the task episode. Areas that are strongly synchronized appear close together in this schematic, and areas that are weakly synchonized, or do not synchronize at all appear far apart. Upper row, areas contralateral to the forepaw that the cat used to respond. Lower row, areas ipsilateral to this forepaw. Thick lines indicate strong correlation (correlation coefficients larger than 0.10), thin and hatched lines show weak, but still significant interactions (correlation coefficients smaller than 0.10 or smaller than 0.05, respectively). The diagram shows that precise synchrony is a global cortical phenomenon that is not restricted to the visual cortex. (Modified from Roelfsema *et al.*, 1997b).

tex, and between areas of the parietal and motor cortex. The pattern of synchronization strength reflects the functional relations among cortical areas rather than their spatial vicinity. Synchronization between parietal area 7 and contralateral visual area 21, an area that occupies a relatively high position in the hierarchy of visual areas, is stronger than synchrony between area 7 and the ipsilateral primary visual cortex, in spite of a much smaller spatial separation of the latter areas (Fig. 10A,C). During the task episodes the predominant type of interareal interaction was synchronization with close to zero ms time-lag. In behavioural epochs during which the animals were reward with cat food, however, zero time-lag synchrony was lost and large, unsystematic phase shifts occurred between field potentials in different areas (Fig. 10B). These changes in the synchronization patterns and their close relation to behavioural conditions indicate that interareal interactions are highly flexible.

It should be noted, however, that in this study no synchronization was found between areas that are functionally most remote, like the primary visual and primary motor cortex (Fig. 10C). In contrast, Bressler *et al.* (1993) reported strong synchronization between the same two areas in awake monkeys. Thus, it remains unclear, at present, whether synchronization on a millisecond time-scale can function as a glue to bind neurons in such remote cortical regions together. An attractive speculation, in this respect, would be that synchronization on a slower time scale is more suitable for incorporating neurons in widely separated cortical regions into a single assembly. Synchronization (or rate-covariations) on a slower time-scale should allow the tag-spreading process to cross the many synapses that separate the visual cortex from the motor cortex.

Concluding Remarks

I have discussed the possible functional significance of assembly labels in the visual cortex, and in other regions of the cerebral cortex. Assembly labels may bind distributed neuronal activity into coherent representational states. For the visual system this translates into integrating visual responses into a coherent percept of a visual image. In the parietal and motor cortex, tag-spreading could serve to bind distributed activity related to movement components into a representation of a compound movement.

At present, these proposals are fiercely debated among neuroscientists. In particular, much controversy exists around the temporal precision of the tag-spreading process (e.g. Shadlen and Newsome, 1994). A number of authors have tried to influence figure-ground segmentation by manipulating synchronization among cortical neurons using stimuli that flicker with high frequencies. These experiments revealed that a temporal offsets of a few milliseconds between flickering image components exert only a small influence (Leonards *et al.*, 1996) or no influence at all (Kiper *et al.*, 1996) on perceptual grouping. Unfortunately, it is unclear at present to which extent synchrony can actually be imposed by the use of flickering stimuli. Most of the studies on synchronization among visual cortical neurons so far have been concerned with synchronization that was not locked to temporal features of the visual stimulus but that was generated by the cortical network itself.

It is not known whether the differences in the strength of synchronization on a millisecond time-scale are strong enough to have a substantial influence on subsequent cortical processing (e.g. Livingstone, 1996). The impact of a change in the strength of synchrony is obviously related to the sensitivity of neurons at other processing stages for the temporal structure of incoming synaptic events. There is considerable debate about this question. Some authors have proposed that cortical neurons are rather insensitive for the precise temporal structure of post-synaptic potentials (Shadlen and Newsome, 1994). However, others have suggested that cortical neurons are exquisitely sensitive to millisecond precise synchrony and behave as coincidence detectors (König *et al.*, 1996; Softky and Koch, 1993; Softky, 1995). The results obtained in squinting cats that were reviewed above are of relevance for this debate. At the early levels of the visual cortical hierarchy responses evoked through an eye that participates in conscious visual perception and responses evoked through an eye that is suppressed only differ in the strength of synchrony (Fries *et al.*, 1997; Roelfsema *et al.*, 1994). In contrast, in higher visual cortical areas neurons responsive to the dominant eye have an enhanced firing rate (Sheinberg *et al.*, 1995). This supports the conjecture that a high degree of synchronicity results in higher activity levels at subsequent processing stages.

Synchronization may have different functions than just feature binding. In the primary auditory cortex, for example, most neurons do not respond to a prolonged tone of constant frequency with a change in their firing rate, but with an enhanced level of synchrony (deCharms and Merzenich, 1996). This finding is, however, not inconsistent with the proposal that the strength of synchronicity among cortical neurons affects firing rates at subsequent processing stages.

In the present article it was argued that the time-scale of the tag-spreading process is not the critical issue. The arguments reviewed above were raised against the involvement of millisecond precise synchronization in perceptual grouping. However, I suggested that tag-spreading also occurs at slower time-scales. At these slower time-scales it presumably corresponds to shifts of visual attention. It seems likely that the time-scale issue cannot be settled based on the experimental evidence that is currently available. Nonetheless, compelling evidence exists for a functional role of tag-spreading at both fast and slow temporal scales. Future experiments should probably attempt to make the link between feature binding and tag-spreading stronger by directly comparing the distribution of assembly labels to the perceptual judgements made by awake experimental animals.

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