The Role of Neuronal Synchronization in Response Selection: A Biologically Plausible Theory of Structured Representations in the Visual Cortex

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Abstract

Recent experimental results in the visual cortex of cats and monkeys have suggested an important role for synchronization of neuronal activity on a millisecond time scale. Synchronization has been found to occur selectively between neuronal responses to related image components. This suggests that not only the firing rates of neurons but also the relative timing of their action potentials is used as a coding dimension. Thus, a powerful relational code would be available, in addition to the rate code, for the representation of perceptual objects. This could alleviate difficulties in the simultaneous representation of multiple objects. In this article we present a set of theoretical arguments and predictions concerning the mechanisms that could group neurons responding to related image components into coherently active aggregates. Synchrony is likely to be mediated by synchronizing connections: we introduce the concept of an interaction skeleton to refer to the subset of synchronizing connections that are rendered effective by a particular stimulus configuration. If the image is segmented into objects, these objects can typically be segmented further into their constituent parts. The synchronization behavior of neurons that represent the various image components may accurately reflect this hierarchical clustering. We propose that the range of synchronizing interactions is a dynamic parameter of the cortical network, so that the grain of the resultant grouping process may be adapted to the actual behavioral requirements.

It can be argued that different aspects of purposeful behavior rely on separable processes by which sensory input is transformed into adjustments of motor activity. Indeed, neurophysiological evidence has suggested separate processing streams originating in the primary visual cortex for object identification and sensorimotor coordination. However, such a separation calls for a mechanism that avoids interference effects in the presence of multiple objects, or when multiple motor programs are simultaneously prepared. In this article we suggest that synchronization between responses of neurons in both the visual cortex and in areas that are involved in response selection and execution might allow for a selective routing of sensory information to the appropriate motor programs.

INTRODUCTION

Neurophysiological research during the last two decades has revealed an unforeseen organizational complexity of the visual cortex (Felleman & Van Essen, 1991; Livingstone & Hubel, 1988; Maunsell & Newsome, 1987; Mishkin et al., 1983; Zeki, 1993; Zeki & Shipp, 1988). The visual field appears to be represented many times, in a multitude of cortical areas that are functionally specialized. This functional subdivision is reflected in the response selectivity of neurons that differs between the various visual areas. Thus, different properties of a visual stimulus are represented in distinct areas of the visual cortex, and a single stimulus is likely to activate neurons in many of these areas. The population of neurons that are activated by a single object may be called a cell assembly (Hebb, 1949). This distributed code is an economic and flexible representational strategy, because combinatorial considerations indicate that a restricted number of neurons suffice to encode a wide range of stimuli. In this coding scheme, a single feature selective neuron can participate at different times in a large number of different assemblies, and newly encountered objects are readily accommodated as new constellations of activated cells.

Natural visual scenes typically contain many objects, and a major disadvantage of the assembly representation as advocated by Hebb is its inability to encode more than a single object without confusion of features that belong to different image components. Von der Malsburg (1981) called this problem the superposition catastrophe (Fig. 1A and B). A representational strategy that resolves these ambiguities should keep track of the features of individual objects and distinguish these from features of other objects or the embedding background. One possible strategy to circumvent such ambiguities relies on cardi-
Figure 1. Schematic illustration of the binding problem and possible solutions. (A) As an example, we consider a network consisting of only 4 feature detectors: two detectors of form and two detectors of texture (bottom). If one object is presented (top) the representation is unambiguous. (B) However, if several objects are presented an ambiguity arises (top): the actual conjunctions of features cannot be inferred from the pattern of active cells (bottom). (C) Resolution of ambiguities by "cardinal cells." Single neurons receive input from a subset of feature selective neurons, and thus acquire selectivity for a feature conjunction. If, for example, a stippled triangle and a hatched square have been presented, convergent connections (thick arrows) activate the appropriate cells. A mechanism is required for restricting activation to those neurons that represent the appropriate conjunctions, since in the presence of a hatched square and a stippled triangle all neurons might receive the same amount of excitatory input. One possibility would be to multiply the architecture and restrict the detection of conjunctions to limited parts of the visual field. Neurons representing conjunctions in a larger aperture, at a subsequent processing stage, may then be constructed by convergence (Fukushima, 1980). (D) Resolution of ambiguities by temporal coding. Neurons that represent features of the same object synchronize their discharges as symbolized by the clocks. Synchronizing interactions are indicated with thick arrows. Note that a different feature constellation would require the activity of the neurons to synchronize in other combinations (stippled arrows). Thus, a mechanism is needed that restricts synchronization to the appropriate groups of cells.

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Experimental and theoretical investigations of the mechanisms responsible for synchronization of the appropriate responses suggest that the topology of intracortical connections plays a prominent role in shaping the assemblies of cells distinguished by synchronous activity (Singer, 1993). In many recent neural network models, synchronizing connections have been proposed to link only those cells that are likely to encode properties of the same object—for example, neurons with a similar orientation preference, receptive field location, disparity tuning, direction selectivity, or color selectivity (Hummel & Biederman, 1992; Murata & Shimizu, 1993; Schillen & König, 1994; Sompolinsky et al., 1990; Sporns et al., 1989; von der Malsburg & Buhmann, 1992). However, single objects may consist of parts that exhibit rather dissimilar features, and it is an open question whether, and if so, how neurons that respond to dissimilar features of a single object get synchronized.

Provided that synchrony is used to selectively associate neuronal responses for further joint processing, it becomes an important issue how synchrony is evaluated by subsequent processing stages. The pattern of synchrony among responses of neurons in visual areas must affect the preparation and execution of motor acts. Evidence is consistent with the proposal that, on the way from sensory to motor cortex, neuronal activity related to sensory stimuli is gradually transformed into premovement activity through parallel pathways (Goldberg & Segraves, 1987; Goodale & Milner, 1992; Mishkin et al., 1983). In the last section of this article we suggest how the pattern of synchronization among visual responses may be exploited for the coordination of these parallel transformations, in particular, in the presence of more than a single object.

**PHYSIOLOGICAL EVIDENCE FOR A FUNCTIONAL ROLE OF NEURONAL SYNCHRONIZATION**

Experimental evidence obtained in the visual cortex of cats and monkeys supports the conjecture that neuronal synchronization might play a prominent role in binding the distributed responses evoked by an object into a coherent percept. When activated with a single coherent stimulus, neurons in the primary visual cortex readily engage in synchronous discharges (Eckhorn et al., 1988; Engel et al., 1990; Gray et al., 1989; Ts'o et al., 1986). If synchronization serves binding, one expects that synchronization should occur selectively between neurons that respond to segments of the same contour, but not between neurons that are activated by segments belonging to different contours. Experiments in cats and monkeys support such a dependence of synchronization on the configurations of a visual stimuli (Engel et al., 1991a; Gray et al., 1989; Kreiter et al., 1992).

In Figure 2, dependence of synchronization on stimulus configuration is illustrated for a pair of neurons in the cat primary visual cortex (Engel et al., 1992a). When the neurons were activated with a single light bar moving over their receptive fields, they fired in close temporal synchrony. However, when the neurons responded to different light bars moving in opposite directions, synchronization was abolished. These results are in accordance with the conjecture that neuronal synchronization depends on the continuity of contours and the coherence of motion, important criteria for perceptual grouping. Subsequent studies (Engel et al., 1991b; Nowak et al., 1995) demonstrated that neuronal synchronization also occurs between neurons in the primary visual cortex of the two hemispheres. This, too, is in agreement with the binding hypothesis: the representation of the visual field is divided between the two hemispheres along the vertical meridian. Therefore, perceptual grouping must involve interactions between different hemispheres. Insight into the pattern of connectivity that supports synchronization was gained in a control experiment, using cats in which the corpus callosum had been sectioned. In these animals interhemispheric interactions were lost, suggesting that synchronization is brought about by cortico–cortical connections (Engel et al., 1991b; Munk et al., 1995).

If synchrony serves to integrate responses to different features of a visual object, it should also occur between visual areas, where neurons are tuned to different aspects of the visual world. Indeed, synchronization has been found between the responses of neurons in various areas of the visual cortex of cats and monkeys (for an extensive overview of the literature see Singer, 1993; Singer & Gray, 1995). For example, neurons in the cat 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., 1991c). 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.

The proposed role of neuronal synchronization implies that its disruption should impair visual perception. Misalignment of the eyes during early development has a pronounced influence on a wide range of visual functions. Studies on the interactions between visual cortical neurons in squinting animals have shed some light on the neurophysiological correlates of these disturbances. Since the pioneering studies of Hubel and Wiesel (1965) it is known that in squinting animals visual cortical neurons lose binocularity and may be activated through one eye only. In a study of intracortical interactions in
cats with divergent squint König et al. (1993) found that synchronization occurs only between cells driven by the same eye, but not between neurons dominated by different eyes. Interactions between cells activated by the deviated eye were of similar strength as those between cells dominated by the nondeviated eye. This agrees with the fact that most animals and humans with divergent squint perform equally well with the two eyes on standard visual tests, but exhibit a remarkable inability to integrate visual information provided by the two eyes (for review, see von Noorden, 1990). The lack of synchronization between neurons driven by different eyes is paralleled by a drastic reduction in the number of intracortical connections linking cells of different ocular dominance (Löwel & Singer, 1992). This is further support for the notion, suggested by the split brain experiments, that synchronization on a millisecond time scale is mediated by cortico-cortical connections.

In contrast to the situation in divergent strabismus, convergent squint often results in a syndrome of perceptual disturbances of the deviated eye that is called strabismic amblyopia. Animals and humans with strabismic amblyopia do not use the deviating eye for fixation. Signals entering through this eye are readily suppressed when both eyes are open, and are not accessible by conscious experience. In search of neurophysiological correlates of strabismic amblyopia, response properties of neurons at various stages along the visual pathways of amblyopic cats and monkeys have been investigated. A surprising finding was that in the visual centers that were studied—including the primary visual cortex—neurons dominated by the amblyopic eye are as numerous as those activated through the normal eye, and do not exhibit gross changes in response characteristics (Blakemore & Vital-Durand, 1992; Chino et al., 1983; Crewther & Crewther, 1990; Freeman & Tsumoto, 1983). In a recent study, we investigated the intracortical interactions in the primary visual cortex of cats with a convergent squint that had developed a behaviorally verified acuity loss of the deviated eye (Roelfsema et al., 1994). In these animals, synchronization between neurons dominated by the amblyopic eye was found to be much weaker than that between neurons dominated by the normal eye. Neurons dominated by the amblyopic eye remained responsive to gratings whose spatial frequency was higher than that resolved by the animals when tested behaviorally through this eye; a seemingly paradoxical finding that is, however, in line with earlier studies (Blakemore & Vital-Durand, 1992; Chino et al., 1983; Crewther & Crewther, 1990). In contrast, the strength of
synchronization between responses evoked through the amblyopic eye was reduced drastically for these fine gratings. These results suggest that synchronization of neuronal responses on a millisecond time scale plays an important role in the normal functioning of the visual cortex. Amblyopic patients report upon closure of their normal eye that continuous lines may appear interrupted, and conversely, that separate contours may appear to be connected (Hess et al., 1978). These visual distortions are fully compatible with the hypothesis that synchronization serves to label the responses that are evoked by a single contour; and to distinguish these from the responses to other image components. Disturbance of synchrony should result in erroneous grouping.

The results reviewed so far were obtained in the visual system. However, synchronization between responses with a precision in the millisecond range has also been found within and between areas of the somatosensory and motor cortex (Georgopoulos et al., 1993; Murthy & Fetz, 1992; Sanes & Donoghue, 1993). This suggests that neuronal synchronization may fulfill similar functions in other sensory modalities, and that it may even play a role in the coordination of motor activity. Synchronization of cortical field potentials that reflect the activity of large populations of cells was even found between areas of the visual, parietal, and motor cortex (Bressler et al., 1993; Roelfsema et al., 1995), suggesting that the assemblages of cells that synchronize their discharges may extend over large regions of the cortex. This temporal coordination of activity in the visual and motor cortex has been suggested to play a role in visuomotor integration (Bressler et al., 1993). We shall return to this hypothesis in the section on Synchrony Selection on the Basis of Synchronizing of this paper.

**THE MICROSTRUCTURE OF NEURONAL SYNCHRONIZATION**

In this section we sketch the raw outlines of a theory on connectional architectures that cause synchronous firing of neurons that respond to related image components.

The rules according to which the visual system groups components of a visual image were explored extensively by the Gestalt psychologists at the beginning of this century (Wertheimer, 1923). More recent psychophysical work on perceptual grouping has concentrated on texture segregation (for review, see Bergen, 1991). Early workers in the field of texture segregation stressed the importance of feature similarity for grouping. Image components with similar color, shape, orientation, or movement direction are likely to be grouped together (Beck, 1966; Julesz, 1984; Olson & Attnave, 1970). Subsequent studies revealed, however, that image regions containing gradually changing features are also perceived as being coherent (Nothdurft, 1993). In this case, segmentation occurs in areas where the texture elements change abruptly. Thus, image components with quite dissimilar properties may be grouped if they are connected through an image region in which texture elements change gradually from one extreme to the other. This suggests that local similarity can override dissimilarities that are manifest at a more global scale.

The evidence reviewed above suggests that synchronization is mediated by intracortical connections. However, cortico-cortical connections are heterogeneous and subserve a range of different functions (Felleman & Van Essen, 1991). Important functions mediated by cortico-cortical connections include the relay of retinal input from one level of processing to the next, and the relay of top-down influences from higher to lower levels in the processing hierarchy. At present, it is unclear what distinguishes intracortical connections that subserve different functions, and whether synchronizing connections belong to a special class of connections. In the following, we shall refer to connections that mediate synchronization between neuronal discharges as synchronizing connections.

To account for the selectivity of synchronization, and in order to accommodate feature similarity as a grouping criterion, many authors have suggested that synchronizing connections should exist between cells with similar feature selectivity (Hummel & Biederman, 1992; Murata & Shimizu, 1993; Schillen & König, 1994; Singer, 1993; Sompolinsky et al., 1990; Sporns et al., 1989; Tononi et al., 1992; von der Malsburg & Buhmann, 1992). In accordance with this prediction, intracortical connections have been found to selectively interconnect neurons with similar orientation or color selectivity (Gilbert & Wiesel, 1989; Gilbert, 1992; Livingstone & Hubel, 1988; Malach et al., 1993, 1994; Ts'o & Gilbert, 1988). One of the most significant features for grouping is probably the position of an image component in the visual field. And there is indeed evidence that the grouping criterion of proximity (Rock & Palmer, 1990) is reflected in the architecture of intracortical connections. Connections within and between the different visual areas typically link neurons with receptive fields at approximately corresponding visual field positions (Salin et al., 1989; Zeki & Shipp, 1988). These considerations lead to the following postulate:

**1. Neurons exhibiting selectivity for similar features should be linked with synchronizing connections.**

Neurons that respond to similar visual features are more likely to be coactivated during the process of perception than cells that respond to unrelated aspects of the visual world. Singer (1993) proposed that the selectivity of the connections that mediate the synchronizing interactions may be shaped by visual experience during development. The plausibility of this conjecture is supported by neural network studies (Hummel & Biederman, 1992; König et al., 1992) that investigated the effects of visual input on the architecture of synchronizing connections using correlation rules of synaptic plas-
ticity. In addition, recent experimental evidence suggests that during early postnatal development synchronizing connections are stabilized according to a correlation rule (Löwel & Singer, 1991). Therefore, (1) may be rephrased as follows:  

(1A) Neurons that are frequently coactivated during perception should be linked with synchronizing connections.

Such an architecture of synchronizing connections is suitable to support grouping of image components that frequently occur simultaneously during perception, but does not suffice as an explanation for the grouping operations in other instances. In Figure 3 another potent grouping criterion, connectedness, is illustrated. Note that there is no a priori reason for biasing synchronizing connections between the nodes that are numbered 1 through 4. Thus, a particular node can be connected to each of the other nodes and similarity of features cannot be the reason for the grouping. Furthermore, connectedness is a property that cannot be computed by neurons receiving information from a subregion of the image. If a neuron’s receptive field covers only a subregion of the visual field, the cell is unable to distinguish between connected and disconnected components, since they may be connected outside the receptive field. This illustrates some of the difficulties encountered in computing connectedness with networks that rely solely on activity propagation. (For a detailed account of computational problems associated with connectedness detection see Minsky & Papert, 1969.) Fortunately, the situation is more favorable for networks consisting of neurons that possess an additional coding dimension, like the precise timing of their action potentials. In order to explain how the dynamics of neuronal synchronization can reflect connectedness in complicated situations (as in Fig. 3) let us consider how the local differences between Figures 3A through D at positions where contours are in close proximity are reflected in the pattern of activity of orientation-selective neurons. In Figures 4A and C, subsets of the neurons that might be activated by two different configurations of neighboring contours are illustrated. It is likely that slightly different groups of neurons will be responsive in the two situations. Since it is plausible that only connections between cells that are activated by a particular stimulus configuration influence the synchronicity, different sets of synchronizing connections are likely to get involved in the two conditions. We refer to this subset of effective connections as the interaction skeleton (Fig. 4B & D). It is in accordance with (1A), psychophysical (Field et al., 1993), and anatomical evidence (Fitzpatrick et al., 1993; Schmidt et al., submitted) to suppose that synchronizing connections predominantly interconnect cells with nearby receptive fields that are approximately collinear (see also Mitchison & Crick, 1982). Thus, the difference between the sets of activated synchronizing connections in Figures 4A and C could account for the experimentally validated notion that synchronization occurs between responses to segments of the same contour, but not between the responses to different contours (Engel et al., 1991a; Gray et al., 1989). A crucial question is whether the local connections between cells with neighboring receptive fields are prone to induce a globally synchronized state in which all neurons responding to different segments of the same contour would participate. Simulation studies indicate that local synchronizing interactions may indeed cause synchronization between all neurons that are connected by the interaction skeleton (König & Schillen, 1991). Thus, the interaction skeleton consists of links; neurons with their synchronizing connections.
These links are switched on by contour segments of appropriate orientation if located within the respective receptive fields. A local change in the configuration of contours results in the activation of different links, which, in turn, results in a global change in the synchronization pattern (Figs. 4B & D). Note that this applies to all positions of Figure 3 where contours are in close proximity. Hence the synchronization behavior of neurons reflects how the numbered nodes are connected.

In short:

(2A) A local change in the subset of active neurons can lead to a global change in synchronization behavior.

(2B) Networks that utilize synchrony as a coding dimension can detect connectedness and use it as a grouping criterion.

Similar arguments may apply to texture segregation. As mentioned above, image regions in which the orientation, movement direction, or color of texture elements changes gradually get segregated from other regions at positions at which these features change abruptly (Nothdurft, 1993). The local similarity of features within a coherent image region may dynamically define an interaction skeleton in which neurons that are selective for differing features are connected through cells with preferences for intermediate features.

We shall now generalize these conjectures to interaction skeletons linking neurons selective for different feature dimensions. If feature domains are unrelated, as is the case for texture and motion, neurons representing a particular feature of the first domain should be able to synchronize with cells representing any feature of the other domain in a stimulus specific way. Thus, if an object with a particular texture moves from left to right, neurons that respond to rightward directed movements should be able to synchronize their responses with those of cells that are selective for that particular texture. But these neurons should not synchronize their responses if activated by different objects, one moving from left to right but lacking the texture, the other having the appropriate texture but being stationary.

In several studies on synchronization in artificial neuronal networks, stimulus dependent synchronization has been achieved by implementing mechanisms that
allow for rapid activity dependent changes in synaptic efficacy of synchronizing connections (Murata & Shimizu, 1993; Sporns et al., 1989; von der Malsburg & Schneider, 1986). Connections between cells that are activated by a new stimulus will be potentiated, and the enhanced efficacy guarantees that synchronization remains restricted to the appropriate assemblies when additional stimuli are introduced.

In our theory, such rapid synaptic changes are not required. We base our argument 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; a large proportion of these cells is, in addition, selective for the color 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 in to particular, shared feature domains and at the same time exhibit tuning to distinct domains. We propose that neurons having a similar selectivity for a shared feature domain should be linked with synchronizing connections (in accordance with (1)). Figure 5 illustrates a network that consists of neuronal groups, each of which is selective for two feature domains. Neurons in one cluster are selective for texture and position, those in the other cluster for shape and position. Thus, visual field position is the feature domain that the two clusters have in common, and synchronizing connections link neurons whose receptive field positions are similar. As a consequence, neurons of the two clusters will synchronize their discharges if coactivated and if their receptive fields are close together (Fig. 5). 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 than one feature dimension. Thus, in Figure 5 visual field position functions as a linking dimension.

The information about the association of a particular texture with a particular shape would also be implicitly available without synchronization because of the common location of the respective receptive fields. But synchronization between responses makes this information explicit, which is advantageous, since it may cause joint processing of these responses. It has been proposed that cortical cells are particularly sensitive to simultaneously arriving synaptic input and act as "coincidence detectors" (Abeles, 1982; Softky & Koch, 1993; but see Shadlen & Newsome, 1994). Synchronization among discharges of converging afferents is therefore likely to enhance the probability that postsynaptic cells are activated. Figure 5C 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 Figure 5C 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. This illustrates how the evaluation of temporal correlation by coincidence detection could be used to generate translational invariant response properties (Hummel & Biederman, 1992). These properties are found, for example, in visual areas of the inferotemporal stream (Ito et al., 1995; Kobatake & Tanaka, 1994; Tošev et al., 1994). In these areas, there are neurons that are selective for the conjunction between a visual shape and a particular texture (Kobatake & Tanaka, 1994; Komatsu & Ideura, 1993). However, their responses to multiple, simultaneously presented objects have not yet been investigated systematically.

The possibility to generate new tuning characteristics by coincidence detection, as illustrated in Figure 5C, is one of the main advantages of neuronal synchronization. If A, B, and C are feature domains, and if conjunctions of the type \( A \cup B \) and \( B \cup C \) have been computed by the network, conjunctions of the type \( A \cup C \) 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 \( A \cup B \cup C \), and only then can construct cells selective for the presence of \( A \cup C \) in a single image component by having responses of neurons \( A \cup B \cup C \) (for all values of \( j \)) converging onto a further set of cells \( A \cup C \) (Fig. 5D). This indicates that networks that utilize synchronous firing in order to express conjunctions are more economic with respect to the number of units required for the computation of invariant receptive field properties.

In summary:

(3A) If neurons with a corresponding selectivity in the feature domains that they share are linked with synchronizing connections, their coincident firing makes further feature conjunctions explicit.

(3B) Coincidence detectors may translate these coincident firing patterns into a conventional rate coded response selectivity.

When activated by a synchronously firing assembly of cells the coincidence detector should participate in this assembly, since it responds to features belonging to the same object. Therefore, we propose that response of the coincidence detector preserves the temporal structure of the afferent spike trains. We shall refer to the process in which neurons are both activated by, and incorporated into, a synchronously firing assembly as assembly capture.

These considerations, however, do not explain stimulus-dependent synchronization between responses to completely unrelated feature domains. The neuronal groups in the two clusters of Figure 5 share selectivity for visual field position. Indeed, it is this statistical dependence of firing probabilities that allows for the specificity of the synchronizing connections. However, under conditions in which local synchronizing influences result in global synchrony (see below) this scheme can also explain stimulus-dependent synchronization between cells that respond to completely different aspects of the visual world. Figure 6 illustrates a network consisting of three clusters of neurons that are selective for two feature domains. As discussed above, the interaction skeleton is composed of synchronizing connections between those cells that are activated by a particular stimulus configuration. Under conditions in which synchronization between the responses of cells in the left and middle cluster and cells in the middle and right cluster implies coincident firing of cells of the left and right cluster (transitivity), synchrony of firing makes conjunctions between texture and stimulus motion explicit. Activation of distinct subsets of cells of the middle cluster renders different patterns of connections effective, which then mediate synchronization between the outer cell groups. Again, local changes in the pattern of activated neurons may lead to global changes in synchronization patterns, similar to the situation in Figures 4 and 5. Thus, because of the response selectivity of activated neurons in the middle cluster, it is possible to infer which responses in the respective outer clusters are evoked by the same stimulus.

A comparison of Figures 4 and 6 suggests an analogy between the mechanism that causes synchronization between neurons selective for different features domains and the mechanism that allows for the detection of connectedness of contour segments, as discussed above. Neurons that are simultaneously selective for multiple feature domains form links between cells that are tuned for only one of those feature domains. These links are
switched on by the occurrence of the respective feature conjunction in one of the image components; in this way, neurons that are tuned to unrelated feature domains characterizing this image component become connected through the interaction skeleton. Provided that synchronization is sufficiently transitive, it may spread through the interaction skeleton, causing all neurons that respond to the various features of a single object to fire in synchrony.

(4) With neurons that are simultaneously selective for more than a single feature domain, the problem of associating cells into coherently firing assemblies representing a single object is equivalent to the problem of detecting connectedness within the interaction skeleton.

It may seem paradoxical that we utilize selectivity for multiple feature dimensions in order to achieve appropriate synchronization, particularly since we wanted to avoid the representational costs associated with cardinal cells (see Introduction). However, it should be noted that the minimal requirement of our scheme is that neurons be selective for at least two feature domains. The number of neurons necessary to represent all possible conjunctions of two feature domains compares favorably to the astronomical number of cells required to represent conjunctions between all feature domains at the same time. It should be stressed that retinal position is treated as equivalent to the other feature domains and, accordingly, that neurons with restricted receptive fields need only be selective for one additional feature domain—a requirement that is certainly biologically plausible. Moreover, further savings on the number of cells can be made, since not all pairwise conjunctions need to be represented by dedicated neurons. Many conjunctions may be represented by the synchronous firing between neurons that are selective for the first and second feature domain, respectively (as in Fig. 6). The minimal requirement of this scheme is that enough pairwise feature conjunctions are represented by selective neurons in order to connect all neurons selective for the various feature domains indirectly, through the interaction skeleton.

We suggest that the neurons of the anterior inferotemporal cortex that are selective for complicated visual shapes, conjunctions of shapes and textures, or conjunctions of shapes and colors (Kobatake & Tanaka, 1994; Komatsu & Ideura, 1993) should not be equated with
cardinal cells. These neurons are typically invariant for other visual properties, like size or position on the retina (Ito et al., 1995; Kobatake & Tanaka, 1994; Tovee et al., 1994), and therefore, do not suffice for the complete representation of a visual object. We instead propose that these neurons serve as links in an interaction skeleton, and are included in coherently firing cell assemblies that as a whole serve as the representation of perceptual objects.

In their feature integration theory of visual attention, Treisman and coworkers (Treisman & Gelade, 1980; Treisman & Sato, 1990) suggested that the responses of feature selective neurons in a restricted region of the visual field (corresponding to the focus of attention) should be integrated into a coherent percept. A prominent role for visual field position in demarcating the responses that originate from a single image component is also implied in our treatment of receptive field position as an important linking dimension. Indeed, the specificity of intracortical connections within and between visual areas, which predominantly link neurons with similar receptive field locations, is consistent with a prominent role for visual field position in recovering those responses that are evoked by a single image component. However, in comparison with theories that incorporate a single focus of attention, the proposal of utilizing synchronous firing to demarcate the responses evoked by a single image component has a number of advantages. First, multiple neuronal assemblies may coexist without getting confounded, since only neurons that belong to the same assembly exhibit synchronous activity. In contrast, if the responses evoked from the focus of attention are selected for joint processing, only the relations between the responses originating from a single contiguous image region may be recovered simultaneously. Second, the outlines of objects may be highly irregular, and it is unclear how the focus of attention should be adapted to include only the object of interest and not other objects that may be in close proximity or even partially overlapping. Third, the view that visual field position alone might suffice in this respect is probably an oversimplification. When responses from different visual field positions need to be integrated, other criteria like collinearity, good continuation (Singer, 1993), disparity (Murata & Shimizu, 1993) and similarity of color (Schillen & König, 1994) or texture have to be taken into account. This is particularly obvious when objects are partially occluded by others and responses from noncontiguous parts of the visual field have to be integrated into a coherent percept. In these situations, an approach that is solely based on visual field position cannot succeed.

An elegant approach to occlusion was proposed by Hummel and Biederman (1992) in their model for shape recognition based on response synchronization. These authors suggested that neurons responsive to complementary distant collinear line terminations—a situation that occurs when a contour is interrupted by an occlud-
linked with synchronizing connections to groups of cells representing its visual shape.

5. **Feature domains that can be exploited as linking dimensions may be as diverse as the feature dimensions used for perceptual grouping.**

In the foregoing, we defined the interaction skeleton as the subset of activated and interconnected neurons. We suggested that the spread of local synchronizing influences through the interaction skeleton is essential, since it gives rise to synchronization between responses of neurons that are not directly connected (Figs. 4, 6, & 7). Synchronization between neurons that are widely separated in the interaction skeleton is beneficial, since this allows them to represent a virtually infinite number of conjunctions between different features.

Up to this point we have only discussed the topology of the network of synchronizing connections. Equally important are the neuronal processes that generate synchrony, because they determine the effective range of synchronizing interactions, that is, the correlation length within the interaction skeleton. We wish to address a few important results that have emerged from studies on synchronization in neural networks, but shall not go into detail because a thorough discussion of network dynamics would be beyond the scope of this paper.

Irregular firing of neurons that are separated by multiple synapses is incompatible with the establishment of precise synchronization. The accumulation of synaptic delays and conduction times in polysynaptic connections prevents synchronization of units that are distant in the interaction skeleton. However, if units exhibit a regular firing pattern—in particular, oscillations within a narrow frequency band—local synchronizing influences may result in global synchrony of the units that constitute the interaction skeleton (Kö nig & Schillen, 1991). If three units A, B, and C oscillate with the same frequency, and if A is synchronous to both B and C, then by necessity B is also oscillating in synchrony with C. In mathematical terms, oscillations of a single frequency imply transitivity of synchronization. Temporal constraints on
the synchronizing interactions are less severe for units engaging in oscillatory activity than for stochastically firing cells, because in the former case even long transmission and synaptic delays are compatible with the generation of synchrony (Bush & Sejnowski, in press; König & Schillen, 1991). Oscillatory neurons with inhibitory action may postpone the firing of postsynaptic neurons up to the predictable moment when they will fire again, thus causing them to fire in synchrony. Similarly, excitatory interactions between oscillators may mediate synchronizing effects, 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; Glünder & Nischwitz, 1993; Sompolinsky et al., 1990). For these reasons, several studies on synchronization in neural networks have adopted oscillators as basic units (König & Schillen, 1991; Murata & Shimizu, 1993; Schillen & König, 1994; Sporns et al., 1989; von der Malsburg & Schneider, 1986). Many studies on the phenomenon of synchronization in networks composed of oscillators were probably prompted by the finding that neurons in the visual cortex often display stimulus-induced oscillatory activity with a frequency of approximately 40 Hz (Brosch et al., 1995; Eckhorn et al., 1988, 1993; Engel et al., 1990, 1992b; Fries et al., 1994; Gray et al., 1989; Kreiter & Singer, 1992; Nakamura et al., 1992). However, in some studies the existence of these gammatone oscillations was questioned (Tové and Rolls, 1992; Young et al., 1992), or considered to be an epiphenomenon of cortical processing (Bair et al., 1994; Ghose and Freeman, 1992). At present, this issue is still controversial. Nonetheless, evidence is consistent with a prominent role of oscillatory activity in mediating synchronization over large cortical distances. In the anaesthetized cat, episodes of oscillatory firing were found to be associated with the appearance of synchrony over large cortical distances, whereas such long-range synchronization did not occur when neurons fired more irregularly (König et al., 1995).

(6) Oscillatory activity facilitates synchronization over long distances in the interaction skeleton.

We have emphasized the benefits of an extensive spread of local synchronizing influences through the interaction skeleton. On the one hand, a long correlation length permits the binding of responses to features of a single object across different dimensions and modalities. On the other hand, very long correlation lengths, which imply transitivity of synchronization, may also lead to synchronized firing of cells that respond to features of different image components, as illustrated in Figure 8. In realistic situations, objects are usually composed of components that are related to each other by numerous different grouping criteria, like connectedness or similarity of color and texture. Extensive spread of synchronization through the interaction skeleton could thus cause false conjunctions between the responses evoked by different object components. In the case of an intermediate correlation length, synchronization between a pair of neurons will depend on their distance in the interaction skeleton and the strength of the synchronizing connections between the interposed positions. Thus, the prevalence of a particular grouping criterion should be reflected by the strength of the respective synchronizing connections. With a suitable choice of synaptic strengths, it can be assured that neurons responding to features of the same image component exhibit stronger synchronization among each other than with neurons responding to different but related parts of the image, and still weaker or no synchronization with neurons that respond to unrelated image components. Thus, gradations in the strength of synchronization within a network can, in principle, be used to express hierarchical clustering, or parsing, of the visual image (von der Malsburg, 1981; Kaneko, 1990).

(7) The synchronization pattern of a network with intermediate correlation length can express the hierarchical clustering of image components.

The degree to which responses to different image components need to be separated certainly depends on the behavioral context. In the example of Figure 8, the task of switching on the vacuum cleaner requires a separation of the switch from the rest of the housing, whereas locating the vacuum cleaner requires one only to distinguish its different components from the background. Therefore, it would be advantageous if the correlation length were a dynamic parameter of the cortical network, so that the grain of the resultant grouping process may be adapted to the actual behavioral requirements. Physiological evidence is consistent with this possibility. Recordings from the visual cortex of anaesthetized cats have revealed that the strength of synchronization between neurons of different hemispheres is quite variable over time (König et al., 1995). 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 anesthesia is probably due to spontaneous changes in the activity of modulatory systems that influence cortical excitability and the regularity of firing. Munk et al. (1996) showed that in the anaesthetized cat activation of the meencephalic reticular formation has a pronounced effect on the strength of the interactions between visual cortical neurons. We propose that in awake animals the correlation length within the interaction skeleton is also variable and is continuously adapted to the actual behavioral requirements. Behavioral conditions that require the integration of information across different feature modalities or over large regions of the visual field should be associated with oscillatory firing patterns of the activated cell groups. In a study on the interactions between transcortical field potentials in awake monkeys, Bressler et al. (1995) found
that the strength of synchronization between widely separated cortical areas fluctuates during the performance of a visuomotor task. Thus, it should be promising to study changes in the firing modes of large populations of neurons as a function of behavioral state in awake animals.

(8) A dynamic control of the correlation length in the interaction skeleton allows for adjustments of the grain of segmentation to behavioral requirements.

In summary, we have indicated how selective synchronizing interactions between groups of neurons that respond to features in more than one domain may accommodate the wide range of grouping criteria that the visual system utilizes when segmenting a visual scene. The subset of neurons that are activated by a particular stimulus configuration, and the functional architecture of synchronizing connections, define an interaction skeleton through which the synchronizing influences may spread, and whereby the extent of this spread may be dynamically regulated. Obviously, it is necessary that the specific relations between the firing times of the neurons in sensory cortices influence the subsequent selection and execution of behavioral responses. Therefore, in the next section we shall describe how the motor system could utilize the synchrony code to avoid erroneous responses, errors that would result if visual responses evoked by different image components are not segregated appropriately.

**RESPONSE SELECTION ON THE BASIS OF SYNCHRONIZATION**

In this section we adopt the position that the visual system evolved not only to obtain adequate descriptions of visual objects, but also to translate visual input into adequate behavioral responses.

Much remains to be learned about the progression of response characteristics of neurons in the different pathways that link the primary visual cortex with the motor system, but studies in awake monkeys have revealed a number of important properties that constrain theories on sensory-motor integration. Many cells in the so-called association areas that link the sensory cortices with the motor cortex cannot be classified as being either sensory or motor neurons, because their activity depends on both sensory input and motor performance. A well-studied example constitutes the neuronal activity that is related to the visual guidance of eye movements. In the parietal and frontal areas related to the generation of saccadic eye movements, neurons respond to visual stimuli at a particular position in the visual field, or are active during the planning of an eye movement toward a particular position in the visual field (Bruce & Goldberg, 1984). Many of the visual neurons exhibit a strong enhancement of their response to a stimulus inside their receptive field if this stimulus becomes the target for the upcoming saccade (Bushnell et al., 1981; Goldberg &
Bushnell, 1981). Goldberg and Segraves (1987) suggested that the activity of these bimodal visuomotor neurons serves as a premotor signal that is related to the planning of the next saccade. In a natural visual environment, many of these bimodal neurons are likely to be active at the same time and, therefore, a selection must take place among such premotor signals before they are permitted to trigger the next eye movement (Goldberg & Segraves, 1987). In line with this hypothesis, it has recently been shown that neurons in the frontal eye fields also respond to distractors that do not become the target for the next saccade, but these responses were found to be attenuated during the selection of the appropriate eye movement (Schall & Hanes, 1993). Thus, if multiple visual stimuli are present, multiple and contradictory premotor signals are generated at the same time. Each signal reflects the option to perform different targeting movements. These conflicting premotor signals appear to engage in a competition in which the most salient, or behaviorally relevant, stimulus will eventually win.

Comparable observations have been made in the motor cortex of monkeys—for example, during the execution of arm movements. Many neurons in the premotor cortex of monkeys exhibit visual responses to cues that instruct the animal to perform a particular arm movement, but fail to respond if the same visual stimulus is behaviorally irrelevant (Boussaoud & Wise, 1993; Kurata & Tanji, 1985). Therefore, these cells do not seem to reflect purely visual aspects of the cue. However, many of these cells are also not unconditionally related to motor performance, since they might not respond if another visual cue (di Pellegrino & Wise, 1993) or a stimulus of another sensory modality instructs the very same movement (Vaaadia et al., 1986). It is apparent that, in analogy to the situation in eye movement control, these neurons exhibit premovement activity signaling the compatibility of a particular movement with a sensory feature.

In summary:

(9A) In the association cortex and in the premotor cortex sensory stimuli evoke neuronal activity signaling the compatibility of a particular movement with this stimulus.

(9B) Multiple stimuli may induce responses in pools of neurons that are related to incompatible movements, and which engage in competitive interactions.

Unlike eye movements, limb and body movements involve multiple joints and have many degrees of freedom. These have to be specified by the visual input if, for example, an arm movement is guided by vision. This implies that the visual signals have to be transformed into a format that can be decoded by the motor system. Let us consider the task of grasping an object that is positioned somewhere in the extrapersonal space. 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. This is relatively independent of the object’s exact location. Conversely, the proximal arm movements have to be specified by the object’s location with respect to the trunk, and are independent of its shape.

At processing stages that are close to the effectors, like the primary motor cortex, neurons related to the proximal and distal arm movements are well separated. This implies that complex activation patterns need to be generated at these stages of processing during the execution of a compound movement comprising both proximal and distal components. One way to coordinate such patterns is to implement command neurons that initiate specific spatio-temporal activity distributions through diverging axonal projections, the architecture of which specifies a particular motor pattern. Such command neurons would represent the motor counterparts of the cardinal cells in the visual cortex. In both cases, constellations of distributed activity are associated with the activity of a few highly specialized neurons. In analogy with the drawbacks of cardinal cells, the representation of compound movements by command neurons is associated with several disadvantages. First, at least one dedicated neuron is required for each conceivable combination of movements. The combinatorial richness of the spatial and temporal degrees of freedom of these movements approximates that of possible feature constellations in perception, and is, in all likelihood, too large for the available number of command neurons. Second, such representations do not permit one to generalize from the ability to perform certain combinations of proximal and distal arm movements to the ability to carry out different combinations of the same components. In other words, the parametric modification of motor performance would lack systematicity (Fodor & Pylyshyn, 1988).

An alternative programming strategy could consist of the extraction of visual information related to different aspects of motor activity, and its transformation into motor commands within parallel architectures that lack convergence onto command units. Indeed, the movement-related responses of neurons in various brain structures of the monkey support such a parallel strategy of movement encoding. It appears that many cortical areas participate in parallel in the programming and execution of arm movements, and that neurons in different areas appear to be related to dissimilar aspects of arm movements (Georgopoulos, 1991; Kalaska & Crammond, 1992). Moreover, even within a single cortical area several functionally dissimilar subpopulations can typically be distinguished. For example, proximal and distal arm movements are represented in different subdivisions of the premotor cortex (Kurata & Tanji, 1986; Rizzolatti et al., 1988). 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). Similarly, neurons related to a specific kind of distal movement—for instance, precision grip—respond before and during the execution of this movement with either arm, and display visual responses to stimuli for which this type of grasping is appropriate (Rizzolatti et al., 1988; Rizzolatti & Gentilucci, 1988). Thus, evidence is consistent with the proposal that the different parameters of a planned movement are programmed within parallel processing streams from the visual to the motor cortex. In the case of visually guided grasping movements, the signals required for the specification of the proximal arm movement and for the programming of the grip are likely to be relayed in parallel via the occipito-parietal pathway of the visual system (Goodale & Milner, 1992; Taira et al., 1990). A different pathway including parts of the temporal lobe is likely to be involved in the recognition of the object (Goodale & Milner, 1992; Mishkin et al., 1983), and therefore might be involved in the decision whether it is worthwhile to grasp this object or to perform a different type of movement.

Thus, the hypothesis is that different features of the visual environment evoke in parallel previously learned movement components, and cause these components to recombine into patterns that match the actual constellation of visual features. This implies an ability to perform compound movements that have not been executed previously, as the respective movement components have, with all likelihood, been learned in different combinations. Thus, relations among visual features and their systematic changes can be translated into systematic variations of the corresponding motor patterns in a very flexible way. However, such parallel architectures are susceptible to interference if several features are present simultaneously, as is the case when more than one object is within reach. In this situation, the various features of different objects may evoke incompatible movement components that should not be combined arbitrarily (Neumann, 1990). We propose that such unwanted interference can be circumvented when the processes extracting the various movement parameters can evaluate the results of perceptual grouping. As our hypothesis implies that this result is reflected in the synchronization behavior of visual cortical neurons, we postulate that the assemblies of neurons representing particular components of movements should be sensitive to the synchronization of afferent activity.

In Figure 9, two objects are depicted that might be manipulated by a monkey. It is assumed that features of the respective objects evoke different patterns of premovement activity in parallel. The banana, for example, might induce neuronal activity that is related to whole-hand prehension, proximal arm movements to the spatial location of the banana and movements associated with feeding, like opening of the mouth. The other object, a leaf, is likely to evoke activity of neurons that are related to different movement components. Neurons that synchronize their discharges according to the rules that were outlined in the previous section have been indicated in Figure 9. As suggested above, the various patterns of premovement activity may be interpreted as representing different sets of features, like “edible” or “grasping, requiring precision grip.” Therefore, it is proposed that neurons with premovement activity should be captured by the assemblies of synchronously firing cells that trigger the premovement assemblies (see the previous section). According to proposal (9B), groups of cells that encode incompatible movement components engage in a competitive interaction. Eventually, the premovement activity in each of the three pathways that are illustrated in Figure 9 should converge to a state in which each of the pathways unambiguously encodes a single movement component. However, meaningful behavior will only result if the competition is won by premovement cells that code for movement components related to the same object. In order to assure this condition, we make an additional assumption (which is the counterpart of 1 in the motor cortex):

(10) Neurons that are related to compatible movement components should be linked with synchronizing connections.

Proposals (9B) and (10) are in accordance with evidence that in the motor cortex of monkeys neurons with similar tuning are likely to be linked with excitatory interconnections, whereas cells that are related to incompatible movements tend to inhibit each other (Georgopoulos et al., 1993).

For the network of Figure 9, this implies that cell assemblies representing, for example, grasping food should be connected with synchronizing connections to neurons with premovement activity for precision grip and whole hand prehension, as well as to cells related to proximal arm movements toward various locations in movement space. Let us assume that activity in the pathway related to the semantic connotation of an object has converged to a state in which a movement for grasping food is being planned (Fig. 9D). On the one hand, neurons that exhibit activity preceding whole hand prehension now receive synchronous synaptic input from both the sensory cells that respond to shape of the banana and from the neurons related to food grasping, neurons that have been captured by the assembly representing the banana (broken lines in Fig. 9D). On the other hand, there is no synchronicity between cells related to food grasping and neurons associated with precision grip, because the latter fire in synchrony with the assembly representing the leaf (continuous lines in Fig. 9D). The asynchronicity of synaptic input between neurons related to precision grip and whole hand prehension is likely to result in a competitive advantage for the cells that are related to whole hand prehension. Thus, when the assembly representing the banana has captured neurons related to food grasping, the likelihood increases that
Figure 9. Synchronization aided response selection in the motor cortex. (A) Visual image composed of two possible targets for a grasping movement. (B) Neurons that are selective for three different feature domains and that evoke premovement activity. Groups of neurons in the left cluster exhibit activity related to the semantical connotation of the stimuli. Neurons in the middle cluster are 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. Similarly, the right cluster indicates the locations of the stimuli in movement space that activate neurons related to proximal arm movements toward the respective positions. Dashed circles represent neurons that are activated by the banana. Solid circles represent neurons activated by the leaf. Inhibitory connections (—one way) exist between neurons, with activity preceding incompatible movement components. Conversely, neurons with compatible premovement activity are linked with excitatory synchronizing connections. Solid lines indicate the excitatory synchronizing connections that emerge from the cells that exhibit activity related to feeding. For clarity, additional connections of this type have been omitted. (C) A more detailed description of the synchronizing excitatory connections that exist between groups of cells related to semantics and to movements of the hand. Neurons that fire synchronously have been indicated with solid and stippled circles, respectively. When all neurons exhibit similar firing rates their input is synchronized to the same extent. Note (that each node receives two inputs from cells that are firing in synchrony, and one input that is not synchronous.) (D) Interactions between the left and middle cluster after activity in the former has converged to a state in which feeding-related neurons predominate. Synchrony of firing between afferents that contact the cells related to precision grip is lost. In contrast, neurons with activity preceding whole hand prehension receive input from neurons that have synchronized their discharges, resulting in a competitive advantage over the neurons related to precision grip.

Neurons encoding a distal movement appropriate for the banana are also captured. This, in turn, increases the likelihood that neurons related to the proximal movement to the location of the banana prevail over neurons encoding a proximal movement towards a different location. Thus, the synchronicity among responses that are evoked by a single object helps to avoid the combination of movement components that are evoked by different objects.

(11) The cooperative interactions among neurons that exhibit activity before the execution of compatible movement components, and that have synchronized their discharges, result in the selection of those movement components that are evoked by a single object.

The cooperative interactions among neurons that exhibit premovement activity evoked by a single object do not imply that these cells should always collaborate. An interchange of the position of the two objects, for example, would promote synchronization between different neurons (as in Figs. 6A & C) and, therefore, cooperative interactions between different combinations of cells in the motor cortex. Thus, systematicity of visually guided movements whose parameters are specified by parallel streams from the visual cortex to the motor cortex is preserved in the presence of multiple objects.

The connections between most cortical areas are reciprocal (Felleman & Van Essen, 1991). Therefore, the selection of a particular movement component is likely to affect the sensory neurons that evoked this premovement activity. For example, the selection of a proximal arm movement towards position 2 in Figure 9 might enhance the activity of neurons that respond to the presence of an object at this position. Similarly, neurons responding to the figural aspects of the banana might increase their activity in this situation. Indeed, neurons in various visual areas have been shown to modulate their discharge rate as a function of the behavioral relevance of the stimuli that evoke their activity (Bushnell et al., 1981; Goldberg & Bushnell, 1981; Moran & Desimone, 1985; Motter, 1993). Thus, these rate modulations
might be a reflection of the competition between incompatible motor programs and the subsequent selection process (Goldberg & Segraves, 1987).

CONCLUSIONS

In this survey we have indicated how neuronal synchronization may contribute to resolve the ambiguity of population codes that arises when multiple image components are present. We propose that neurons responding to related image components synchronize their discharges due to reciprocal interactions that are mediated by intracortical connections (Engel et al., 1992a; Singer, 1993). This implies that the Gestalt criteria for perceptual grouping should reside in the architecture of these connections. Part of this architecture is certainly determined genetically, but certain features are likely to be modified by learning, according to a Hebbian learning rule (Hummel & Biederman, 1992; König et al., 1992; Löwel & Singer, 1992; Singer, 1993; for review, see Singer, 1995).

We propose that the neurons activated by the features of an object define an interaction skeleton in which synchronization can propagate across several synaptic links. It should be stressed that it is the transitivity of neuronal synchronization within the interaction skeleton that can account for additional grouping criteria. Transitivity allows the detection of connectedness between widely separated contour segments that cannot be grouped on the basis of local criteria like similarity of orientation or collinearity. In addition, transitivity of neuronal synchronization allows for the correct grouping of responses across feature domains and modalities. Tuning of cortical neurons to more than one feature domain—a well established experimental finding (Zohary, 1992; Leventhal et al., 1995)—reduces the problem of establishing synchronously firing ensembles of neurons with widely differing feature selectivities to the detection of connectedness in the interaction skeleton. Another advantage of this proposal is the possibility of dynamically adjusting the correlation length within the interaction skeleton, thus influencing the grain of perceptual grouping.

It has been suggested that cortical neurons should be particularly sensitive to synchronicity among discharges in afferents that project onto them (Abeles, 1982; Softky & Koch, 1993; Softky, 1995). Coincidence detecting neurons may acquire selectivity for specific feature constellations of single objects, while integrating information over large regions of the visual field, without becoming sensitive to the co-occurrence of the same features in different image components. Hummel and Biederman (1992) have indicated how this mechanism may be utilized for recognition of objects despite changes in size, viewpoint, or position in the visual field. Thus, by taking the temporal relation between afferent discharge patterns into consideration, neurons can acquire useful receptive field properties in a very economic way. The reason is that neurons sensitive to the synchrony of converging input transform this synchrony code into a rate code; they respond more vigorously to synchronized than to nonsynchronized input. Conversely, firing rates influence the pattern of synchronization (Boven & Aertsen, 1990). The discharge rate of neurons determines the composition of the interaction skeleton by selecting the neurons that serve as links in an interaction skeleton. Hence the activity of cell groups determines the probability of synchronization between discharges of other cells. Our proposal concerning the role of synchronization in the selection of an appropriate compound movement illustrates this point. The subset of neurons that is activated by a particular stimulus configuration defines an interaction skeleton through which synchrony is established. This pattern of synchronization, in turn, may influence the activity of neurons of the motor cortex. We hypothesize that the interplay between firing rates of neurons and the temporal relations between them accounts for the flexibility with which coherent representational states can be established.

This flexibility is reflected in, for example, the adaptability of motor performance. Akin to the distributed and parallel representation of visual features, the various components of movements may be planned in parallel. Just as sensory features can be combined to generate representations of a large number of different perceptual objects, movement components can be combined to generate large numbers of compound movements, resulting in a systematization of both sensory representations and motor programs. New compound movements can be readily assembled from components that were learned in different combinations. The temporal relations between the responses of cortical neurons are suggested to play an important role in the selection of the appropriate combination of movement components. Thus, population responses representing components of movements may be bound together in the same way by dynamic transitory synchronization as population responses representing component features of perceptual objects.

In a recent simulation study, Tononi et al. (1992) investigated the role of synchronization among responses of neurons in various areas of the visual cortex in the selection of saccadic eye movements. Neurons that carried information about the shape and color of stimuli were located in other areas than cells representing their spatial position. In order to make a saccade to a stimulus of a particular shape or color, information about these visual features has to be combined with information about the spatial position of stimuli. In their study, Tononi et al. (1992) elegantly demonstrated that selective synchronization among the responses of the respective cells may result in the selection of a saccade to an image component with a particular shape or color. To date, few studies have addressed the question of how synchroni-
zation may help to assemble complicated motor programs from simpler movement components. Our hypotheses about the virtues of synchronization in this respect are a first attempt in this direction. Clearly, these proposals also need to be backed up with simulation studies and the predictions have to be tested experimentally.

Many neurons in the parietal (Mountcastle et al., 1975; Taira et al., 1990) and premotor cortex (Boussaoud & Wise, 1993; Crammond & Kalaska, 1994; di Pellegrino & Wise, 1993; Gentiliucci et al., 1988; Rizzolatti et al., 1988) appear to signal the compatibility of a particular movement with a visual stimulus. A subset of these cells fire up to the moment at which the respective movement is executed, or the moment at which the animal interrupts the preparation of this movement (Wise & Mauritz, 1985). We suggest that such premovement activity might be handled in the same way as the activity of neurons that are selective for other feature domains like color or motion. Thus, neurons that exhibit premovement activity should synchronize their discharges with neurons that respond to the visual features of the object that triggers their activity. Thus, neurons that exhibit premovement activity should be captured by the assemblies of synchronously firing neurons that trigger their activity. For the extraction of the relevant movement parameters from the visual input numerous coordinate transformations are required (Andersen et al., 1993; Graziano et al., 1994; Kalaska & Crammond, 1992; Soechting & Flanders, 1992). For example, for the visual guidance of arm movements the position of the eyes in the orbit and the position of the head on the trunk need to be taken into account. For the sake of simplicity, we did not include coordinate transformations explicitly in our scheme for visuomotor integration (Fig. 9). However, the temporal relations between responses that label the features of different objects may be preserved during coordinate transformation, as was indicated in Figure 7. Bressler et al. (1993) have shown that field potentials that are recorded in the visual and motor cortex of a monkey may indeed synchronize during the performance of a visuomotor task. In a recent study, Roelfsema et al. (1995) also showed that in the awake cat synchronization with precision in the millisecond range occurs between field potentials in various areas of the visual cortex, between areas of the visual and parietal cortex and also between areas of the parietal and motor cortex. One prediction of our hypothesis is that only visual responses to objects that give rise to behavioral responses should synchronize their activity with neurons in areas that are related to response selection and execution. A core assumption in the concept of response selection by synchronization is that neurons, once they have synchronized their activity, cooperate in activating neurons of the motor cortex (Tononi et al., 1992). The hypothesized synchronizing connections between motor cortical neurons related to compatible movement components, and the competitive interactions between incompatible premovement activity are thought to facilitate the selection of the appropriate compound movement. The cooperative interactions between premovement activity evoked by a single object increase the likelihood that the appropriate movement components are selected simultaneously.

We implied a mutual dependence between firing rates and synchrony. The firing rates of neurons determine the routes along which synchrony may spread. The amount of synchronicity between action potentials in converging afferents in turn influences firing rates. This interdependence may help to close the gap between theories that rely predominantly on firing rates and others that emphasize the importance of neuronal synchrony. The brain may take advantage of the specific features of both rate and synchrony.

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Notes

1. (1) and (1A) are not entirely equivalent. For example, (1A)—but not (1)—predicts that orientation selective neurons with collinear receptive fields should be selectively interconnected.

2. How exactly feature dimensions are defined can be a matter of debate. For instance, retinal position can be considered as a single feature or also as the combination of two feature domains, azimuth and elevation. The argument developed does not depend on a specific assignment of features to particular dimensions.

3. In the present discussion, selectivity of neurons for more than a single feature domain implies selectivity for feature conjunctions. Thus, given feature domains A and B, the selectivity of a neuron that responds to a value of 1 on the former, and a value of 3 on the latter feature dimension may be expressed as A₁B₃. In this notation the neuron would only respond if A₁ and B₃ are features of a single object. For the conjunction of retinal position R with another feature domain A, like texture, this definition of simultaneous selectivity matches the response properties of cortical neurons. Obviously, selectivity for the conjunction of R and A pertains if the computation of the value of A is restricted to a limited number of retinal afferents.

4. In a different approach to this problem, Hummel & Biederman (1992) incorporated synchronizing connections with infinite propagation velocity in their network for shape recognition. These physiologically implausible connections can probably be avoided if oscillatory units are used as building blocks.

5. With correlation length we denote the distance over which synchronization due to local interactions spreads through the interaction skeleton. If the correlation length is long synchronization develops among neurons that are far apart in the interaction skeleton. The correlation length depends on the dynamics of the units that constitute a network.

6. It has been argued convincingly (Andersen et al., 1993) that in the process of transforming the retinal image into premovement activity various coordinate transformations need to take
place. The temporal relations among neurons that are activated by a single image component may be preserved under these conditions, as was demonstrated in Figure 7. Note that in the example of Figure 9 premovement activity of neurons in one pathway is compatible with premovement activity of both groups of cells of the other two pathways, respectively. In general, this does not need to be the case. For example, a hitting arm movement is not compatible with movement activity associated with feeding.

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