

# The Psychophysical Evidence for a Binding Problem in Human Vision

## Review

Jeremy M. Wolfe\*<sup>‡</sup> and Kyle R. Cave<sup>†</sup>

\*Center for Ophthalmic Research  
Harvard Medical School  
Boston, Massachusetts 02115

<sup>†</sup>Department of Psychology  
University of Southampton  
Highfield  
Southampton SO17 1BJ  
United Kingdom

### What Is “Binding” and Why Might It Be a Problem?

Imagine that you are looking at two women. One has an oval face with striking green eyes framed by long blond hair. The other has a round face with piercing blue eyes framed by wavy red hair. Long before we reach the realms of social psychology, several potential problems present themselves to the visual system. Did those blue eyes go with the blond hair? Was that blond hair wavy? If one woman is Lynn and the other is Anne, which is which? Coherent perception of even a single object requires that the properties of that object be coordinated or *bound* together. As discussed elsewhere in this issue of *Neuron*, information about these properties appears to be distributed across many different brain areas. This separation of different types of information about a single object raises the possibility of a “binding problem.” This paper will review some of the psychophysical evidence indicating that this is a real problem that is faced and, under most circumstances, solved by the visual system. We will also discuss contrary evidence that suggests that the visual system has no such binding problem. Finally, we will provide a theoretical framework within which to understand these apparently contradictory data. (Other issues like texture grouping and contour completion might be considered to be examples of binding. In this paper, however, we are restricting ourselves to the binding of features to objects.)

### Evidence that There Is a Binding Problem

#### *Illusory Conjunctions*

Some of the most striking evidence for a binding problem in vision comes from a class of apparent misperceptions labeled “illusory conjunctions.” When subjects must report on the identity of items in briefly presented arrays of colored shapes, they often report seeing a stimulus made up of the color from one array element and the shape from a different array element. Apparently, perceptual features can become unbound from their original objects and can be recombined to form a new object representation.

In Treisman and Schmidt’s (1982) classic version of the illusory conjunction paradigm, subjects viewed a line of colored shapes or letters, flanked by two black digits (see Figure 1). Treisman and Schmidt told the

subjects that their primary task was to report the two digits, so that their attention would be diverted from the colored shapes. Subjects were very accurate in reporting the digits, but their reports of the stimuli between the digits included a large number of illusory conjunctions. Illusory conjunctions occurred with both letters and abstract shapes and included all the features tested (color, shape, size, and solidity). Treisman and Schmidt concluded that when attention is not available to combine features correctly, they can be put together to form combinations not actually present in the stimulus.

Illusory conjunctions have arisen in a variety of different visual tasks. For instance, Prinzmetal (1981) presented subjects with arrays of circles, with two of the circles each containing a single horizontal or vertical line. Although the lines were at different locations, subjects sometimes perceived them as forming a plus sign. Interestingly, the two lines were more likely to combine into an illusory plus sign if they were both part of the same perceptual group of circles. Prinzmetal and Millis-Wright (1984) demonstrated a different grouping effect in a task in which subjects searched for one of two target letters in an array and then reported its color. Subjects’ reports included more illusory conjunctions when the letters formed a word or a pronounceable nonword than when the letter string was unpronounceable. Treisman and Paterson (1984) found that some subjects perceived an arrow when presented with arrays containing the appropriate shape components (a line and an angle). Some of their subjects could also combine an angle and a line into an illusory triangle, but only if circles were also present in the array, presumably to supply a closure feature (for additional demonstrations of illusory conjunctions, see Prinzmetal et al., 1986; Briand and Klein, 1987; Cohen and Ivry, 1989).

While illusory conjunctions have been demonstrated with a number of different methods by a number of different experimenters, there is disagreement over what these errors tell us about visual processes and representations. In the original formulation of Treisman’s Feature Integration Theory (Treisman and Gelade, 1980), illusory conjunctions were taken as evidence that binding features into the representation of an object required attention. Preattentively, features were somehow “free floating” and, consequently, capable of arbitrary rearrangement if attention was diverted.

Various aspects of this position have been challenged. For example, Tsal (1989) argued that features could be correctly conjoined without attention and the presence of attention might not always assure correct feature combinations. He and others have argued that illusory conjunctions might reflect a coarse coding of some aspects of feature information (Cohen and Ivry, 1989; Prinzmetal and Keysar, 1989; Ashby et al., 1996). A second important point raised by Tsal and echoed elsewhere is that illusory conjunctions might be failures of memory as much as failures of vision. In a standard illusory conjunction display, the stimuli are presented briefly and the subject is asked to describe what was seen (but see Prinzmetal et al., 1995).

<sup>‡</sup>To whom correspondence should be addressed (e-mail: wolfe@search.bwh.harvard.edu).

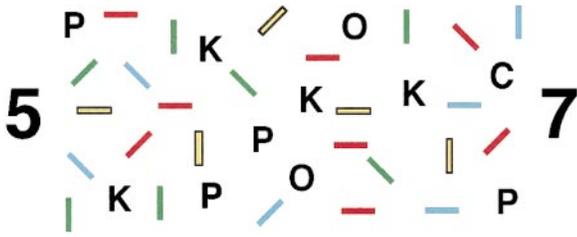


Figure 1. Illusory Conjunction Demonstration

(1) There are two large numbers on the left and right of this figure. Determine if they are both odd and then read ahead for more instructions.

(2) Without looking back at the figure, ask yourself if it contains the letters "R," "P," or "Q"? Did you see a vertical yellow bar? Did you see a horizontal green bar? If you thought you saw an "R," a "Q," or a horizontal green bar, you have made an "illusory conjunction" error.

In a somewhat similar vein, Butler, Mewhort, and Browse (1991) claimed that illusory conjunction errors demonstrate more about the encoding strategy used in a particular task than about the basic properties of visual representations. They showed that the same stimuli could produce different patterns of errors depending on subjects' expectations. When subjects knew that they would see only uppercase letters in each trial, they would sometimes combine a bar from a letter Q with a letter P and report a letter R. However, when subjects did not know whether to expect upper- or lowercase letters, then their errors with the same uppercase stimuli consisted mainly of mislocating entire letters rather than combining features from different letters. Butler, Mewhort, and Browse concluded that subjects encode the stimuli as features in the first task and as letters in the second task.

Illusory conjunctions are not limited to basic preattentive features: just as features can travel from object to object, letters can travel from word to word (Mozer, 1983; McClelland and Mozer, 1986). When Mozer's subjects viewed the two words "LINE" and "LACE," they sometimes reported seeing "LICE" or "LANE." As in the earlier demonstrations of illusory conjunctions, these letter migrations occurred more often when attention was diverted to other stimuli. They were also more likely to occur when the two words shared some letters, and they occurred just as often whether the letters in the two words matched in case or not, indicating that the confusion occurred within abstract word representations rather than between representations of individual letters or features (see also Treisman and Souther, 1986; Fang and Wu, 1989). Even more abstract errors appeared in experiments by Virzi and Egeth (1984), in which subjects confused the color named by a word and the color of the ink with which it was written (see also Intraub, 1985; Goolkasian, 1988).

To summarize, illusory conjunctions are clear evidence for *some sort of* problem with the correct binding of features to objects. The original conception of "free floating" preattentive features bound together by the glue of attention has been replaced by a view that illusory conjunction phenomena can occur when linkages break down at any of a number of levels of processing.

These linkages may be built and maintained by attention, at least at some levels, thus preventing illusory conjunctions.

#### *Dissociating Detection and Localization of Features*

If binding is a problem, then it should be possible to find evidence of unbound features. What would such evidence look like? If some process like attention is needed in order to associate features with the correct locations, then it should be possible to dissociate the identification and localization of features. The strong form of this hypothesis would hold that there exists a preattentive stage of processing at which features are identified but represented completely independently of location. Original Feature Integration Theory argued for a position of this sort. Treisman and Gormican (1988), for example, argued that detection of features and localization of features were separate operations, though Treisman's more recent views are less absolute (Treisman, 1996). Still, one of the main claims of Feature Integration Theory (Treisman and Gelade, 1980) and related models like Guided Search (Wolfe, 1994a) is that the features belonging to visual objects cannot be accurately bound together into object representations in the early, preattentive stage of visual processing.

Treisman and Gelade (1980) originally predicted that subjects performing a feature search might be able to report the presence of a target feature in a display even if they were unable to localize the target. The feature would be detected preattentively without the localizing effects of spatial attention. In conjunction search, however, this dissociation would not be possible because conjunctions could not be detected without spatial attention. Thus, if a subject could detect a conjunction target, then they should also be able to localize it. Treisman and Gelade tested their prediction in two experiments in which each search array contained one of two possible targets. In the *feature search* condition, the target had a color or shape not shared by any of the distractors. Here, accuracy in reporting the target feature was above chance, even on those trials with large errors in the report of the target location. However, in the *conjunction search* task, subjects did not report the conjunction features accurately unless they also correctly reported the location of those features.

Nissen (1985) provided additional evidence that color and shape features from an object were combined via location. She presented subjects with an array of four objects, each with a unique shape and unique color. In one condition, one of the four possible locations was cued before each trial, and the subject reported the color and shape at that location. Nissen predicted that accuracy of the color and shape reports should be independent of one another, because subjects did not need to determine one feature in order to determine the other. The data were consistent with that prediction. In a second condition, a color was cued at the beginning of each trial. Subjects were asked to report the location and the shape of the object with the cued color. In this condition, Nissen predicted that the accuracy of the shape reports would depend in part on the accuracy of the location reports, because subjects would have to determine the target location before they could determine its shape. The data showed that the shape and accuracy reports were not independent, and that shape

accuracy was very low when the location was reported incorrectly. From the first condition, Nissen estimated the proportion of targets for which the shape would be correctly reported once the location was known. Using this estimate and the proportion of correctly reported locations in the second condition, she was able to work out predictions for the second condition that corresponded fairly closely to the actual results.

Taken together, the Treisman and Gelade (1980) and Nissen (1985) results suggested that features could be represented without being bound to their locations, so that subjects could report feature identities without locations. Subsequent work, however, has raised questions about these free-floating features. Johnston and Pashler (1990) questioned whether Treisman and Gelade were correct in concluding that features could be identified without being located. They suggested that even if a feature's location had been correctly determined, subjects might not always be able to report its position accurately using Treisman and Gelade's system for reporting location. They also conjectured that accuracy in reporting features may have been deceptively high in Treisman and Gelade's experiment, because when subjects were unable to detect either of the possible target features, they might guess and report the target that was more difficult to detect (a "negative information" strategy). Johnston and Pashler performed their own version of the experiment in which the stimulus elements were arranged so that each location occupied a unique corner or side, making it easier to remember and report each location. They also tried to equalize the discriminability of each of the two target features (although they concluded from their results that they were only partially successful). They found only weak evidence for identification without localization and concluded that the phenomenon was rare, at best.

Just as Johnston and Pashler (1990) raised doubts about Treisman and Gelade's evidence for unbound features, a later study by Monheit and Johnston (1994) raised doubts about Nissen's claims for the independent reporting of color and shape. With a careful analysis of Nissen's task, Monheit and Johnston demonstrated that any effects of nonindependence between color and shape would be very small if the subjects used a reasonable guessing strategy when they failed to identify the features present. They then conducted their own versions of Nissen's experiments with some changes to increase their ability to detect nonindependence effects. They increased the number of trials per subject, and they selected their stimulus elements from a set of six colors and six shapes (rather than the four used by Nissen) to limit the effects of guessing. They found the nonindependence effects they expected: in many trials, subjects either reported both the color and shape correctly or got them both wrong.

The experiments discussed here are only a small portion of the literature on the independence or lack of independence between identification and localization tasks. The Treisman and Nissen studies argue for a precedence for identification over localization. Other studies have argued for the opposite (Sagi and Julesz, 1985; but see also Folk and Egeth, 1989) or for an equality between the operations (Green, 1992). Saarinen has argued that it is futile to search for a clear answer in

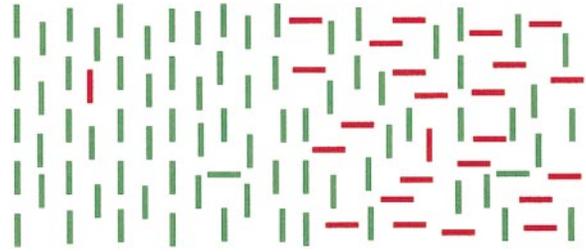


Figure 2. Feature and Conjunction Search

It is very easy to find the red and vertical items on the left of this figure. On the right, the item defined by the conjunction of red and vertical does not "pop out" in the same way.

this line of research (Saarinen, 1996a, 1996b). The area suffers from a pair of seemingly insurmountable problems. First, accuracy and reaction time data, the measures of choice, can be readily altered by task manipulations. Second, data about the state of vision *prior* to the deployment of attention are derived from measures taken *after* the stimulus is gone, just as in the illusory conjunction experiments. This makes it hard to know if a failure to report the locus or identity of a stimulus is the result of a failure to process or a failure to remember. We cannot be sure if subjects misperceive a combination of two features or misremember that combination.

To summarize this section, there is some evidence for a dissociation between identification and localization of basic feature information. For present purposes, this evidence supports the notion that there is a binding problem in early vision. However, interpretation of these data has proven to be ambiguous and the experiments, taken as a whole, make for a somewhat unsatisfying meal. Clearer evidence that the visual system faces problems in binding features into object representations comes from the visual search literature.

#### *Search for Conjunctions of Basic Features*

One of the pillars of support for the existence of a binding problem in human vision was the apparent inefficiency of searches for targets defined by conjunctions of basic features. A search for a target among distractors is very easy if the target is defined by a single salient feature. Thus, as shown in Figure 2, it is easy to find the red item among green distractors or the horizontal item among vertical distractors. However, Treisman and Gelade (1980) reported that the same features failed to produce efficient search when those features conjunctively defined the target (see the right side of Figure 2). They found that a search for a red vertical target among red horizontal and green vertical distractors produced an inefficient search, consistent with a serial, self-terminating search through the items. In the original Feature Integration Theory, this apparent seriality was taken as evidence that features were unbound prior to the arrival of attention.

Subsequent research complicated the picture from the vantage point of the binding problem. Houck and Hoffman (1986) demonstrated that unattended conjunctions of color and orientation could produce a McCollough effect, a visual aftereffect dependent on the contingent relationship between color and orientation. Even more troubling was the data from numerous labs showing efficient search for conjunctions (e.g., Nakayama

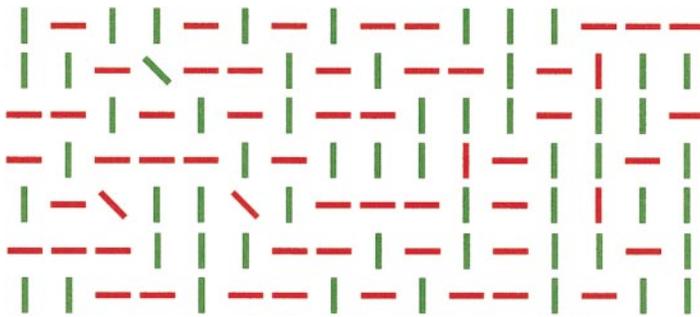


Figure 3. Texture Segmentation by Feature and Conjunction

In the left half of the figure, it is quite easy to see the triangle formed by the three oblique elements. On the right, the three red vertical elements never form a triangle of comparable clarity.

and Silverman, 1986b; Quinlan and Humphreys, 1987; Wolfe et al., 1989; Zohary and Hochstein, 1989; Treisman and Sato, 1990; Cohen and Ivry, 1991; McLeod et al., 1991). At first, it appeared that these results might be specific exceptions to the general rule of inefficient conjunction search (Nakayama and Silverman, 1986a; McLeod et al., 1988). However, subsequent work indicates that *any* search for conjunctions of basic features is efficient if the features are salient enough (see discussions in Wolfe, 1994a, 1998). Indeed, there are several published reports of conjunction searches that yield search efficiencies that are indistinguishable from those produced by basic features (e.g., Wolfe, 1992; von der Heydt and Dursteler, 1993; Theeuwes and Kooi, 1994).

Do these findings argue against the existence of a binding problem? Do they show that features are conjoined prior to the arrival of attention? Perhaps not. Efficient search for conjunctions can occur even if features cannot be bound together without attention. Consider the search for a red vertical item among green vertical and red horizontal items. Suppose that a parallel color processor biases the deployment toward red items and an orientation processor biases the deployment of attention toward vertical items. Even though color and orientation are being handled entirely separately, the combination of these two sources of attentional *guidance* will tend to deploy attention to loci containing both red and vertical. This concept of guidance is, not surprisingly, at the heart of the eponymous Guided Search model (Wolfe et al., 1989; Cave and Wolfe, 1990; Wolfe, 1994a; Wolfe and Gancarz, 1996). It is also a part of later versions of Feature Integration Theory (e.g., Treisman and Sato, 1990) and the more recent FeatureGate model (Cave, 1999) and is anticipated by the work of Hoffman (1979; see also Tsotsos et al., 1995).

These developments in the understanding of conjunction search render ambiguous the role of attention in conjoining features. Is item-by-item attention needed to bind features into objects or not? More recent conjunction experiments suggest that Treisman's original claim is correct even if the original empirical support for the claim is open to reinterpretation.

The first case, illustrated in Figure 3, is derived from Wolfe et al. (1995). On the left side of the figure, the three items of odd orientation form a virtual triangle that is detected without noticeable effort (Nothdurft, 1992). Wolfe et al. (1995) had subjects describe the orientation of a briefly presented triangle of this sort. The task was easy even when three different orientations formed the vertices of the triangle. However, when the vertices were

defined by conjunctions of color and orientation, as they are on the right side of this figure, no impression of a triangle was instantly available. Instead, subjects seemed to need to attend to each red vertical in turn in order to describe the position of the triangle as a whole. In a brief presentation, the task was essentially impossible.

Figure 4 shows a second illustrative case. Wolfe and Bennett (1997) had subjects search for red vertical lines in displays similar to those shown here. On the left of Figure 4 is a typical conjunction search. On the right, the same elements have been combined into "pluses." Search was much less efficient in the latter case. Wolfe and Bennett argued that this case represented conjunction search in the absence of useful guidance. On the left, it is possible to guide attention toward "red" items and toward "vertical" items. On the right, *all* items contain "red" and "vertical." Prior to the arrival of attention, each plus is the same preattentive bundle of "red" and "green" and "vertical" and "horizontal." It is only when attention is deployed to an item that it is possible to correctly bind colors and orientations.

To summarize this section, recent research supports a modified version of Treisman's position on conjunctions. When Feature Integration Theory was first proposed, it was unclear if subjects searched from object to object in the visual field or from location to location. In that context, Treisman could propose that features were initially "free floating." As will be discussed later in this paper, subsequent work has made it clear that search generally proceeds from object to object (e.g., Behrmann and Tipper, 1994; Tipper et al., 1994; Vecera and Farah, 1994; Wolfe, 1994b, 1996; Yantis and Gibson, 1994; Wolfe and Bennett, 1997; Tipper and Weaver,

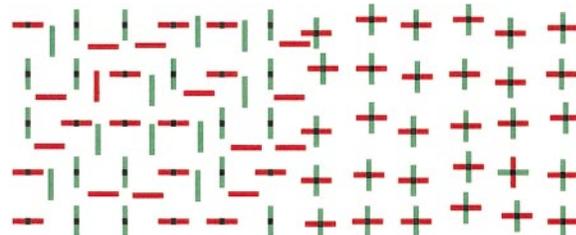


Figure 4. Preattentive Objects Are Just Bundles of Features

Search for red vertical items. On the left side of this figure, the task is a relatively easy "guided" search. On the right, the same red vertical element is very difficult to find because all of the elements contain the features "red," "green," "vertical," and "horizontal."

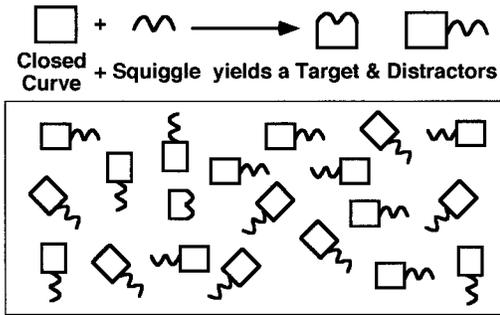


Figure 5. An Example of Inefficient Search for a Shape  
From Wolfe and Bennett (1997).

1998) (more specifically, attention appears to be directed to locations defined by objects; reviewed by Cave and Bichot, 1999). In this light, we can describe the preattentive world as populated by unrecognized bundles of features loosely held together by virtue of their shared location. Thus, all of the pluses in Figure 4 are bundles of red, green, vertical, and horizontal. Attention is required to correctly *bind* the features into a red-vertical, green-horizontal plus or into its 90° rotation. Similarly, while objects like faces may be composed of basic features that are processed without attention, it is only with the deployment of attention that these features can be bound together into a representation that can be recognized (Nothdurft, 1993; Suzuki and Cavanagh, 1995; Cave and Bichot, 1999).

#### **Objects as Bundles of Features**

The idea that objects are represented only as bundles of basic features prior to the arrival of attention can be used to explain failures to search efficiently for targets defined by the spatial arrangement of their parts. Searches for Ts among Ls and for Ss among mirror-reversed Ss are standards of inefficient search (e.g., Braun and Julesz, 1998; Kwak et al., 1991), though there are some reports of efficient search for targets defined by spatial relations (Wang et al., 1994) or even by their conceptual category (Jonides and Gleitman, 1972; but see Duncan, 1983; Dixon and Shedden, 1987; but then see Krüger, 1984).

The same pattern is seen in objects that are not alphanumeric characters. Target shapes that are quite different from distractor shapes yield inefficient search if they are composed of the same bundle of features. For example, a closed curve and a squiggle, as shown in Figure 5, can be combined to make two very different objects. Nevertheless, because they are both composed of the same preattentive bundle of features, search for one of these among the other is quite inefficient (Wolfe and Bennett, 1997).

#### **Evidence that There Is Not an Absolute Binding Problem**

The evidence discussed thus far indicates that the visual system struggles with a binding problem and sometimes loses. Prior to the arrival of attention, the features of an object seem to be rather loosely affiliated with each other. The relationship of color to orientation or squiggle to closed curve seems to be properly appreciated only

after attention is deployed to an object. However, as noted above, features are not entirely independent in the absence of attention. Houck and Hoffman (1986), cited earlier, showed that attentional manipulation did not disrupt the McCollough effect, an aftereffect dependent on a firm, contingent relationship of color and orientation (McCollough, 1965). If preattentive features were utterly unbound, it should not be possible to produce an effect that requires the association of, say, red and vertical (Dodwell and Humphrey, 1992).

Like the Houck and Hoffman experiments, there are other studies showing a relationship between features in the absence of attention. We would argue that these studies show that features of an object are *bundled* together preattentively but that explicit knowledge of the relationship of one feature to another requires spatial attention.

#### **Features Linked to Other Features of the Same Object**

A number of studies demonstrating object-based attention suggest that all of the features belonging to an object are bundled and selected together. For instance, Treisman, Kahneman, and Burkell (1983) asked subjects to perform two tasks: reading a word aloud and localizing the gap in a rectangle. Performance was better when the rectangle surrounded the word, making them a single object. This advantage could not be attributed to distance, because the distance between the word and the gap was the same whether the rectangle surrounded the word or not.

Further evidence for object-based attention came from another dual-task experiment by Duncan (1984). The stimuli consisted of a diagonal line and a rectangle superimposed. Depending on the condition, subjects reported either two properties of the line, two properties of the rectangle, or one property of each. Reports were more accurate when both properties were from the same object. Because the objects were superimposed, Duncan argued that the same-object advantage could not result from selecting the object's location. Many subsequent studies have produced similar results (for a useful review, see Goldsmith, 1998; see also Tipper et al., 1994; Vecera and Farah, 1994; Lavie and Driver, 1996; Tipper and Weaver, 1998) (although Cave and Kosslyn, 1989, argued that the object is selected by a very specific selection of locations).

Recent evidence about the extent of feature bundling can be found in the experiments by Luck and Vogel (1997). On each trial, their subjects viewed two multielement displays, with a delay of less than a second between them, and monitored one feature dimension for changes between the two displays. With set sizes of up to four, subjects could keep track of the color or shape or size or orientation of four objects without much trouble. Interestingly, performance was just as good when subjects had to look for changes that could occur in any of the four features. Seemingly, subjects were now remembering 16 pieces of information. We know, however, that subjects could not remember the colors of 16 distinct objects, so the results suggest that visual short-term memory can hold approximately four objects and that all of the features of each object are recorded and bundled together.

### When Is Binding a Problem?

The psychophysical research reviewed here makes it clear that there is a binding problem in human vision. There are circumstances under which observers behave as if basic features that are tightly linked in the world are, at best, loosely linked in the visual system. At the same time, the orderly and reasonable nature of routine visual perception demonstrates that the visual system solves the binding problem successfully most of the time. By “successfully,” in this case, we mean that the problem does not interfere with our usual uses of our visual systems. The visual system may be rife with unbound features but, under normal circumstances, they do not intrude. Why not?

We propose that there are two answers to this question: a preattentive or, perhaps, unattended answer and an attentive answer. In the early stages of visual processing (i.e., primary visual cortex), visual information is represented within spatially organized maps of the visual field. Each feature is represented as occupying a fairly specific location, and thus location serves as a means for linking all of the features belonging to a single object. Although the representations at this level contain all of the information necessary to determine the relationships between the features in an object, those relationships are not explicitly represented at this level. Without explicit representations of the feature combinations, target objects defined by a combination of features cannot be found easily in visual search, although a feature combination may produce some form of priming or adaptation. We can think of the features at this early level as being loosely “bundled” together rather than tightly “bound.”

In the absence of visual attention, the spatially organized maps of the visual field would prevent features from becoming truly “free floating.” However, without the explicit representation of the relationships among features, or “binding,” permitted by the deployment of attention, it may not be possible to recognize these spatially correlated bundles of features. The processes of object recognition require that features be tightly “bound” rather than loosely “bundled,” as they were in the earlier levels. The binding, however, is only possible for objects selected by attention, and not for all of the objects present at unselected locations in the visual field.

The simple spatial association used in early vision may not help in later stages of object recognition (i.e., the inferior temporal lobe), because specific information about the location of each feature is no longer available. In order to avoid the combinatorial disaster of representing *all* objects in *all* orientations at *all* locations, cells with complex response properties respond to those properties across large portions of the visual field. If information from multiple objects in the visual field were represented simultaneously at this level, it would be difficult to determine which features belonged to which objects. Selective attention is the apparent solution to this aspect of the binding problem. If visual selection mechanisms allow only selected objects or locations to be represented at this level, then the specific relationships among features can be represented explicitly. In this way, a mechanism that is specialized for face recognition, for example, can receive two eyes, a nose, and

a mouth. If attention did not regulate the input into the face recognizer, it might receive six eyes, three noses, and three mouths. In the absence of the tight spatial information of earlier visual stages, it might be quite unable to associate the correct facial features with each other.

Thus, across the great bulk of the visual field, unrecognized objects are held together by the spatial organization of the early visual system. At later stages, a recognized object is held together by the explicit binding of a selected set of features. Working in tandem, these processes of bundling and binding deliver a coherent perceptual world. The data described above suggest that problems in feature binding arise in two circumstances. The first occurs when explicit representations of feature combinations are needed before the objects have been selected. This situation can happen in visual searches for targets defined by feature combinations. We can't easily search for one face in a field of distractor faces with similar features, because the featural configuration for each face cannot be represented until that face is individually selected and its representation is built in the later stages of the visual system. Guidance by basic features limits this problem in most cases. Thus, the search for a face is only noticeably inefficient if there are many faces. Otherwise, basic feature information can guide attention to the few faces in the scene. Similarly, recognition of a specific car in the parking lot requires explicit binding of its features. However, in the search for your yellow Volkswagon (Weisstein, 1973), attention will be guided to items of the appropriate color. The visual search examples that point to failures of binding (e.g., the pluses of Figure 4) must be carefully contrived to require binding without permitting guidance.

The second set of circumstances that produces a binding problem is exemplified by illusory conjunctions. When information is presented briefly or when sustained information is not recoded into memory, the spatial glue that holds bundled features together becomes degraded. Basic features with uncertain positions can combine to produce illusory conjunctions. Recall that the stimuli are gone in most cases of illusory conjunctions, making accurate updating of spatial position impossible.

We make no specific claims here about the neural substrate of binding. This account neither requires nor contradicts a feature binding role for oscillations or some other form of synchronous neural firing, as has been proposed in a number of different contexts (e.g., von der Malsburg, 1981; Crick and Koch, 1990a, 1990b). Whatever the mechanism, we would be surprised if it did not produce an early, parallel bundling of features into objects at specific spatial locations followed by a later selection of one or more of those bundles for more precise binding.

In summary, this paper has described some of the psychophysical evidence for binding problems in human vision. Other papers in this issue deal with the physiological and/or computational solutions to these problems. Psychophysics points to two aspects of those solutions. Early stages of visual processing appear to be able to divide the world into proto-objects that are little more than loosely organized feature bundles at specific locations in space. These initial object parsing operations

are apparently performed in parallel across the visual field and prevent features from floating freely by tying them to spatial locations. Later stages, responsible for object recognition, require tighter, more accurate binding of features and more explicit representations of the relationships among the features. This more demanding stage is capacity limited. Attentional selection is used to restrict this more complete binding to the current object (or objects) of attention.

#### Acknowledgments

This work was supported by grants from the National Institutes of Health—National Eye Institute, the National Institutes of Mental Health, the National Science Foundation, the Air Force Office of Scientific Research, and the Human Frontiers Science Program. We thank Bill Phillips for comments on an earlier draft.

#### References

A comprehensive reference list for all reviews can be found on pages 111–125.

## References for Reviews on the Binding Problem

- Abeles, M. (1982a). Role of cortical neuron: integrator or coincidence detector? *Israel J. Med. Sci.* *18*, 83–92.
- Abeles, M. (1982b). *Studies of Brain Function, Volume 6, Local Cortical Circuits: An Electrophysiological Study* (Berlin: Springer-Verlag).
- Abeles, M. (1991). *Corticomics: Neural Circuits of Cerebral Cortex* (Cambridge: Cambridge University Press).
- Abeles, M., Prut, Y., Bergman, H., and Vaadia, E. (1994). Synchronization in neuronal transmission and its importance for information processing. *Prog. Brain Res.* *102*, 395–404.
- Adam, H. (1998). *Figur-Grund-Abtrennung mit rückgekoppelten Merkmalsfeldern*. PhD Thesis, Department of Physics and Astronomy, Ruhr University, Bochum, Germany.
- Adelson, E.H. (1993). Perceptual organization and the judgment of brightness. *Science* *262*, 2042–2044.
- Adelson, E.H. (1999). Lightness perception and lightness illusions. In *The Cognitive Neurosciences*, M.S. Gazzaniga, ed. (Cambridge, MA: MIT Press).
- Adelson, E.H., and Movshon, J.A. (1982). Phenomenal coherence of moving visual patterns. *Nature* *300*, 523–525.
- Aertsen, A., Gerstein, G.L., Habib, M.K., and Palm, G. (1989). Dynamics of neuronal firing correlation: modulation of “effective connectivity.” *J. Neurophysiol.* *61*, 900–917.
- Aertsen, A., Diesmann, M., and Gewaltig, M.-O. (1996). Propagation of synchronous spiking activity in feedforward neural networks. *J. Physiol. (Paris)* *90*, 243–247.
- Aiple, F., and Krüger, J. (1988). Neuronal synchrony in monkey striate cortex: interocular signal flow and dependency on spike rates. *Exp. Brain Res.* *72*, 141–149.
- Alais, D., Blake, R., and Lee, S.-H. (1998). Visual features that vary together over time group together over space. *Nat. Neurosci.* *1*, 160–164.
- Albright, T.D., and Stoner, G.R. (1995). Visual motion perception. *Proc. Natl. Acad. Sci. USA* *92*, 2433–2440.
- Alonso, J.-M., and Martinez, L.M. (1998). Functional connectivity between simple cells and complex cells in cat striate cortex. *Nat. Neurosci.* *1*, 395–403.
- Alonso, J.-M., Usrey, W.M., and Reid, R.C. (1996). Precisely correlated firing in cells of the lateral geniculate nucleus. *Nature* *383*, 815–819.
- Andersen, R.A. (1995). Encoding of intention and spatial location in the posterior parietal cortex. *Cereb. Cortex* *5*, 457–469.
- Andersen, R.A. (1997). Multimodal integration for the representation of space in the posterior parietal cortex. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* *352*, 1421–1428.
- Anderson, C.H., and Van Essen, D.C. (1987). Shifter circuits: a computational strategy for dynamic aspects of visual processing. *Proc. Natl. Acad. Sci. USA* *84*, 6297–6301.
- Arbib, M. (1964). *Brains, Machines and Mathematics* (New York: McGraw-Hill).
- Arguin, M., Cavanagh, P., and Joannette, Y. (1994). Visual feature integration with an attention deficit. *Brain Cogn.* *24*, 44–56.
- Arieli, A., Sterkin, A., Grinvald, A., and Aertsen, A. (1996). Dynamics of ongoing activity: explanation of the large variability in evoked cortical responses. *Science* *273*, 1868–1871.
- Ashby, F.G., Prinzmetal, W., Ivry, R., and Maddox, W.T. (1996). A formal theory of feature binding in object perception. *Psychol. Rev.* *103*, 165–192.
- Assad, J., and Maunsell, J. (1995). Neuronal correlates of inferred motion in primate posterior parietal cortex. *Nature* *373*, 518–521.
- Bair, W. (1999). Spike timing in the mammalian visual system. *Curr Opin. Neurobiol.*, in press.
- Bair, W. and Koch, C. (1995). Precision and reliability of neocortical spike trains in the behaving monkey. In *The Neurobiology of Computation*, B.J. Kluwer, ed. (New York: Academic Publishers).
- Bair, W., and Koch, C. (1996). Temporal precision of spike trains in extrastriate cortex of the behaving monkey. *Neural Comput.* *8*, 44–66.
- Bair, W., and O’Keefe, L.P. (1998). The influence of fixational eye movements on the response of neurons in area MT of the macaque. *Vis. Neurosci.* *15*, 779–786.
- Bair, W., Koch, C., Newsome, W., and Britten, K. (1994). Power spectrum analysis of bursting cells in area MT in the behaving monkey. *J. Neurosci.* *14*, 2870–2892.
- Bair, W., Cavanaugh, J.R., and Movshon, J.A. (1997). Reconstructing stimulus velocity from neuronal responses in area MT. In *Advances in Neural Information Processing Systems*, M.C. Mozer, M.I. Jordan, and T. Petsche, eds. (Cambridge, MA: MIT Press).
- Baldi, P., and Meir, R. (1990). Computing with arrays of coupled oscillators: an application to preattentive texture discrimination. *Neural Comput.* *2*, 458–471.
- Ballard, D.H., Hinton, G.E., and Sejnowski, T.J. (1983). Parallel visual computation. *Nature* *306*, 21–26.
- Barbas, H. (1988). Anatomic organization of basoventral and medio-dorsal visual recipient prefrontal regions in the rhesus monkey. *J. Comp. Neurol.* *276*, 313–342.
- Barbas, H., and Pandya, D.N. (1989). Architecture and intrinsic connections of the prefrontal cortex in the rhesus monkey. *J. Comp. Neurol.* *286*, 353–375.
- Barlow, H.B. (1972). Single units and cognition: a neurone doctrine for perceptual psychology. *Perception* *1*, 371–394.
- Barlow, H.B. (1981). Critical limiting factors in the design of the eye and visual cortex. *Proc. R. Soc. Lond. B Biol. Sci.* *212*, 1–34.
- Barlow, H.B. (1985). The twelfth Bartlett memorial lecture: the role of single neurons in the psychology of perception. *Quart. J. Exp. Psychol.* *37*, 121–145.
- Bauer, H.-U., and Pawelzik, K. (1993). Alternating oscillatory and stochastic dynamics in a model for a neuronal assembly. *Physica D69*, 380–393.
- Baylis, G.C., Rolls, E.T., and Leonard, C.M. (1985). Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. *Brain Res.* *342*, 91–102.
- Baylis, G.C., Rolls, E.T., and Leonard, C.M. (1987). Functional subdivisions of the temporal lobe neocortex. *J. Neurosci.* *7*, 330–342.
- Beck, J. (1966). Perceptual grouping produced by changes in orientation and shape. *Science* *154*, 538–540.
- Beck, J. (1967). Perceptual grouping produced by line figures. *Percept. Psychophys.* *2*, 491–495.
- Behrmann, M., and Tipper, S.P. (1994). Object-based attentional mechanisms: evidence from patients with unilateral neglect. In *Attention and Performance, Volume 15, Conscious and Nonconscious Information Processing*, C. Umiltà and M. Moscovitch, eds. (Cambridge, MA: MIT Press).
- Bergen, J.R., and Adelson, E.H. (1988). Early vision and texture perception. *Nature* *333*, 363–364.
- Bergen, J.R., and Julesz, B. (1983). Parallel versus serial processing in rapid pattern discrimination. *Nature* *303*, 696–698.
- Best, J., Reuss, S., and Dinse, H.R.O. (1986). Lamina-specific differences of visual latencies following photic stimulation in the cat striate cortex. *Brain Res.* *385*, 356–360.
- Biederman, I. (1981). On the semantics of a glance at a scene. In *Perceptual Organization*, M. Kubovy and J. Pomerantz, eds. (Hillsdale, NJ: Lawrence Erlbaum Associates).
- Biederman, I. (1987). Recognition by components: A theory of human image understanding. *Psychol. Rev.* *94*, 115–147.
- Biederman, I. and Kalocsai, P. (1997). Neurocomputational bases of object and face recognition. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* *352*, 1203–1219.
- Bienenstock, E. (1995). A model of neocortex. *Network* *6*, 179–224.

- Bienenstock, E., and von der Malsburg, C. (1987). A neural network for invariant pattern recognition. *Europhys. Lett.* **4**, 121–126.
- Blake, R., and Yang, Y. (1997). Spatial and temporal coherence in perceptual binding. *Proc. Natl. Acad. Sci. USA* **94**, 7115–7119.
- Booth, M., and Rolls, E. (1998). View-invariant representations of familiar objects by neurons in the inferior temporal visual cortex. *Cereb. Cortex* **8**, 510–523.
- Borg-Graham, L., Monier, C., and Fregnac, Y. (1996). Voltage-clamp measurement of visually-evoked conductances with whole-cell patch recordings in primary visual cortex. *J. Physiol. (Paris)* **90**, 185–188.
- Borg-Graham, L.J., Monier, C., and Fregnac, Y. (1998). Visual input evokes transient and strong shunting inhibition in visual cortical neurons. *Nature* **393**, 369–373.
- Borisyuk, R.M., Borisyuk, G.N., and Kazanovich, Y.B. (1998). The synchronization principle in modelling of binding and attention. *Membr. Cell Biol.* **11**, 753–761.
- Bosking, W.H., Zhang, Y., Schofield, B., and Fitzpatrick, D. (1997). Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex. *J. Neurosci.* **17**, 2112–2127.
- Boussaoud, D., Ungerleider, L.G., and Desimone, R. (1990). Pathways for motion analysis: cortical connections of the medial superior temporal and fundus of the superior temporal visual area in the macaque. *J. Comp. Neurol.* **296**, 462–495.
- Bouyer, J.J., Montaron, M.F., and Rougeul, A. (1981). Fast frontoparietal rhythms during combined focused attentive behaviour and immobility in cat: cortical and thalamic localizations. *Electroencephalogr. Clin. Neurophysiol.* **51**, 244–252.
- Bradley, D.C., Chang, G.C., and Andersen, R.A. (1998). Encoding of three-dimensional structure-from-motion by primate area MT neurons. *Nature* **392**, 714–717.
- Bragin, A., Jando, G., Nadasdy, Z., Hetke, J., Wise, K., and Buzsaki, G. (1995). Gamma (40–100 Hz) oscillation in the hippocampus of the behaving rat. *J. Neurosci.* **15**, 47–60.
- Braitenberg, V. (1978). Cell assemblies in the cerebral cortex. In *Lecture Notes in Biomathematics, Volume 21, Theoretical Approaches in Complex Systems*, R. Heim and G. Palm, eds. (Berlin: Springer).
- Braitenberg, V., and Schuz, A. (1991). *Anatomy of the Cortex: Statistics and Geometry* (Berlin: Springer).
- Braun, J., and Julesz, B. (1998). Dividing attention at little cost: detection and discrimination tasks. *Percept. Psychophys.* **60**, 1–23.
- Bravo, M., and Blake, R. (1990). Preattentive vision and perceptual groups. *Perception* **19**, 515–522.
- Brecht, M., Singer, W., and Engel, A.K. (1998). Correlation analysis of corticotectal interactions in the cat visual system. *J. Neurophysiol.* **79**, 2394–2407.
- Bressler, S.L., Coppola, R., and Nakamura, R. (1993). Episodic multi-regional cortical coherence at multiple frequencies during visual task performance. *Nature* **366**, 153–156.
- Briand, K.A., and Klein, R.M. (1987). Is Posner's "beam" the same as Triesman's "glue"? On the relation between visual orienting and feature integration theory. *J. Exp. Psychol. Hum. Percept. Perform.* **13**, 228–241.
- Britten, K.H., Shadlen, M.N., Newsome, W.T., and Movshon, J.A. (1992). The analysis of visual motion: a comparison of neuronal and psychophysical performance. *J. Neurosci.* **12**, 4745–4765.
- Britten, K.H., Newsome, W.T., Shadlen, M.N., Celebrini, S., and Movshon, J.A. (1996). A relationship between behavioral choice and the visual responses of neurons in macaque MT. *Vis. Neurosci.* **13**, 87–100.
- Brody, C.D. (1998). Slow covariations in neuronal resting potentials can lead to artefactually fast cross-correlations in their spike trains. *J. Neurophysiol.* **80**, 3345–3351.
- Brody, C.D. (1999a). Disambiguating different covariation types. *Neural Comput.* **11**, 1527–1535.
- Brody, C.D. (1999b). Correlations without synchrony. *Neural Comput.* **11**, 1537–1551.
- Brody, C.D. (1999c). Latency, excitability, and spike timing covariations. *Neural Comput.*, in press.
- Bruce, C., Desimone, R., and Gross, C. (1981). Visual properties of neurons in a polysensory area in the superior temporal sulcus of the macaque. *J. Neurophysiol.* **46**, 369–384.
- Bülthoff, H., and Edelman, S. (1992). Psychophysical support for a two-dimensional view interpolation theory of object recognition. *Proc. Natl. Acad. Sci. USA* **89**, 60–64.
- Bülthoff, H.H., Edelman, S.Y., and Tarr, M.J. (1995). How are three-dimensional objects represented in the brain? *Cereb. Cortex* **3**, 247–260.
- Buračas, G., Zador, A., DeWeese, M., and Albright, T. (1998). Efficient discrimination of temporal patterns by motion-sensitive neurons in primate visual cortex. *Neuron* **20**, 959–969.
- Burr, D. (1979). Acuity for apparent vernier offset. *Vision Res.* **19**, 835–837.
- Bush, P., and Sejnowski, T. (1996). Inhibition synchronizes sparsely connected cortical neurons within and between columns in realistic network models. *J. Comput. Neurosci.* **3**, 91–110.
- Bushnell, M.C., Goldberg, M.E., and Robinson, D.L. (1981). Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. *J. Neurophysiol.* **46**, 755–772.
- Buzsaki, G. (1996). The hippocampo-neocortical dialogue. *Cereb. Cortex* **6**, 81–92.
- Buzsaki, G., and Chrobak, J.J. (1995). Temporal structure in spatially organized neuronal ensembles: a role for interneuronal networks. *Curr. Opin. Neurobiol.* **5**, 504–510.
- Buzsaki, G., Leung, L.S., and Vanderwolf, C.H. (1983). Cellular basis of hippocampal EEG in the behaving rat. *Brain Res.* **6**, 139–171.
- Caminiti, R., Ferraina, S., and Johnson, P.B. (1996). The sources of visual information to the primate frontal lobe: a novel role for the superior parietal lobule. *Cereb. Cortex* **6**, 319–328.
- Carney, T., Paradiso, M., and Freeman, R. (1989). A physiological correlate of the Pulfrich effect in cortical neurons of the cat. *Vision Res.* **29**, 155–165.
- Carney, T., Silverstein, D., and Klein, S. (1995). Vernier acuity during image rotation and translation: visual performance limits. *Vision Res.* **35**, 1951–1964.
- Castelo-Branco, M., Neuenschwander, S., and Singer, W. (1998). Synchronization of visual responses between the cortex, lateral geniculate nucleus, and retina in the anesthetized cat. *J. Neurosci.* **18**, 6395–6410.
- Cave, K.R. (1999). The Feature Gate model of visual selection. *Psychol. Res.*, in press.
- Cave, K.R., and Bichot, N.P. (1999). Visuo-spatial attention: beyond a spotlight model. *Psychonom. Bull. Rev.*, in press.
- Cave, K.R., and Kosslyn, S.M. (1989). Varieties of size-specific visual selection. *J. Exp. Psychol. Gen.* **118**, 148–164.
- Cave, K.R., and Wolfe, J.M. (1990). Modeling the role of parallel processing in visual search. *Cogn. Psychol.* **22**, 225–271.
- Chance, F., Nelson, S., and Abbott, L. (1999). Complex cells as cortically amplified simple cells. *Nat. Neurosci.* **2**, 277–282.
- Chelazzi, L., Miller, E.K., Duncan, J., and Desimone, R.C. (1993). A neural basis for visual search in inferior temporal cortex. *Nature* **363**, 345–347.
- Chelazzi, L., Duncan, J., Miller, E.K., and Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *J. Neurophysiol.* **80**, 2918–2940.
- Cheng, K., Hasegawa, T., Saleem, K.S., and Tanaka, K. (1994). Comparison of neuronal selectivity for stimulus speed, length, and contrast in the prestriate visual cortex areas V4 and MT of the macaque monkey. *J. Neurophysiol.* **71**, 2269–2280.
- Chino, Y., Shansky, M., Jankowski, W., and Banser, F. (1983). Effects of rearing kittens with convergent strabismus on development of receptive-field properties in striate cortex neurons. *J. Neurophysiol.* **50**, 265–286.
- Chino, Y.M., Smith, E.L., Wada, H., Ridder, W.H., Langston, A.L., and Leshner, G.A. (1991). Disruption of binocularly correlated signals alters the postnatal development of spatial properties in cat striate cortical neurons. *J. Neurophysiol.* **65**, 841–859.

- Chrobak, J.J., and Buzsaki, G. (1998). Gamma oscillations in the entorhinal cortex of the freely behaving rat. *J. Neurosci.* *18*, 388–398.
- Churchland, P.S., Ramachandran, V.S., and Sejnowski, T.J. (1994). A critique of pure vision. In *Large-Scale Neuronal Theories of the Brain*, C. Koch and J.L. Davis, eds. (Cambridge, MA: MIT Press).
- Cobb, S.R., Buhl, E.H., Halasy, K., Paulsen, O., and Somogyi, P. (1995). Synchronization of neuronal activity in hippocampus by individual GABAergic interneurons. *Nature* *378*, 75–78.
- Cohen, A., and Ivry, R.B. (1989). Illusory conjunctions inside and outside the focus of attention. *J. Exp. Psychol. Hum. Percept. Perform.* *15*, 650–663.
- Cohen, A., and Ivry, R.B. (1991). Density effects in conjunction search: evidence for coarse location mechanism of feature integration. *J. Exp. Psychol. Hum. Percept. Perform.* *17*, 891–901.
- Colby, C.L., and Goldberg, M.E. (1999). Space and attention in parietal cortex. *Annu. Rev. Neurosci.* *22*, 319–349.
- Colby, C.L., Duhamel, J.-R., and Goldberg, M.E. (1996). Visual, presaccadic, and cognitive activation of single neurons in monkey lateral intraparietal area. *J. Neurophysiol.* *76*, 2841–2852.
- Connor, C.E., Gallant, J.L., Preddie, D.C., and Van Essen, D.C. (1996). Responses in area V4 depend on the spatial relationship between stimulus and attention. *J. Neurophysiol.* *75*, 1306–1308.
- Connor, C., Preddie, D., Gallant, J., and van Essen, D. (1997). Spatial attention effects in macaque area V4. *J. Neurosci.* *17*, 3201–3214.
- Connors, B.W., and Gutnick, M.J. (1990). Intrinsic firing patterns of diverse neocortical neurons. *Trends Neurosci.* *13*, 99–104.
- Connors, B.W., Gutnick, M.J., and Prince, D.A. (1982). Electrophysiological properties of neocortical neurons in vitro. *J. Neurophysiol.* *48*, 1302–1320.
- Corbetta, M., Miezin, F.M., Shulman, G.L., and Petersen, S.E. (1993). A PET study of visuospatial attention. *J. Neurosci.* *13*, 1202–1226.
- Corbetta, M., Shulman, G.L., Miezin, F.M., and Petersen, S.E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science* *270*, 802–805.
- Cowey, A., and Gross, C.G. (1970). Effects of foveal prestriate and inferotemporal lesions on visual discrimination by rhesus monkeys. *Exp. Brain Res.* *11*, 128–144.
- Creutzfeldt, O.D., Garey, L.J., Kuroda, R., and Wolff, J.R. (1977). The distribution of degenerating axons after small lesions in the intact and isolated visual cortex of the cat. *Exp. Brain Res.* *27*, 419–440.
- Crewther, D., and Crewther, S. (1990). Neural site of strabismic amblyopia in cats: spatial frequency deficit in primary cortical neurons. *Exp. Brain Res.* *79*, 615–622.
- Crick, F. (1984). Function of the thalamic reticular complex: the searchlight hypothesis. *Proc. Natl. Acad. Sci. USA* *81*, 4586–4590.
- Crick, F., and Koch, C. (1990a). Some reflections on visual awareness. *Cold Spring Harbor Symp. Quant. Biol.* *55*, 953–962.
- Crick, F., and Koch, C. (1990b). Towards a neurobiological theory of consciousness. *Sem. Neurosci.* *2*, 263–275.
- Damasio, A.R. (1985). Disorders of complex visual processing: agnosia, achromatopsia, Balint's syndrome, and related difficulties of orientation and construction. In *Principles of Behavioral Neurology*, M.M. Mesulam, ed. (Philadelphia: Davis).
- Das, A., and Gilbert, C.D. (1995). Receptive field expansion in adult visual cortex is linked to dynamic changes in strength of cortical connections. *J. Neurophysiol.* *74*, 779–792.
- Das, A., and Gilbert, C.D. (1999). Topography of contextual modulations mediated by short-range interactions in primary visual cortex. *Nature* *399*, 655–661.
- Dean, P. (1976). Effects of inferotemporal lesions on the behavior of monkeys. *Psychol. Bull.* *83*, 41–71.
- DeAngelis, G.C., Ghose, G.M., Ohzawa, I., and Freeman, R.D. (1999). Functional micro-organization of primary visual cortex: receptive field analysis of nearby neurons. *J. Neurosci.* *19*, 4046–4064.
- deCharms, R., and Merzenich, M. (1996). Primary cortical representation of sounds by the coordination of action-potential timing. *Nature* *381*, 610–613.
- deCharms, R.C., Blake, D.T., and Merzenich, M.M. (1998). Optimizing sound features for cortical neurons. *Science* *280*, 1439–1443.
- De Oliveira, S.C., Thiele, A., and Hoffmann, K.P. (1997). Synchronization of neuronal activity during stimulus expectation in a direction discrimination task. *J. Neurosci.* *17*, 9248–9260.
- Deppisch, J., Bauer, H.-U., Schillen, T.B., König, P., Pawelzik, K., and Geisel, T. (1993). Alternating oscillatory and stochastic states in a network of spiking neurons. *Network* *4*, 243–257.
- Desimone, R. (1991). Face-selective cells in the temporal cortex of monkeys. *J. Cogn. Neurosci.* *3*, 1–8.
- Desimone, R., and Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* *18*, 193–222.
- Desimone, R., and Schein, S. (1987). Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. *J. Neurophysiol.* *57*, 835–868.
- Desimone, R., and Ungerleider, L. (1986). Multiple visual areas in the caudal superior temporal sulcus of the macaque. *J. Comp. Neurol.* *248*, 164–189.
- Desimone, R., Albright, T.D., Gross, C.G., and Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *J. Neurosci.* *4*, 2051–2062.
- Desimone, R., Schein, S.J., Moran, J., and Ungerleider, L.G. (1985). Contour, color and shape analysis beyond the striate cortex. *Vision Res.* *25*, 441–452.
- Dev, P. (1975). Perception of depth surfaces in random-dot stereograms: a neural model. *Int. J. Man-Machine Stud.* *7*, 511–528.
- DeValois, R.L., and DeValois, K.K. (1988). *Spatial Vision* (New York: Oxford University Press).
- DeValois, R.L., Albrecht, D.G., and Thorell, L.G. (1982a). Spatial frequency selectivity of cells in macaque visual cortex. *Vision Res.* *22*, 545–559.
- DeValois, R.L., Yund, E.W., and Hepler, N. (1982b). The orientation and direction selectivity of cells in macaque visual cortex. *Vision Res.* *22*, 531–544.
- DeYoe, E.A., and Van Essen, D.C. (1985). Segregation of efferent connections and receptive field properties in visual area V2 of the macaque. *Nature* *317*, 58–61.
- DeYoe, E.A., and Van Essen, D.C. (1988). Concurrent processing streams in monkey visual cortex. *Trends Neurosci.* *11*, 219–226.
- Diesmann, M., Gewaltig, M.-O., and Aertsen, A. (1997). Cortical synfire activity—a two dimensional state space analysis. In *From Membrane to Mind: Proceedings of the 25th Gottinger Neurobiology Conference*, H. Wässle and N. Elsner, eds. (Stuttgart: Thieme-Verlag).
- Dixon, P., and Shedden, J.M. (1987). Conceptual and physical differences in the category effect. *Percept. Psychophys.* *42*, 457–464.
- Dodwell, P.C., and Humphrey, G.K. (1992). A functional theory of the McCollough effect. *Psych. Rev.* *97*, 78–89.
- Donnelly, N., Humphreys, G.W., and Riddoch, M.J. (1991). Parallel computation of primitive shape descriptions. *J. Exp. Psychol. Hum. Percept. Perform.* *17*, 561–570.
- Donoghue, J.P., Sanes, J.N., Hatsopoulos, N.G., and Gaal, G. (1998). Neural discharge and local field potential oscillations in primate motor cortex during voluntary movement. *J. Neurophysiol.* *79*, 159–173.
- Doupe, A.J. (1997). Song- and order-selective neurons in the songbird anterior forebrain and their emergence during vocal development. *J. Neurosci.* *17*, 1147–1167.
- Dubner, R., and Zeki, S.M. (1971). Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus. *Brain Res.* *35*, 528–532.
- Duncan, J. (1983). Category effects in visual search: a failure to replicate the “oh-zero” phenomenon. *Percept. Psychophys.* *34*, 221–232.
- Duncan, J. (1984). Selective attention and the organization of visual information. *J. Exp. Psychol. Gen.* *113*, 501–517.
- Eckes, C., and Vorbrüggen, C.V. (1996). Combining data-driven and model-based cues for segmentation of video sequences. In *WCNN 1996* (San Diego: Lawrence Erlbaum).
- Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M., and Reitboeck, H.J. (1988). Coherent oscillations: a mechanism for feature linking in the visual cortex? *Biol. Cybern.* *60*, 121–130.

- Eckhorn, R., Frien, A., Bauer, R., Woelbern, T., and Kehr, H. (1993). High frequency 60–90 Hz oscillations in primary visual cortex of awake monkey. *Neuroreport* 4, 243–246.
- Edelman, G.M. (1978). Group selection and phasic reentrant signaling: a theory of higher brain function. In *The Mindful Brain: Cortical Organization and the Group-Selective Theory of Higher Brain Function*. G.M. Edelman and V.B. Mountcastle, eds. (Cambridge, MA: MIT Press).
- Edelman, G.M. (1987). *Neural Darwinism: The Theory of Neuronal Group Selection* (New York: Basic Books).
- Edelman, G.M. (1989). *The Remembered Present: A Biological Theory of Consciousness* (New York: Basic Books).
- Edwards, D.P., Purpura, K.P., and Kaplan, E. (1995). Contrast sensitivity and spatial frequency response of primate cortical neurons in and around the cytochrome oxidase blobs. *Vision Res.* 35, 1501–1523.
- Eggers, H., and Blakemore, C. (1978). Physiological basis of an isometric amblyopia. *Science* 201, 264–267.
- Elder, J., and Zucker, S. (1993). The effect of contour closure on the rapid discrimination of two-dimensional shapes. *Vision Res.* 33, 981–991.
- Engel, A.K., König, P., Gray, C.M., and Singer, W. (1990). Stimulus-dependent neuronal oscillations in cat visual cortex: inter-columnar interaction as determined by cross-correlation analysis. *Eur. J. Neurosci.* 2, 588–606.
- Engel, A.K., König, P., Kreiter, A.K., and Singer, W. (1991a). Inter-hemispheric synchronization of oscillatory neuronal responses in cat visual cortex. *Science* 252, 1177–1179.
- Engel, A.K., Kreiter, A.K., König, P., and Singer, W. (1991b). Synchronization of oscillatory neuronal responses between striate and extrastriate visual cortical areas of the cat. *Proc. Natl. Acad. Sci. USA* 88, 6048–6052.
- Engel, A.K., König, P., and Singer, W. (1991c). Direct physiological evidence for scene segmentation by temporal coding. *Proc. Natl. Acad. Sci. USA* 88, 9136–9140.
- Engel, A.K., König, P., and Singer, W. (1992a). Reply to: The functional nature of neuronal oscillations. *Trends Neurosci.* 15, 387–388.
- Engel, A.K., König, P., Kreiter, A.K., Chillen, T.B., and Singer, W. (1992b). Temporal coding in the visual cortex: new vista on integration in the nervous system. *Trends Neurosci.* 15, 218–225.
- Engel, A.K., Roelfsema, P.R., Fries, P., Brecht, M., and Singer, W. (1997). Role of the temporal domain for response selection and perceptual binding. *Cereb. Cortex* 7, 571–582.
- Eskandar, E.N., and Assad, J.A. (1999). Dissociation of visual motor and predictive signals in parietal cortex during visual guidance. *Nat. Neurosci.* 2, 88–93.
- Fahle, M., and Koch, C. (1995). Spatial displacement, but not temporal asynchrony, destroys figural binding. *Vision Res.* 35, 491–494.
- Fahle, M., and Poggio, T. (1981). Visual hyperacuity: spatio-temporal interpolation in human vision. *Proc. R. Soc. Lond. B Biol. Sci.* 213, 451–477.
- Fang, S.-P., and Wu, P. (1989). Illusory conjunctions in the perception of Chinese characters. *J. Exp. Psychol. Hum. Percept. Perform.* 15, 434–447.
- Felleman, D.J., and Van Essen, D.C. (1987). Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex. *J. Neurophysiol.* 57, 889–920.
- Felleman, D.J., and van Essen, D.C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cereb. Cortex* 1, 1–47.
- Ferrera, V.P., and Lisberger, S.G. (1995). Attention and target selection for smooth pursuit eye movements. *J. Neurosci.* 15, 7472–7484.
- Ferrera, V.P., Rudolph, K.K., and Maunsell, J.H.R. (1994). Responses of neurons in the parietal and temporal visual pathways during a motion task. *J. Neurosci.* 14, 6171–6186.
- Fetz, E., Toyama, K., and Smith, W. (1991). Synaptic interactions between cortical neurons. In *Cerebral Cortex*, A. Peters and E.G. Jones, eds. (New York: Plenum Press).
- Fodor, J.A., and Pylyshyn, Z.W. (1988). Connectionism and cognitive architecture: a critical analysis. *Cognition* 28, 3–71.
- Folk, C.L., and Egeth, H. (1989). Does the identification of simple features require serial processing? *J. Exp. Psychol. Hum. Percept. Perform.* 15, 97–110.
- Foster, K.H., Gaska, J.P., Nagler, M., and Pollen, D.A. (1985). Spatial and temporal frequency selectivity of neurones in visual cortical areas V1 and V2 of the macaque monkey. *J. Physiol. (Lond.)* 365, 331–363.
- Franz, V., Gegenfurtner, K.R., Fahle, M., and Buelthoff, H.H. (1999). Grasping visual illusions: no evidence for a dissociation between perception and action. *Psychol. Sci.*, in press.
- Freeman, W.J. (1975). *Mass Action in the Nervous System* (New York: Academic Press).
- Freeman, W.J., and Skarda, C.A. (1985). Spatial EEG-patterns, nonlinear dynamics and perception: the neo-Sherrington view. *Brain Res. Rev.* 10, 147–175.
- Freiwald, W.A., Kreiter, A.K., and Singer, W. (1995). Stimulus dependent intercolumnar synchronization of single unit responses in cat area 17. *Neuroreport* 6, 2348–2352.
- Friedman-Hill, S.R., Robertson, L.C., and Treisman, A. (1995). Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions. *Science* 269, 853–855.
- Friedman-Hill, S., Maldonado, P.E., and Gray, C.M. (1999). Temporal dynamics of neuronal activity in the striate cortex of alert macaque: I. Incidence and stimulus-dependence of oscillations. *J. Neurosci.*, in press.
- Frien, A., Eckhorn, R., Bauer, R., Woelbern, T., and Kehr, H. (1994). Stimulus-specific fast oscillations at zero phase between visual areas V1 and V2 of awake monkey. *Neuroreport* 5, 2273–2277.
- Fries, P., Roelfsema, P.R., Engel, A.K., König, P., and Singer, W. (1997). Synchronization of oscillatory responses in visual cortex correlates with perception in interocular rivalry. *Proc. Natl. Acad. Sci. USA* 94, 12699–12704.
- Fuji, H., Ito, H., Aihara, K., Ichinose, N., and Tsukada, M. (1996). Dynamical cell assembly hypothesis-theoretical possibility of spatio-temporal coding in the cortex. *Neural Network* 9, 1303–1350.
- Fujita, I., Tanaka, K., Ito, M., and Cheng, K. (1992). Columns for visual features of objects in monkey inferotemporal cortex. *Nature* 360, 343–346.
- Fukushima, K. (1980). Neocognitron: a self-organizing neural network model for a mechanism of pattern recognition unaffected by shift in position. *Biol. Cybern.* 36, 193–202.
- Gallant, J.L., Connor, C.E., Rakshit, S., Lewis, J.W., and Van Essen, D.C. (1996). Neural responses to polar, hyperbolic, and cartesian gratings in area V4 of the macaque monkey. *J. Neurophysiol.* 76, 2718–2739.
- Gattass, R., Sousa, A.P., and Gross, C.G. (1988). Visuotopic organization and extent of V3 and V4 of the macaque. *J. Neurosci.* 8, 1831–1845.
- Gawne, T.J., Kjaer, T.W., and Richmond, B.J. (1996). Latency: another potential code for feature binding in striate cortex. *J. Neurophysiol.* 76, 1356–1360.
- Geesaman, B.J., and Andersen, R.A. (1996). The analysis of complex motion patterns by form/cue invariant MSTd neurons. *J. Neurosci.* 16, 4716–4732.
- Geisler, W.S., and Albrecht, D.G. (1995). Bayesian analysis of identification performance in monkey visual cortex: nonlinear mechanisms and stimulus certainty. *Vision Res.* 35, 2723–2730.
- Georgopoulos, A.P., Ashe, J., Smyrnis, N., and Taira, M. (1992). The motor cortex and the coding of force. *Science* 256, 1692–1695.
- Gerstein, G.L., Bedenbaugh, P., and Aertsen, M.H. (1989). Neuronal assemblies. *IEEE Trans. Biomed. Eng.* 36, 4–14.
- Gerstner, W., and van Hemmen, J.L. (1993). Coherence and incoherence in a globally coupled ensemble of pulse-emitting units. *Phys. Rev. Lett.* 7, 312–315.
- Gerstner, W., Kempter, R., Van Hemmen, J.L., and Wagner, H. (1996). A neuronal learning rule for sub-millisecond temporal coding. *Nature* 383, 76–78.
- Ghose, G.M., and Freeman, R.D. (1992). Oscillatory discharge in the visual system: does it have a functional role? *J. Neurophysiol.* 68, 1558–1574.

- Ghose, G.M., and Freeman, R.D. (1997). Intracortical connections are not required for oscillatory activity in the visual cortex. *Vis. Neurosci.* 14, 963R-979R.
- Ghose, G.M., and Maunsell, J. (1999). Specialized representations in visual cortex: a role for binding? *Neuron* 24, this issue, 79-85.
- Ghose, G.M., and Ts'o, D.Y. (1997). Form processing modules in primate area V4. *J. Neurophysiol.* 77, 2191-2196.
- Gibson, J.R., and Maunsell, J.H.R. (1997). The sensory modality specificity of neural activity related to memory in visual cortex. *J. Neurophysiol.* 78, 1263-1275.
- Gilbert, C.D., and Wiesel, T.N. (1979). Morphology and intracortical projections of functionally characterized neurones in the cat visual cortex. *Nature* 280, 120-125.
- Gilbert, C.D., and Wiesel, T.N. (1983). Clustered intrinsic connections in cat visual cortex. *J. Neurosci.* 3, 1116-1133.
- Gilbert, C.D., and Wiesel, T.N. (1989). Columnar specificity of intrinsic horizontal and cortico-cortical connections in cat visual cortex. *J. Neurosci.* 9, 2432-2442.
- Givre, S.J., Arezzo, J.C., and Schroeder, C.E. (1995). Effects of wavelength on the timing and laminar distribution of illuminance-evoked activity in macaque V1. *Vis. Neurosci.* 12, 229-239.
- Gizzi, M.S., Newsome, W.T., and Movshon, J.A. (1983). Directional selectivity of neurons in macaque MT. *Invest. Ophthalm. Vis. Sci.* 24 (suppl.), 107.
- Gizzi, M.S., Katz, E., Schumer, R.A., and Movshon, J.A. (1990). Selectivity for orientation and direction of motion of single neurons in cat striate and extrastriate visual cortex. *J. Neurophysiol.* 63, 1529-1543.
- Goldsmith, M. (1998). What's in a location? Comparing object-based and space-based models of feature integration in visual search. *J. Exp. Psychol.* 127, 189-219.
- Goldstone, R.L. (1998). Perceptual learning. *Annu. Rev. Psychol.* 49, 585-612.
- Goodale, M. (1993). Visual pathways supporting perception and action in the primate cerebral cortex. *Curr. Opin. Neurobiol.* 3, 578-585.
- Goodale, M., and Humphrey, G. (1998). The objects of action and perception. *Cognition* 67, 181-207.
- Goodale, M.A., and Milner, A.D. (1992). Separate visual pathways for perception and action. *Trends Neurosci.* 15, 20-25.
- Goodale, M.A., Milner, A.D., Jakobson, L.S., and Carey, D.P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature* 349, 154-156.
- Goodale, M.A., Meenan, J.P., Bulthoff, H.H., Nicolle, D.A., Murphy, K. J., and Racicot, C.I. (1994). Separate neural pathways for visual analysis of object shape in perception and prehension. *Curr. Biol.* 4, 604-610.
- Goolkasian, P. (1988). Illusory conjunctions in the processing of clock times. *J. Gen. Psychol.* 115, 341-353.
- Gottlieb, J.P., Kusunoki, M., and Goldberg, M.E. (1998). The representation of visual salience in monkey parietal cortex. *Nature* 397, 481-484.
- Graham, N. (1989). *Visual Pattern Analyzers* (New York: Oxford University Press).
- Gray, C.M. (1994). Synchronous oscillations in neuronal systems: mechanisms and functions. *J. Comput. Neurosci.* 7, 11-38.
- Gray, C.M. (1999). The temporal correlation hypothesis of visual feature integration: still alive and well. *Neuron* 24, this issue, 31-47.
- Gray, C.M., and McCormick, D.A. (1996). Chattering cells: superficial pyramidal neurons contributing to the generation of synchronous oscillations in the visual cortex. *Science* 274, 109-113.
- Gray, C.M., and Singer, W. (1989). Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex. *Proc. Natl. Acad. Sci. USA* 86, 1698-1702.
- Gray, C.M., and Viana Di Prisco, G. (1997). Stimulus-dependent neuronal oscillations and local synchronization in striate cortex of the alert cat. *J. Neurosci.* 17, 3239-3253.
- Gray, C.M., Koenig, P., Engel, A.K., and Singer, W. (1989). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature* 338, 334-337.
- Gray, C.M., Engel, A.K., Koenig, P., and Singer, W. (1990). Stimulus-dependent neuronal oscillations in cat visual cortex: receptive field properties and feature dependence. *Eur. J. Neurosci.* 2, 607-619.
- Gray, C.M., Engel, A.K., Koenig, P., and Singer, W. (1992). Synchronization of oscillatory neuronal responses in cat striate cortex: temporal properties. *Vis. Neurosci.* 8, 337-347.
- Green, M. (1992). Visual search: detection, identification and localization. *Perception* 21, 765-777.
- Gregory, R.L. (1970). *The Intelligent Eye* (London: Weidenfield and Nicholson).
- Gross, C.G., Cowey, A., and Manning, F.J. (1971). Further analysis of visual discrimination deficits following foveal prestriate and inferotemporal lesions in rhesus monkeys. *J. Comp. Physiol. Psychol.* 76, 1-7.
- Gross, C.G., Rocha-Miranda, C.E., and Bender, D.B. (1972). Visual properties of neurons in inferotemporal cortex of the macaque. *J. Neurophysiol.* 35, 96-111.
- Grossberg, S. (1995). The attentive brain. *Am. Scientist* 83, 438-449.
- Grossberg, S. (1999a). The link between brain learning, attention, and consciousness. *Conscious. Cogn.*, in press.
- Grossberg, S. (1999b). How does the cerebral cortex work? *Spat. Vis.*, in press.
- Grossberg, S., and Somers, D. (1991). Synchronized oscillations during cooperative feature linking in a cortical model of visual perception. *Neural Networks* 4, 453-466.
- Haenny, P.D., Maunsell, J.H.R., and Schiller, P.H. (1988). State dependent activity in monkey visual cortex. II. Retinal and extraretinal factors in V4. *Exp. Brain Res.* 69, 245-259.
- Hata, Y., Tsumoto, T., Sato, H., and Tamura, H. (1991). Horizontal interactions between visual cortical neurones studied by cross-correlation analysis in the cat. *J. Physiol.* 441, 593-614.
- Hatsopoulos, N.G., Ojakangas, C.L., Paninski, L., and Donoghue, J.P. (1998). Information about movement direction obtained from synchronous activity of motor cortical neurons. *Proc. Natl. Acad. Sci. USA* 95, 15706-15711.
- Hayek, F.A. (1952). *The Sensory Order* (Chicago: University of Chicago Press).
- Hebb, D.O. (1949). *The Organization of Behavior* (New York: Wiley).
- Heeger, D. (1992). Normalization of cell responses in cat striate cortex. *Vis. Neurosci.* 9, 181-197.
- Hellwig, B., Schuz, A., and Aertsen, A. (1994). Synapses on axon collaterals of pyramidal cells are spaced at random intervals: a Golgi study in the mouse cerebral cortex. *Biol. Cybern.* 71, 1-12.
- Herculano-Houzel, S., Munk, M.H., Neuenschwander, S., and Singer, W. (1999). Precisely synchronized oscillatory firing patterns require electroencephalographic activation. *J. Neurosci.* 19, 3992-4010.
- Hess, R., Campbell, F., and Greenhalgh, T. (1978). On the nature of the neural abnormality in human amblyopia: neural aberrations and neural sensitivity loss. *Pflügers Arch.* 377, 201-207.
- Hinton, G.E.A. (1981). A parallel computation that assigns canonical object-based frames of reference. In *Proceedings of the Seventh International Joint Conference on Artificial Intelligence, Volume 2* (Vancouver).
- Hoffman, J.E. (1979). A two-stage model of visual search. *Percept. Psychophys.* 25, 319-327.
- Hoffman, D.A., Magee, J.C., Colbert, C.M., and Johnston, D. (1997). K<sup>+</sup> channel regulation of signal propagation in dendrites of hippocampal pyramidal neurons. *Nature* 387, 869-875.
- Hommel, B. (1998). Event files: evidence for automatic integration of stimulus-response episodes. *Vis. Cogn.* 5, 183-216.
- Hopfield, J.J., and Hertz, A.V.M. (1995). Rapid local synchronization of action potentials: toward computation with coupled integrate-and-fire neurons. *Proc. Natl. Acad. Sci. USA* 92, 6655-6662.
- Hoppensteadt, F.C., and Izhikevich, E.M. (1998). Thalamo-cortical interactions modeled by weakly connected oscillators: could the brain use FM radio principles? *Biosystems* 48, 85-94.
- Horwitz, G.D., and Newsome, W.T. (1999). Separate signals for target selection and movement specification in the superior colliculus. *Science* 284, 1158-1161.

- Houck, M.R., and Hoffman, J.E. (1986). Conjunction of color and form without attention. Evidence from an orientation-contingent color aftereffect. *J. Exp. Psychol. Hum. Percept. Perform.* *12*, 186–199.
- Howard, I.P., and Rogers, B.J. (1995). *Binocular Vision and Stereopsis* (Oxford: Oxford University Press).
- Hubel, D., and Wiesel, T. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* *160*, 106–154.
- Hubel, D., and Wiesel, T. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *J. Neurophysiol.* *28*, 229–289.
- Hubel, D.H., and Wiesel, T.N. (1968). Receptive fields and functional architecture of monkey striate cortex. *J. Physiol. (Lond.)* *195*, 215–243.
- Hubel, D.H., and Wiesel, T.N. (1974). Sequence regularity and geometry or orientation columns in the monkey striate cortex. *J. Comp. Neurol.* *158*, 267–294.
- Huerta, P.T., and Lisman, J.E. (1996). Low-frequency stimulation at the throughs of Q-oscillation induces long-term depression of previously potentiated CA1 synapses. *J. Neurophysiol.* *75*, 877–884.
- Hummel, J.E., and Biederman, I. (1992). Dynamic binding in a neural network for shape recognition. *Psychol. Rev.* *99*, 480–517.
- Hummel, J.E., and Stankiewicz, B.J. (1996). An architecture for rapid, hierarchical structural description. In *Attention and Performance*, Volume XVI, T. Inui and J. McClelland, eds. (Cambridge, MA: MIT Press).
- Intraub, H. (1981). Identification and naming of briefly glimpsed visual scenes. In *Eye Movement: Cognition and Visual Perception*, D.F. Fisher, R.A. Monty, and J.W. Senders, eds. (Hillsdale, NJ: Lawrence Erlbaum Associates).
- Intraub, H. (1985). Visual dissociation: an illusory conjunction of pictures and forms. *J. Exp. Psychol. Hum. Percept. Perform.* *11*, 431–442.
- Ito, M., and Gilbert, C.D. (1999). Attention modulates contextual influences in the primary visual cortex of alert monkeys. *Neuron* *22*, 593–604.
- Ivry, R.B., and Prinzmetal, W. (1991). Effect of feature similarity on illusory conjunctions. *Percept. Psychophys.* *49*, 105–116.
- Jensen, O., and Lisman, J.E. (1998). An oscillatory short-term memory buffer model can account for data on the Sternberg task. *J. Neurosci.* *18*, 10688–10699.
- Johnston, D., Magee, J.C., Colbert, C.M., and Christie, B.R. (1996). Active properties of neuronal dendrites. *Annu. Rev. Neurosci.* *19*, 165–186.
- Jones, J., and Palmer, L. (1987). An evaluation of the two-dimensional Gabor filter model of simple receptive fields in cat striate cortex. *J. Neurophysiol.* *58*, 1233–1258.
- Jonides, J., and Gleitman, H. (1972). A conceptual category effect in visual search: O as letter or digit. *Percept. Psychophys.* *12*, 457–460.
- Julesz, B. (1975). Experiments in the visual perception of texture. *Sci. Am.* *232*, 34–43.
- Kahneman, D. (1973). *Attention and Effort* (Englewood Cliffs, NJ: Prentice-Hall).
- Kahneman, D., and Henik, A. (1981). Perceptual organization and attention. In *Perceptual Organization*, M. Kubovy and J. Pomerantz, eds. (Hillsdale, NJ: Lawrence Erlbaum Associates).
- Kahneman, D., Treisman, A., and Gibbs, B. (1992). The reviewing of object files: object-specific integration of information. *Cogn. Psychol.* *24*, 175–219.
- Kammen, D.M., Holmes, P.J., and Koch, C. (1989). Origin of oscillations in visual cortex: feedback versus local coupling. In *Models of Brain Functions*, R.M.J. Cotterill, ed. (Cambridge: Cambridge University Press).
- Kanisza, G. (1979). *The Organization of Vision* (New York: Praeger).
- Kapadia, M.K., Ito, M., Gilbert, C.D., and Westheimer, G. (1995). Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys. *Neuron* *15*, 843–856.
- Kastner, S., De Weerd, P., Desimone, R., and Ungerleider, L.G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science* *282*, 108–111.
- Kastner, S., Pinsk, M.A., De Weerd, P., Desimone, R., and Ungerleider, L.G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* *22*, 751–761.
- Kefalea, E. (1998). Object localization and recognition for a grasping robot. In *Proceedings of the 24th Annual Conference of the IEEE Industrial Electronics Society* (Aachen, Germany).
- Keil, K., Müller, M.M., Ray, W.J., Gruber, T., and Elbert, T. (1999). Human gamma band activity and perception of a Gestalt. *J. Neurosci.* *19*, 7152–7161.
- Kersten, D. (1999). High-level vision as statistical inference. In *The Cognitive Neurosciences*, M.S. Gazzaniga, ed. (Cambridge, MA: MIT Press).
- Kilgard, M.P., and Merzenich, M.M. (1998). Plasticity of temporal information processing in the primary auditory cortex. *Nat. Neurosci.* *1*, 727–731.
- Kim, J.-N., and Shadlen, M.N. (1999). Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque. *Nat. Neurosci.* *2*, 176–185.
- Kiorpes, L., and McKee, S.P. (1999). Amblyopia and its neural basis. *Curr. Opin. Neurobiol.*, in press.
- Kiorpes, L., and Movshon, J.A. (1996). Amblyopia: a developmental disorder of the central visual pathways. *Cold Spring Harbor Symp. Quant. Biol.* *61*, 39–48.
- Kiorpes, L., Kiper, D., O'Keefe, L., Cavanaugh, J., and Movshon, J. (1998). Neuronal correlates of amblyopia in the visual cortex of macaque monkeys with experimental strabismus and anisometropia. *J. Neurosci.* *18*, 6411–6424.
- Kiper, D.C., Gegenfurtner, K.R., and Movshon, J.A. (1996). Cortical oscillatory responses do not affect visual segmentation. *Vision Res.* *36*, 539–544.
- Kisvarday, Z.F., Toth, E., Rausch, M., and Eysel, U.T. (1997). Orientation-specific relationship between populations of excitatory and inhibitory lateral connections in the visual cortex of the cat. *Cereb. Cortex* *7*, 605–618.
- Kobatake, E., and Tanaka, K. (1994). Neuronal selectivities to complex object features in the ventral visual pathway of the macaque cerebral cortex. *J. Neurophys.* *71*, 856–857.
- Kobatake, E., Wang, G., and Tanaka, K. (1998). Effects of shape-discrimination training on the selectivity of inferotemporal cells in adult monkeys. *J. Neurophysiol.* *80*, 324–330.
- Koch, C. (1999). *Biophysics of Computation* (New York: Oxford University Press).
- Koch, C., and Poggio, T. (1999). Predicting the visual world: silence is golden. *Nat. Neurosci.* *2*, 9–10.
- Koch, C., and Ullman, S. (1985). Shifts in selective visual attention: towards the underlying neural circuitry. *Hum. Neurobiol.* *4*, 219–227.
- Koch, C., Rapp, M., and Segev, I. (1996). A brief history of time (constants). *Cereb. Cortex* *6*, 93–101.
- Koffka, K. (1935). *Principles of Gestalt Psychology* (New York: Harcourt, Brace and World).
- Koffka, K. (1969). *The Task of Gestalt Psychology* (Princeton: Princeton University Press).
- Köhler, W. (1930). *Gestalt Psychology* (London: Bell and Sons).
- Köhler, W., and Held, R. (1949). The cortical correlate of pattern vision. *Science* *110*, 414–419.
- Konen, W., and von der Malsburg, C. (1993). Learning to generalize from single examples in the dynamic link architecture. *Neural Comput.* *5*, 719–735.
- Konen, W., Maurer, T., and von der Malsburg, C. (1994). A fast dynamic link matching algorithm for invariant pattern recognition. *Neural Networks* *7*, 1019–1030.
- König, P., and Schillen, T.B. (1991). Stimulus-dependent assembly formation of oscillatory responses: I. Synchronization. *Neural Comput.* *3*, 155–166.
- König, P., Engel, A.K., and Singer, W. (1996). Integrator or coincidence detector? The role of the cortical neuron revisited. *Trends Neurosci.* *19*, 130–137.

- König, P., Engel, A.K., and Singer, W. (1995). Relation between oscillatory activity and long-range synchronization in cat visual cortex. *Proc. Natl. Acad. Sci. USA* *92*, 290–294.
- König, P., Engel, A.K., Löwel, S., and Singer, W. (1993). Squint affects synchronization of oscillatory responses in cat visual cortex. *Eur. J. Neurosci.* *5*, 501–508.
- Kovacs, I., and Julesz, B. (1993). A closed curve is much more than an incomplete one: effect of closure in figure-ground segmentation. *Proc. Natl. Acad. Sci. USA* *90*, 7495–7497.
- Kreiter, A.K., and Singer, W. (1992). Oscillatory neuronal responses in the visual cortex of the awake macaque monkey. *Eur. J. Neurosci.* *4*, 369–375.
- Kreiter, A.K., and Singer, W. (1996). Stimulus-dependent synchronization of neuronal responses in the visual cortex of the awake macaque monkey. *J. Neurosci.* *16*, 2381–2396.
- Krüger, L.E. (1984). The category effect in visual search depends on physical rather than conceptual differences. *Percept. Psychophys.* *35*, 558–564.
- Krüger, J., and Aiple, F. (1988). Multimicroelectrode investigation of monkey striate cortex: spike train correlations in the infragranular layers. *J. Neurophysiol.* *60*, 798–828.
- Kwak, H., Dagenbach, D., and Egeth, H. (1991). Further evidence for a time-independent shift of the focus of attention. *Percept. Psychophys.* *49*, 473–480.
- Lades, M., Vorbrüggen, J.C., Buhmann, J., Lange, J., von der Malsburg, C., Würtz, R., and Konen, W. (1993). Distortion invariant object recognition in the dynamic link architecture. *IEEE Trans. Comput.* *42*, 300–311.
- Lamme, V.A. (1995). The neurophysiology of figure-ground segregation in primary visual cortex. *J. Neurosci.* *15*, 1605–1615.
- Lamme, V.A.F., and Spekreijse, H. (1999). Neuronal synchrony does not represent texture segregation. *Nature* *396*, 362–366.
- Lampl, I., Reichova, I., and Ferster, D. (1999). Synchronous membrane potential fluctuations in neurons of the cat visual cortex. *Neuron* *22*, 361–374.
- Larkum, M.E., Zhu, J.J., and Sakmann, B. (1999). A new cellular mechanism for coupling inputs arriving at different cortical layers. *Nature* *398*, 338–341.
- Lashley, K.S., Chow, K.L., and Semmes, J. (1951). An examination of the electrical field theory of cerebral integration. *Psychol. Rev.* *58*, 128–136.
- Laufer, M., and Verzeano, M. (1967). Periodic activity in the visual system of the cat. *Vision Res.* *7*, 215–229.
- Laurent, G. (1996). Dynamical representation of odors by oscillating and evolving neural assemblies. *Trends Neurosci.* *19*, 489–496.
- Laurent, G., Wehr, M., and Davidowitz, H. (1996). Temporal representations of odors in an olfactory network. *J. Neurosci.* *16*, 3837–3847.
- Lavie, N., and Driver, J. (1996). On the spatial extent of attention in object-based visual selection. *Percept. Psychophys.* *58*, 1238–1251.
- Lee, S.-H., and Blake, R. (1999). Visual form created solely from temporal structure. *Science* *284*, 1165–1168.
- Lee, C., Rohrer, W.H., and Sparks, D.L. (1988). Population coding of saccadic eye movements by neurons in the superior colliculus. *Nature* *332*, 357–360.
- Lee, D., Itti, L., Koch, C., and Braun, J. (1999). Attention activates winner-take-all competition among visual filters. *Nat. Neurosci.* *2*, 375–381.
- Legendy, C. (1970). The brain and its information trapping device. In *Progress in Cybernetics*, Volume 1, J. Rose, ed. (New York: Gordon and Breach).
- Lennie, P. (1981). The physiological basis of variations in visual latency. *Vision Res.* *21*, 815–824.
- Lennie, P., Krauskopf, J., and Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *J. Neurosci.* *10*, 649–669.
- Leon, M.I., and Shadlen, M.N. (1998). Exploring the neurophysiology of decisions. *Neuron* *21*, 669–672.
- Leonards, U., Singer, W., and Fahle, M. (1996). The influence of temporal phase differences on texture segmentation. *Vision Res.* *36*, 2689–2697.
- Leonards, U., and Singer, W. (1998). Two segmentation mechanisms with differential sensitivity for colour and luminance contrast. *Vision Res.* *38*, 101–109.
- Leonards, U., Singer, W., and Fahle, M. (1996). The influence of temporal phase differences on texture segmentation. *Vision Res.* *36*, 2689–2697.
- Leopold, D.A., and Logothetis, N.K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature* *379*, 549–553.
- Leventhal, A.G., Thompson, K.G., Liu, D., Zhou, Y., and Ault, S.J. (1995). Concomitant sensitivity to orientation, direction, and color of cells in Layers 2, 3, and 4 of monkey striate cortex. *J. Neurosci.* *15*, 1808–1818.
- Levi, D., and Sharma, V. (1998). Integration of local orientation in strabismic amblyopia. *Vision Res.* *38*, 775–781.
- Levick, W.R., and Zacks, J.L. (1970). Responses of cat retinal ganglion cells to brief flashes of light. *J. Physiol. (Lond.)* *206*, 677–700.
- Levitt, J.B., and Lund, J.S. (1997). Contrast dependence of contextual effects in primate visual cortex. *Nature* *387*, 73–76.
- Levitt, J.B., Kiper, D.C., and Movshon, J.A. (1994). Receptive field and functional architecture of macaque V2. *J. Neurophysiol.* *71*, 2517–2542.
- Levitt, J.B., Lund, J.S., and Yoshioka, T. (1996). Anatomical substrates for early stages in cortical processing of visual information in the macaque monkey. *Behav. Brain Res.* *76*, 5–19.
- Li, C.-Y., and Li, W. (1994). Extensive integration field beyond the classical receptive field of cat striate cortical neurons-classification and tuning properties. *Vision Res.* *34*, 2337–2355.
- Li, Z. (1999a). Visual segmentation by contextual influences via intracortical interactions in the primary visual cortex. *Network Comput. Neural Syst.* *10*, 187–212.
- Li, Z. (1999b). A neural model of contour integration in the primary visual cortex. *Neural Comput.*, in press.
- Lisberger, S.G., and Movshon, J.A. (1999). Visual motion analysis for pursuit eye movements in area MT of macaque monkeys. *J. Neurosci.* *19*, 2224–2246.
- Lisman, J.E. (1997). Bursts as a unit of neural information: making unreliable synapses reliable. *Trends Neurosci.* *20*, 38–43.
- Lisman, J.E., and Idiart, M.A. (1995). Storage of  $7 \pm 2$  short-term memories in oscillatory subcycles. *Science* *267*, 1512–1515.
- Livingstone, M.S. (1996). Oscillatory firing and interneuronal correlations in squirrel monkey striate cortex. *J. Neurophysiol.* *75*, 2467–2485.
- Livingstone, M.S., and Hubel, D.H. (1983). Specificity of cortico-cortical connections in monkey visual system. *Nature* *304*, 531–534.
- Livingstone, M.S., and Hubel, D.H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *J. Neurosci.* *4*, 309–356.
- Livingstone, M.S., and Hubel, D.H. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science* *240*, 740–749.
- Llinas, R.R. (1988). The intrinsic electrophysiological properties of mammalian neurons: insights into central nervous system function. *Science* *242*, 1654–1664.
- Llinas, R., and Ribary, U. (1993). Coherent 40 Hz oscillation characterizes dream state in humans. *Proc. Natl. Acad. Sci. USA* *90*, 2078–2081.
- Llinas, R.R., Grace, A.A., and Yarom, Y. (1991). In vitro neurons in mammalian cortical layer 4 exhibit intrinsic oscillatory activity in the 10- to 50-Hz frequency range. *Proc. Natl. Acad. Sci. USA* *88*, 897–901.
- Löwel, S., and Singer, W. (1992). Selection of intrinsic horizontal connections in the visual cortex by correlated neuronal activity. *Science* *255*, 209–212.
- Logothetis, N.K. (1998). Single units and conscious vision. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* *353*, 1801–1818.
- Logothetis, N.K., and Pauls, J. (1995). Psychophysical and physiological evidence for viewer-centered object representations in the primate. *Cereb. Cortex* *5*, 270–288.

- Logothetis, N.K., and Schall, J.D. (1989a). Neuronal activity related to motion perception in the middle temporal (MT) visual area of the macaque. In *Neural Mechanisms of Visual Perception: Proceedings of the Retina Research Foundation*, D.M.-K. Lam and C.D. Gilbert, eds. (The Woodlands, TX: Portfolio Publishing Company).
- Logothetis, N.K., and Schall, J.D. (1989b). Neuronal correlates of subjective visual perception. *Science* **245**, 761–763.
- Logothetis, N.K., Pauls, J., and Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. *Curr. Biol.* **5**, 552–563.
- Luck, S.J., and Vogel, E.K. (1997). The capacity of visual working memory for features and conjunctions. *Nature* **390**, 279–281.
- Luck, S.J., Chelazzi, L., Hillyard, S.A., and Desimone, R. (1997a). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *J. Neurophysiol.* **77**, 24–42.
- Luck, S.J., Girelli, M., McDermott, M.T., and Ford, M.A. (1997b). Bridging the gap between monkey neurophysiology and human perception: an ambiguity resolution theory of visual selective attention. *Cogn. Psychol.* **33**, 64–87.
- Lumer, E.D., Edelman, G.M., and Tononi, G. (1997a). Neural dynamic in a model of the thalamocortical system. I. Layers, loops and the emergence of fast synchronous rhythms. *Cereb. Cortex* **7**, 207–227.
- Lumer, E.D., Edelman, G.M., and Tononi, G. (1997b). Neural dynamics in a model of the thalamocortical system. II. The role of neural synchrony tested through perturbations of spike timing. *Cereb. Cortex* **7**, 228–236.
- Luthi, A., and McCormick, D.A. (1998). H-current: properties of a neuronal and network pacemaker. *Neuron* **21**, 9–12.
- Lytton, W.W., and Sejnowski, T.J. (1991). Simulations of cortical pyramidal neurons synchronized by inhibitory interneurons. *J. Neurophysiol.* **66**, 1059–1079.
- MacLeod, K., and Laurent, G. (1996). Distinct mechanisms for synchronization and temporal patterning of odor-encoding neural assemblies. *Science* **274**, 976–979.
- MacLeod, K., Backer, A., and Laurent, G. (1998). Who reads temporal information contained across synchronized and oscillatory spike trains? *Nature* **395**, 693–698.
- Madler, C., and Poppel, E. (1987). Auditory evoked potentials indicate the loss of neuronal oscillations during general anesthesia. *Naturwissenschaften* **74**, 42–43.
- Magee, J.C., and Johnston, D.A. (1997). A synaptically controlled, associative signal for Hebbian plasticity in hippocampal neurons. *Science* **275**, 209–213.
- Mainen, Z.F., and Sejnowski, T.J. (1995). Reliability of spike timing in neocortical neurons. *Science* **268**, 1503–1506.
- Malach, R., Amir, Y., Harel, M., and Grinvald, A. (1993). Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate striate cortex. *Proc. Natl. Acad. Sci. USA* **90**, 10469–10473.
- Maldonado, P.E., Friedman-Hill, S.R., and Gray, C.M. (1999). Temporal dynamics of neuronal activity in the striate cortex of alert macaque: II. Short and long-range temporally-correlated activity. *J. Neurosci.*, in press.
- Marcelja, S. (1980). Mathematical description of the responses of simple cortical cells. *J. Optic. Soc. Am.* **70**, 1297–1300.
- Margulis, M., and Tang, C.-M. (1998). Temporal integration can readily switch between sublinear and supralinear summation. *J. Neurophysiol.* **79**, 2809–2813.
- Markram, H., Lübke, J., Frotscher, M., and Sakmann, B. (1997). Regulation of synaptic efficacy by coincidence of postsynaptic APs and EPSPs. *Science* **275**, 213–215.
- Marr, D. (1982). *Vision* (San Francisco: Freeman).
- Marsalek, P., Koch, C., and Maunsell, J.H.R. (1997). On the relationship between synaptic input and spike output jitter in individual neurons. *Proc. Natl. Acad. Sci. USA* **94**, 735–740.
- Mason, A., Nicoll, A., and Stratford, K. (1991). Synaptic transmission between individual pyramidal neurons of the rat visual cortex in vitro. *J. Neurosci.* **11**, 72–84.
- Massad, A., Mertsching, B., and Schmalz, S. (1998). Combining multiple views and temporal associations for 3-D object recognition. In *Proceedings of the ECCV 1998, Volume 2 Stockholm*.
- Matsumura, M., Chen, D.-F., Sawaguchi, T., Kubota, K., and Fetz, E.E. (1996). Synaptic interactions between primate precentral cortex neurons revealed by spike-triggered averaging of intracellular membrane potentials in vivo. *J. Neurosci.* **16**, 7757–7767.
- Maunsell, J.H.R., and Gibson, J.R. (1992). Visual response latencies in striate cortex of the macaque monkey. *J. Neurophysiol.* **68**, 1332–1344.
- Maunsell, J.H.R., and Newsome, W.T. (1987). Visual processing in monkey extrastriate cortex. *Annu. Rev. Neurosci.* **10**, 363–401.
- Maunsell, J.H., Sclar, G., Nealey, T.A., and DePriest, D.D. (1991). Extraretinal representations in area V4 in the macaque monkey. *Vis. Neurosci.* **7**, 561–573.
- Maunsell, J.H.R., Ghose, G.M., Assad, J.A., McAdams, C.J., Boudreau, C.E., and Noerager, B.D. (1999). Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. *Vis. Neurosci.* **16**, 1–14.
- McAdams, C.J., and Maunsell, J.H.R. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *J. Neurosci.* **19**, 431–441.
- McClelland, J.L., and Mozer, M.C. (1986). Perceptual interactions in two-word displays: familiarity and similarity effects. *J. Exp. Psychol. Hum. Percept. Perform.* **12**, 18–35.
- McCullough, C. (1965). Color adaptation of edge-detectors in the human visual system. *Science* **149**, 1115–1116.
- McCulloch, W., and Pitts, W. (1943). A logical calculus of the ideas immanent in nervous activity. *Bull. Math. Biophys.* **5**, 115–133.
- McCormick, D.A., Connors, B.W., Lighthall, J.W., and Prince, D.A. (1985). Comparative electrophysiology of pyramidal and sparsely spiny stellate neurons of the neocortex. *J. Neurophysiol.* **54**, 782–806.
- McLeod, P., Driver, J., and Crisp, J. (1988). Visual search for conjunctions of movement and form is parallel. *Nature* **332**, 154–155.
- McLeod, P., Driver, J., Dienes, Z., and Crisp, J. (1991). Filtering by movement in visual search. *J. Exp. Psychol. Hum. Percept. Perform.* **17**, 55–64.
- Mel, B., and Fiser, J. (1999). Minimizing binding errors using learned conjunctive features. *Neural Comput.*, in press.
- Melssen, W.J., and Epping, W.J.M. (1987). Detection and estimation of neural connectivity based on cross correlation analysis. *Biol. Cybern.* **57**, 403–414.
- Merigan, W.H., and Maunsell, J.H. (1993). How parallel are the primate visual pathways? *Annu. Rev. Neurosci.* **16**, 369–402.
- Michalski, A., Gerstein, G.L., Czarkowska, J., and Tarnecki, R. (1983). Interactions between cat striate cortex neurons. *Exp. Brain Res.* **51**, 97–107.
- Mikami, A., Newsome, W.T., and Wurtz, R.H. (1986). Motion selectivity in macaque visual cortex. I. Mechanisms of direction and speed selectivity in extrastriate area MT. *J. Neurophysiol.* **55**, 1308–1327.
- Miles, R., and Wong, R.K.S. (1986). *J. Physiol.* **380**, 373–397.
- Miller, E.C., Gochin, P.M., and Gross, C.G. (1993). Suppression of visual responses of neurons in inferior temporal cortex of the awake macaque monkey by addition of a second stimulus. *Brain Res.* **616**, 25–29.
- Milner, P. (1974). A model for visual shape recognition. *Psychol. Rev.* **81**, 521–535.
- Milner, A.D., and Goodale, M.A. (1993). Visual pathways to perception and action. *Prog. Brain Res.* **95**, 317–337.
- Miltner, W.H.R., Braun, C., Arnold, M., Witte, H., and Taub, E. (1999). Coherence of gamma-band EEG activity as a basis for associative learning. *Nature* **397**, 434–436.
- Minsky, M. (1961). Steps toward artificial intelligence. *Proc. Inst. Radio Engr.* **49**, 8–30.
- Missal, M., Vogels, R., and Orban, G. (1997). Responses of macaque inferior temporal neurons to overlapping shapes. *Cereb. Cortex* **7**, 758–767.
- Moore, G.P., Segundo, J.P., Perkel, D.H., and Levitan, H. (1970). Statistical signs of synaptic interactions in neurones. *Biophys. J.* **10**, 876–900.
- Moran, J., and Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science* **229**, 782–784.

- Motter, B.C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *J. Neurophysiol.* *70*, 909–919.
- Motter, B.C., and Mountcastle, V.B. (1981). The functional properties of the light-sensitive neurons of the posterior parietal cortex studied in waking monkeys: foveal sparing and opponent vector organization. *J. Neurosci.* *1*, 3–26.
- Mountcastle, V.B. (1978). An organizing principle for cerebral function: the unit module and the distributed system. In *The Mindful Brain*, G.M. Edelman and V.B. Mountcastle, eds. (Cambridge, MA: MIT Press).
- Movshon, J.A., Adelson, E.H., Gizzi, M.S., and Newsome, W.T. (1985). The analysis of moving visual patterns. *Exp. Brain Res.* *71*, 117–151.
- Movshon, J., Eggers, H., Gizzi, M., Hendrickson, A., Kiorpes, L., and Boothe, R. (1987). Effects of early unilateral blur on the macaque's visual system. III. Physiological observations. *J. Neurosci.* *7*, 1340–1351.
- Mozer, M.C. (1983). Letter migration in word perception. *J. Exp. Psychol. Hum. Percept. Perform.* *9*, 531–546.
- Mozer, M. (1991). *The Perception of Multiple Objects: A Connectionist Approach* (Cambridge, MA: MIT Press).
- Munk, M.H.J., Roelfsema, P.R., König, P., Engel, A.K., and Singer, W. (1996). Role of reticular activation in the modulation of intracortical synchronization. *Science* *272*, 271–274.
- Murata, A., Gallese, V., Kaseda, M., and Sakata, H. (1996). Parietal neurons related to memory-guided hand manipulation. *J. Neurophysiol.* *75*, 2180–2186.
- Murthy, V.N., and Fetz, E.E. (1996a). Oscillatory activity in sensorimotor cortex of awake monkeys: synchronization of local field potentials and relation to behavior. *J. Neurophysiol.* *76*, 3949–3967.
- Murthy, V.N., and Fetz, E.E. (1996b). Synchronization of neurons during local field potential oscillations in sensorimotor cortex of awake monkeys. *J. Neurophysiol.* *76*, 3968–3982.
- Nakayama, K., and Silverman, G.H. (1986a). Serial and parallel processing of visual feature conjunctions. *Nature* *320*, 264–265.
- Navon, D. (1975). Forest before trees: the precedence of global features in visual perception. *Cogn. Psychol.* *9*, 353–383.
- Neisser, U. (1963). Decision-time without reaction-time: experiments in visual scanning. *Am. J. Psychol.* *76*, 376–385.
- Neisser, U. (1967). *Cognitive Psychology* (New York: Appleton-Century-Crofts).
- Neisser, U., and Becklen, R. (1975). Selective looking: attending to visually specified events. *Cogn. Psychol.* *7*, 480–494.
- Nelson, J.I., Salin, P.A., Munk, M.H.J., Arzi, M., and Bullier, J. (1992). Spatial and temporal coherence in cortico-cortical connections: a cross-correlation study in areas 17 and 18 in the cat. *Vis. Neurosci.* *9*, 21–38.
- Neuenschwander, S., and Singer, W. (1996). Long-range synchronization of oscillatory light responses in the cat retina and lateral geniculate nucleus. *Nature* *379*, 728–733.
- Neuenschwander, S., Castelo-Branco, M., and Singer, W. (1999). Synchronous oscillations in the cat retina. *Vision Res.* *39*, 2485–2497.
- Neven, H., and Aertsen, A. (1992). Rate coherence and event coherence in the visual cortex: a neuronal model of object recognition. *Biol. Cybern.* *67*, 309–322.
- Newsome, W.T., Britten, K.H., and Movshon, J.A. (1989). Neuronal correlates of a perceptual decision. *Nature* *341*, 52–54.
- Nicolelis, M.A.L., and Chapin, J.K. (1994). Spatiotemporal structure of somatosensory responses of many-neuron ensembles in the rat ventral posterior medial nucleus of the thalamus. *J. Neurosci.* *14*, 3511–3532.
- Nicolelis, M.A., Ghazanfar, A.A., Stambaugh, C.R., Oliveira, L.M., Laubach, M., Chapin, J.K., Nelson, R.J., and Kaas, J.H. (1998). Simultaneous encoding of tactile information by three primate cortical areas. *Nat. Neurosci.* *1*, 621–630.
- Nicoll, A., and Blakemore, C. (1993). Single-fiber EPSPs in layer 5 of rat visual cortex in-vitro. *Neuroreport* *4*, 167–170.
- Niebur, E., Kammen, D.M., and Koch, C. (1990). Phase-locking in 1-D and 2-D networks of oscillating neurons. In *Nonlinear Dynamics and Neuronal Networks*, H.G. Schuster, ed. (Weinheim: VCH Publishers).
- Niebur, E., Koch, C., and Rosin, C. (1993). An oscillation-based model for the neuronal basis of attention. *Vision Res.* *33*, 2789–2802.
- Nobre, A.C., Sebestyen, G.N., Gitelman, D.R., Mesulam, M.M., Frackowiak, R.S., and Frith, C.D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain* *120*, 515–533.
- Nothdurft, H.C. (1992). Feature analysis and the role of similarity in pre-attentive vision. *Percept. Psychophys.* *52*, 355–375.
- Nothdurft, H.C. (1993). Faces and facial expression do not pop-out. *Perception* *22*, 1287–1298.
- Nowak, L.G., Munk, M.H., Girard, P., and Bullier, J. (1995a). Visual latencies in areas V1 and V2 of the macaque monkey. *Vis. Neurosci.* *12*, 371–384.
- Nowak, L.G., Munk, M.H., Nelson, J.I., James, A.C., and Bullier, J. (1995b). Structural basis of cortical synchronization. I. Three types of interhemispheric coupling. *J. Neurophysiol.* *74*, 2379–2400.
- Nowak, L.G., Munk, M.H., James, A.C., Girard, P., and Bullier, J. (1999). Cross-correlation study of the temporal interactions between areas V1 and V2 of the macaque monkey. *J. Neurophysiol.* *81*, 1057–1074.
- Nowlan, S., and Sejnowski, T. (1995). A selection model for motion processing in area MT of primates. *J. Neurosci.* *15*, 1195–1214.
- Okada, K., Steffens J., Maurer, T., Hong, H., Elagin, E., Neven, H., and von der Malsburg, C. (1998). The Bochum/USC face recognition system and how it fared in the FERET phase III test. In *Face Recognition: From Theory to Applications*, H. Wechsler, P.J. Phillips, V. Bruce, F. Fogelman-Souli, and T.S. Huang, eds. (New York: Springer-Verlag).
- O'Keefe, L.P., and Movshon, J.A. (1998). Processing of first- and second-order motion signals by neurons in area MT of the macaque monkey. *Vis. Neurosci.* *15*, 305–317.
- Oliva, A., and Schyns, P.G. (1997). Coarse blobs or fine edges? Evidence that information diagnosticity changes the perception of complex visual stimuli. *Cogn. Psychol.* *34*, 72–107.
- Olshausen, B.A., Anderson, C.H., and Van Essen, D.C. (1993). A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information. *J. Neurosci.* *13*, 4700–4719.
- Olshausen, B., Anderson, C., and Van Essen, D. (1995). A multiscale dynamic routing circuit for forming size- and position-invariant object representations. *J. Comput. Neurosci.* *2*, 45–62.
- Orban, G.A., Kennedy, H., and Bullier, J. (1986). Velocity sensitivity and direction selectivity of neurons in areas V1 and V2 of the monkey: influence of eccentricity. *J. Neurophysiol.* *56*, 462–480.
- Pal, N.R., and Pal, S.K. (1993). A review of image segmentation techniques. *Pattern Recog. Lett.* *26*, 1277–1294.
- Palm, G. (1981). Towards a theory of cell assemblies. *Biol. Cybern.* *39*, 181–194.
- Palm, G. (1990). Cell assemblies as a guideline for brain research. *Concepts Neurosci.* *1*, 133–137.
- Palm, G., Aertsen, A., and Gerstein, G.L. (1988). On the significance of correlations among neuronal spike trains. *Biol. Cybern.* *59*, 1–11.
- Parker, A.J., and Newsome, W.T. (1998). Sense and the single neuron: probing the physiology of perception. *Annu. Rev. Neurosci.* *21*, 227–277.
- Perkel, D.H., Gerstein, G.L., and Moore, G.P. (1967). Neuronal spike trains and stochastic point processes. I. The single spike train. *Biophys. J.* *7*, 391–418.
- Perrett, D., and Oram, M. (1993). Neurophysiology of shape processing. *Imag. Vis. Comput.* *11*, 317–333.
- Perrett, D., and Oram, M. (1998). Visual recognition based on temporal cortex cells: viewer-centred processing of pattern configuration. *Z. Naturforsch.* *53c*, 518–541.
- Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1984). Neurones responsive to faces

- in the temporal cortex: studies of functional organization, sensitivity to identity and relation to perception. *Hum. Neurobiol.* 3, 197–208.
- Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., and Jeeves, M.A. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proc. R. Soc. Lond. B Biol. Sci.* 223, 293–317.
- Perrett, D.I., Mistlin, A.J., and Chitty, A.J. (1987). Visual neurones responsive to faces. *Trends Neurosci.* 10, 358–364.
- Perrett, D., Oram, M., Harries, M., Bevan, R., Hietanen, J., Benson, P., and Thomas, S. (1991). Viewer-centred and object-centred coding of heads in the macaque temporal cortex. *Exp. Brain Res.* 86, 159–173.
- Peterhans, E., and von der Heydt, R. (1993). Functional organization of area V2 in the alert macaque. *J. Neurosci.* 5, 509–524.
- Peters, A., and Sethares, C. (1991). Organization of pyramidal neurons in area 17 of monkey visual cortex. *J. Comp. Neurol.* 306, 1–23.
- Peters, A., and Yilmaz, E. (1993). Neuronal organization in area 17 of cat visual cortex. *Cereb. Cortex* 3, 49–68.
- Phillips, W.A., and Singer, W. (1997). In search of common foundations for cortical computation. *Behav. Brain Sci.* 20, 657–722.
- Phillips, W.A., Hancock, P.J.B., Willson, N.J., and Smith, L.S. (1988). On the acquisition of object concepts from sensory data. In *Neural Computers*. R. Eckmiller and C. von der Malsburg, eds. (Heidelberg: Springer).
- Phillips, P.J., Moon, H., Rizvi, S., and Rauss, P. (1998). The FERET valuation. In *Face Recognition: From Theory to Applications*. H. Wechsler, P.J. Phillips, V. Bruce, F. Fogelman-Souli, and T.S. Huang, eds. (New York: Springer-Verlag).
- Platt, M.L., and Glimcher, P.W. (1997). Responses of intraparietal neurons to saccadic targets and visual distractors. *J. Neurophysiol.* 78, 1574–1589.
- Plenz, D., and Kitai, S.T. (1996). Generation of high-frequency oscillations in local circuits of rat somatosensory cortex cultures. *J. Neurophysiol.* 76, 4180–4184.
- Poggio, T., and Edelman, S. (1990). A network that learns to recognize 3D objects. *Nature* 343, 263–266.
- Poggio, G.F., and Fischer, B. (1977). Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. *J. Neurophysiol.* 40, 1392–1405.
- Poggio, T., Reichardt, W., and Hausen, W. (1981). A neuronal circuitry for relative movement discrimination by the visual system of the fly. *Naturwissenschaften* 68, 443–466.
- Polat, U., Sagi, D., and Norcia, A. (1997). Abnormal long-range spatial interactions in amblyopia. *Vision Res.* 37, 737–744.
- Polat, U., Mizobe, K., Pettet, M.W., Kasamatsu, T., and Norcia, A.M. (1998). Collinear stimuli regulate visual responses depending on a cell's contrast threshold. *Nature* 391, 580–584.
- Pomerantz, J. (1981). Perceptual organization in information processing. In *Perceptual Organization*, M. Kubovy and J. Pomerantz, eds. (Hillsdale, NJ: Lawrence Erlbaum Associates).
- Potter, M. (1975). Meaning in visual search. *Science* 187, 565–566.
- Potter, M.C., and Levy, E.I. (1969). Recognition memory for a rapid sequence of pictures. *J. Exp. Psychol.* 81, 10–15.
- Pouget, A., and Sejnowski, T.J. (1997). A new view of hemineglect based on the response properties of parietal neurones. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 352, 1449–1459.
- Prinzmetal, W. (1981). Principles of feature integration in visual perception. *Percept. Psychophys.* 30, 330–340.
- Prinzmetal, W., and Keysar, B. (1989). Functional theory of illusory conjunctions and neon colors. *J. Exp. Psychol. Gen.* 118, 165–190.
- Prinzmetal, W., Presti, D.E., and Posner, M.I. (1986). Does attention affect visual feature integration? *J. Exp. Psychol. Hum. Percept. Perform.* 12, 361–369.
- Prinzmetal, W., Henderson, D., and Ivry, R. (1995). Loosening the constraints on illusory conjunctions: assessing the roles of exposure duration and attention. *J. Exp. Psychol. Hum. Percept. Perform.* 21, 1362–1375.
- Prut, Y., Vaadia, E., Bergman, H., Haalman, I., Slovlin, H., and Abeles, M. (1998). Spatiotemporal structure of cortical activity: properties and behavioral relevance. *J. Neurophysiol.* 7, 2857–2874.
- Pulvermüller, F., Birbaumer, N., Lutzenberger, W., and Mohr, B. (1997). High frequency brain activity: its possible role in attention, perception and language processing. *Prog. Neurobiol.* 52, 427–445.
- Purves, D., and LaMantia, A.-S. (1990). Number of 'blobs' in the primary visual cortex of neonatal and adult monkeys. *Proc. Natl. Acad. Sci. USA* 87, 5764–5767.
- Qian, N., and Andersen, R.A. (1994). Transparent motion perception as detection of unbalanced motion signals. II. Physiology. *J. Neurosci.* 14, 7367–7380.
- Quinlan, P.T., and Humphreys, G.W. (1987). Visual search for targets defined by combinations of color, shape, and size: an examination of the task constraints on feature and conjunction searches. *Percept. Psychophys.* 41, 455–472.
- Rafal, R.D. (1997). Balint syndrome. In *Behavioral neurology and Neuropsychology*, T.E. Feinberg and M.J. Farah, eds. (New York: McGraw-Hill).
- Rager, G., and Singer, W. (1998). The response of cat visual cortex to flicker stimuli of variable frequency. *Eur. J. Neurosci.* 10, 1856–1877.
- Raiguel, S.E., Lagae, L., Gulyas, B., and Orban, G.A. (1989). Response latencies of visual cells in macaque areas V1, V2 and V5. *Brain Res.* 493, 155–159.
- Rainer, G., Asaad, W.F., and Miller, E.K. (1998). Memory fields of neurons in the primate prefrontal cortex. *Proc. Natl. Acad. Sci. USA* 95, 15008–15013.
- Recanzone, G.H., Wurtz, R.H., and Schwarz, U. (1997). Responses of MT and MST neurons to one and two moving objects in the receptive field. *J. Neurophysiol.* 78, 2904–2915.
- Reitboeck, H.J., Eckhorn, R., and Pabst, M. (1987). A model of figure/ground separation based on correlated neural activity in the visual system. In *Synergetics of the Brain*, H. Haken, ed. (New York: Springer).
- Rensink, R.A., and Enns, J.T. (1995). Preemption effects in visual search: evidence for low-level grouping. *Psychol. Rev.* 102, 101–130.
- Reyes, A.D., and Fetz, E.E. (1993). Two modes of interspike interval shortening by brief transient depolarizations in cat neocortical neurons. *J. Neurophysiol.* 69, 1661–1672.
- Reyes, A., Rubel, E., and Spain, W. (1994). Membrane properties underlying the firing of neurons in the avian cochlear nucleus. *J. Neurosci.* 14, 5352–5364.
- Reyes, A., Rubel, E., and Spain, W. (1996). In vitro analysis of optimal stimuli for phase-locking and time-delayed modulation of firing in avian nucleus laminaris neurons. *J. Neurosci.* 16, 993–1007.
- Reynolds, J.H., and Desimone, R. (1999). The role of neural mechanisms of attention in solving the binding problem. *Neuron* 24, this issue, 19–29.
- Reynolds, J., Chelazzi, L., and Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *J. Neurosci.* 19, 1736–1753.
- Rhodes, P., and Gray, C.M. (1994). Simulations of intrinsically bursting neocortical pyramidal neurons. *Neural Comput.* 6, 1086–1110.
- Ribary, U., Joannides, A.A., Singh, K.D., Hasson, R., Bolton, J.P.R., Lado, F., Mogilner, A., and Llinas, R. (1991). Magnetic field tomography of coherent thalamocortical 40 Hz oscillations in humans. *Proc. Natl. Acad. Sci. USA* 88, 11037–11041.
- Riehle, A., Grun, S., Diesmann, M., and Aertsen, A. (1997). Spike synchronization and rate modulation differentially involved in motor cortical function. *Science* 278, 1950–1953.
- Riesenhuber, M., and Poggio, T. (1998a). Just one view: invariances in inferotemporal cell tuning. In *Advances in Neural Information Processing Systems*, Volume 10, M. Jordan, M. Kearns, and S. Solla, eds. (Cambridge, MA: MIT Press).
- Riesenhuber, M., and Poggio, T. (1998b). Modeling Invariances in Inferotemporal Cell Tuning, Technical Report 1629 (Cambridge, MA: MIT Artificial Intelligence Laboratory).
- Riesenhuber, M., and Poggio, T. (1999a). Are cortical models really bound by the "binding problem"? *Neuron* 24, this issue, 87–93.
- Riesenhuber, M., and Poggio, T. (1999b). Hierarchical models of object recognition in cortex. *Nat. Neurosci.*, in press.
- Rizzolatti, G., Fogassi, L., and Gallese, V. (1997). Parietal cortex: from sight to action. *Curr. Opin. Neurobiol.* 7, 562–567.

- Robertson, L., Treisman, A., Freidman-Hill, S., and Grabowecky, M. (1997). The interaction of spatial and object pathways: evidence from Balint's syndrome. *J. Cogn. Neurosci.* *9*, 254–276.
- Rock, I., and Brosgole, L. (1964). Grouping based on phenomenal proximity. *J. Exp. Psychol.* *67*, 531–538.
- Rockel, A.J., Hiorns, R.W., and Powell, T.P.S. (1980). The basic uniformity in structure of the neocortex. *Brain* *103*, 221–244.
- Rockland, K.S. (1997). Elements of cortical architecture: hierarchy revisited. In *Cerebral Cortex: Extrastriate Cortex in Primate*, K. Rockland, J. Kaas, and A. Peters, eds. (New York: Plenum Publishing Corporation).
- Rockland, K.S., and Lund, J.S. (1982). Widespread periodic intrinsic connections in the tree shrew visual cortex. *Science* *215*, 1532–1534.
- Rockland, K.S., and Van Hoesen, G.W. (1994). Direct temporal-occipital feedback connections to striate cortex (V1) in the macaque monkey. *Cereb. Cortex* *4*, 300–313.
- Rodman, H.R., and Albright, T.D. (1989). Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). *Exp. Brain Res.* *75*, 53–64.
- Rodriguez, E., George, N., Lachaux, J.-P., Martinerie, J., Renault, B., and Varela, F.J. (1999). Perception's shadow: long-distance gamma band synchronization of human brain activity. *Nature* *397*, 430–433.
- Roe, A.W., and Ts'o, D.Y. (1995). Visual topography in primate V2: multiple representation across functional stripes. *J. Neurosci.* *15*, 3689–3715.
- Roelfsema, P.R., and Singer, W. (1998). Detecting connectedness. *Cereb. Cortex* *8*, 385–396.
- Roelfsema, P.R., König, P., Engel, A.K., Sireteanu, R., and Singer, W. (1994). Reduced synchronization in the visual cortex of cats with strabismic amblyopia. *Eur. J. Neurosci.* *6*, 1645–1655.
- Roelfsema, P.R., Engel, A.K., König, P., and Singer, W. (1996). The role of neuronal synchronization in response selection: A biologically plausible theory of structured representations in the visual cortex. *J. Cogn. Neurosci.* *8*, 603–625.
- Roelfsema, P.R., Engel, A.K., König, P., and Singer, W. (1997). Visuo-motor integration is associated with zero time-lag synchronization among cortical areas. *Nature* *385*, 157–161.
- Rolls, D.T., and Tovee, M.J. (1994). Processing speed in the cerebral cortex and the neurophysiology of visual masking. *Proc. R. Soc. Lond. B Biol. Sci.* *257*, 9–15.
- Rolls, E., and Tovee, M. (1995). The responses of single neurons in the temporal visual cortical areas of the macaque when more than one stimulus is present in the receptive field. *Exp. Brain Res.* *103*, 409–420.
- Rosenblatt, F. (1961). *Principles of Neurodynamics: Perceptions and the Theory of Brain Mechanisms*. (Washington, CD: Spartan Books).
- Rosenquist, A.C. (1985). Connections of visual cortical areas in the cat. In *Cerebral Cortex*, A. Peters and E.G. Jones, eds. (New York: Plenum Press).
- Rougeul, A., Bouyer, J.J., Dedet, L., and Debray, O. (1979). Fast somato-parietal rhythms during combined focal attention and immobility in baboon and squirrel monkey. *Electroenceph. Clin. Neurophysiol.* *46*, 310–319.
- Saarinen, J. (1996a). Localization and discrimination of "pop-out" target. *Vision Res.* *36*, 313–316.
- Saarinen, J. (1996b). Target localization and identification in rapid visual search. *Perception* *25*, 305–312.
- Sagi, D., and Julesz, B. (1985). "Where" and "what" in vision. *Science* *228*, 1217–1219.
- Saito, H., Yukie, M., Tanaka, K., Hikosaka, K., Fukada, Y., and Iwai, E. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *J. Neurosci.* *6*, 145–157.
- Sakai, K., and Miyashita, Y. (1991). Neural organization for the long-term memory of paired associates. *Nature* *354*, 152–155.
- Sakai, K., and Miyashita, Y. (1994). Neuronal tuning to learned complex forms in vision. *Neuroreport* *5*, 829–832.
- Sakata, H., Taira, M., Murata, A., and Mine, S. (1995). Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cereb. Cortex* *5*, 429–438.
- Salin, P.A., and Bullier, J. (1995). Corticocortical connections in the visual system: structure and function. *Physiol. Rev.* *75*, 107–154.
- Sanes, J.N., and Donoghue, J.P. (1993). Oscillations in local field potentials of the primate motor cortex during voluntary movement. *Proc. Natl. Acad. Sci. USA* *90*, 4470–4474.
- Sato, T. (1989). Interactions of visual stimuli in the receptive fields of inferior temporal neurons in awake monkeys. *Exp. Brain Res.* *77*, 23–30.
- Schein, S.J., and Desimone, R. (1990). Spectral properties of V4 neurons in the macaque. *J. Neurosci.* *10*, 3369–3389.
- Schein, S.J., Marrocco, R.T., and de Monasterio, F.M. (1982). Is there a high concentration of color-selective cells in area V4 of monkey visual cortex? *J. Neurophysiol.* *47*, 193–213.
- Schiller, J., Schiller, Y., Stuart, G., and Sakmann, B. (1997). Calcium action potentials restricted to distal apical dendrites of rat neocortical pyramidal neurons. *J. Physiol.* *505*, 605–616.
- Schmidt, K.E., Goebel, R., Löwel, S., and Singer, W. (1997a). The perceptual grouping criterion of collinearity is reflected by anisotropies of connections in the primary visual cortex. *Eur. J. Neurosci.* *9*, 1083–1089.
- Schmidt, K.E., Kim, D.-S., Singer, W., Bonhoeffer, T., and Löwel, S. (1997b). Functional specificity of long-range intrinsic and interhemispheric connections in the visual cortex of strabismic cats. *J. Neurosci.* *17*, 5480–5492.
- Schmolesky, M.T., Wang, Y., Hanes, D.P., Thompson, K.G., Leutgeb, S., Schall, J.D., and Leventhal, A.G. (1998). Signal timing across the macaque visual system. *J. Neurophysiol.* *79*, 3272–3278.
- Schroeder, C.E., Mehta, A.D., and Givre, S.J. (1998). A spatiotemporal profile of visual system activation revealed by current source density analysis in the awake macaque. *Cereb. Cortex* *8*, 575–592.
- Schuster, H.G., and Wagner, P. (1990). A model for neuronal oscillations in the visual cortex. 2. Phase description of the feature dependent synchronization. *Biol. Cybern.* *64*, 83–85.
- Schwarz, C., and Bolz, J. (1991). Functional specificity of the long-range horizontal connections in cat visual cortex: a cross-correlation study. *J. Neurosci.* *11*, 2995–3007.
- Schwindt, P.C., and Crill, W.E. (1995). Amplification of synaptic current by persistent sodium conductance in apical dendrite of neocortical neurons. *J. Neurophysiol.* *74*, 2220–2224.
- Seidemann, E., and Newsome, W.T. (1999). Effect of spatial attention on the responses of area MT neurons. *J. Neurophysiol.* *81*, 1783–1794.
- Sejnowski, T.J. (1981). Skeleton filters in the brain. In *Parallel Models of Associative Memory*, G.E. Hinton and J.A. Anderson, eds. (Hillsdale, NJ: Lawrence Erlbaum Associates).
- Sereno, M.I., and Allman, J.M. (1991). Cortical visual areas in mammals. In *The Neural Basis of Visual Function*, A. Leventhal, ed. (New York: MacMillan).
- Sereno, A.B., and Maunsell, J.H.R. (1998). Shape selectivity in primate lateral intraparietal cortex. *Nature* *395*, 500–503.
- Sestokas, A.K., and Lehmkuhle, S. (1988). Response variability of X- and Y-cells in the dorsal lateral geniculate nucleus of the cat. *J. Neurophysiol.* *59*, 317–325.
- Shadlen, M.N., and Movshon, J.A. (1999). Synchrony unbound: a critical evaluation of the temporal binning hypothesis. *Neuron* *24*, this issue, 67–77.
- Shadlen, M.N., and Newsome, W.T. (1994). Noise, neural codes and cortical organization. *Curr. Opin. Neurobiol.* *4*, 569–579.
- Shadlen, M., and Newsome, W. (1995). Is there a signal in the noise? *Curr. Opin. Neurobiol.* *5*, 248–250.
- Shadlen, M.N., and Newsome, W.T. (1996). Motion perception: seeing and deciding. *Proc. Natl. Acad. Sci. USA* *93*, 628–633.
- Shadlen, M.N., and Newsome, W.T. (1998). The variable discharge of cortical neurons: implications for connectivity, computation, and information coding. *J. Neurosci.* *18*, 3870–3896.
- Shastri, L., and Ajanagadde, V. (1993). From simple associations to systematic reasoning. *Behav. Brain Sci.* *16*, 417–494.
- Sheinberg, D.L., and Logothetis, N.K. (1997). The role of temporal cortical areas in perceptual organization. *Proc. Natl. Acad. Sci. USA* *94*, 3408–3413.

- Shimojo, S., Silverman, G.H., and Nakayama, K. (1989). Occlusion and the solution to the aperture problem for motion. *Vision Res.* **29**, 619–626.
- Sillito, A.M., Grieve, K.L., Jones, H.L., Cuderio, J., and Davis, J. (1995). Visual cortical mechanisms detecting focal orientation discontinuities. *Nature* **378**, 492–496.
- Silverman, M.S., Grosf, D.H., DeValois, R.L., and Elfar, S.D. (1989). Spatial-frequency organization in primate striate cortex. *Proc. Natl. Acad. Sci. USA* **86**, 711–715.
- Simons, D.J., and Levin, D.T. (1997). Change blindness. *Trends Cogn. Sci.* **1**, 261–268.
- Singer, W. (1993). Synchronization of cortical activity and its putative role in information processing and learning. *Annu. Rev. Physiol.* **55**, 349–374.
- Singer, W. (1994). Putative functions of temporal correlations in neocortical processing. In *Large-Scale Neuronal Theories of the Brain*, C. Koch and J.L. Davis, eds. (Cambridge, MA: MIT Press).
- Singer, W. (1995). Development and plasticity of cortical processing architectures. *Science* **270**, 758–764.
- Singer, W. (1999a). Response synchronization: a universal coding strategy for the definition of relations. In *The Cognitive Neurosciences*, M.S. Gazzaniga, ed. (Cambridge, MA: MIT Press).
- Singer, W. (1999b). Neuronal synchrony: a versatile code for the definition of relations? *Neuron* **24**, this issue, 49–65.
- Singer, W., and Gray, C.M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annu. Rev. Neurosci.* **18**, 555–586.
- Singer, W., Engel, A.K., Kreiter, A.K., Munk, M.H.J., Neuenschwander, S., and Roelfsema, P.R. (1997). Neuronal assemblies: necessity, signature and detectability. *Trends Cogn. Sci.* **1**, 252–261.
- Skottun, B.C., Bradley, A., Sclar, G., Ohzawa, I., and Freeman, R.D. (1987). The effects of contrast on visual orientation and spatial frequency discrimination: a comparison of single cells and behavior. *J. Neurophysiol.* **57**, 773–786.
- Snyder, L.H., Batista, A.P., and Andersen, R.A. (1997). Coding of intention in the posterior parietal cortex. *Nature* **386**, 167–170.
- Sompolinsky, H., Golomb, D., and Kleinfeld, D. (1990). Global processing of visual stimuli in a neural network of coupled oscillators. *Proc. Natl. Acad. Sci. USA* **87**, 7200–7204.
- Sperry, R.W., Miner, N., and Myers, R.E. (1955). Visual pattern perception following subpial slicing and tantalum wire implantations in the visual cortex. *J. Comp. Physiol. Psychol.* **48**, 50–58.
- Spitzer, H., Desimone, R., and Moran, J. (1988). Increased attention enhances both behavioral and neuronal performance. *Science* **240**, 338–340.
- Sporns, O., Gally, J.A., Reeke, G.N., and Edelman, G.M. (1989). Reentrant signaling among simulated neuronal groups leads to coherency in their oscillatory activity. *Proc. Natl. Acad. Sci. USA* **86**, 7265–7269.
- Sporns, O., Tononi, G., and Edelman, G.M. (1991). Modeling perceptual grouping and figure ground segregation by means of active reentrant connections. *Proc. Natl. Acad. Sci. USA* **88**, 129–133.
- Stemmler, M., Usher, M., and Niebur, E. (1995). Lateral interactions in primary visual cortex: a model bridging physiology and psychophysics. *Science* **269**, 1877–1880.
- Steriade, M., Timofeev, I., Durmuller, N., and Grenier, F. (1998). Dynamic properties of corticothalamic neurons and local cortical interneurons generating fast rhythmic (30–40 Hz) spike-bursts. *J. Neurophysiol.* **79**, 483–490.
- Steriade, M. (1999). Coherent oscillations and short-term plasticity in corticothalamic networks. *Trends Neurosci.* **22**, 337–345.
- Stevens, C.F., and Wang, Y. (1995). Facilitation and depression at single central synapses. *Neuron* **14**, 795–802.
- Stevens, C.F., and Zador, A.M. (1998). Input synchrony and the irregular firing of cortical neurons. *Nat. Neurosci.* **1**, 210–217.
- Stoner, G.R., and Albright, T.D. (1992). Neural correlates of perceptual motion coherence. *Nature* **358**, 412–414.
- Stoner, G.R., Albright, T.D., and Ramachandran, V.S. (1990). Transparency and coherence in human motion perception. *Nature* **344**, 153–155.
- Stopfer, M., Bhagavan, S., Smith, B.H., and Laurent, G. (1997). Impaired odor discrimination on desynchronization of odor-encoding neural assemblies. *Nature* **390**, 70–74.
- Storm, J.F. (1990). Potassium currents in hippocampal pyramidal cells. *Prog. Brain Res.* **83**, 161–187.
- Stryker, M.P. (1989). Cortical physiology: is grandmother an oscillation? *Nature* **338**, 297–298.
- Stuart, G., and Sakmann, B. (1995). Amplification of EPSPs by axosomatic sodium channels in neocortical pyramidal neurons. *Neuron* **15**, 1065–1076.
- Suzuki, S., and Cavanagh, P. (1995). Facial organization blocks access to low-level features: an object inferiority effect. *J. Exp. Psychol. Hum. Percept. Perform.* **21**, 901–913.
- Szentagotai, J. (1973). Synaptology of the visual cortex. In *Handbook of Sensory Physiology VII/3B: Visual Centers in the Brain*, R. Jung, ed. (New York: Springer-Verlag).
- Tallon-Baudry, C., and Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends Cogn. Sci.* **3**, 151–162.
- Tallon-Baudry, C., Bertrand, O., Delpuech, C., and Pernier, J. (1996). Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *J. Neurosci.* **16**, 4240–4249.
- Tallon-Baudry, C., Bertrand, O., Delpuech, C., and Pernier, J. (1997). Oscillatory gamma band (30–70 Hz) activity induced by a visual search task in humans. *J. Neurosci.* **17**, 722–734.
- Tallon-Baudry, C., Bertrand, O., Peronnet, F., and Pernier, J. (1998). Induced gamma band activity during the delay of a visual short-term memory task in humans. *J. Neurosci.* **18**, 4244–4254.
- Tallon-Baudry, C., Kreiter, A.K., and Bertrand, O. (1999). Sustained and transient oscillatory responses in the gamma and beta bands in a visual short-term memory task in humans. *Vis. Neurosci.*, in press.
- Tanaka, K. (1993). Neuronal mechanisms of object recognition. *Science* **262**, 685–688.
- Tanaka, K. (1996). Inferotemporal cortex and object vision: stimulus selectivity and columnar organization. *Annu. Rev. Neurosci.* **19**, 109–139.
- Tanaka, K., and Saito, H.-A. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *J. Neurophysiol.* **62**, 626–641.
- Tanaka, K., Hikosaka, K., Saito, H., Yukie, M., Fukada, Y., and Iwai, E. (1986a). Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *J. Neurosci.* **6**, 134–144.
- Tanaka, M., Weber, H., and Creutzfeldt, O.D. (1986b). Visual properties and spatial distribution of neurones in the visual association area on the prelunate gyrus of the awake monkey. *Exp. Brain Res.* **65**, 11–37.
- Tanaka, K., Fukada, Y., and Saito, H.A. (1989). Underlying mechanisms of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal area of the macaque monkey. *J. Neurophysiol.* **62**, 642–656.
- Tarr, M.J., and Bulthoff, H.H. (1995). Is human object recognition better described by geon-structural-descriptions or by multiple-views? *J. Exp. Psychol. Hum. Percept. Perform.*, in press.
- Theeuwes, J., and Kooi, J.L. (1994). Parallel search for a conjunction of shape and contrast polarity. *Vision Res.* **34**, 3013–3016.
- Thomson, A.M., and Deuchars, J. (1997). Synaptic interactions in neocortical local circuits: dual intracellular recordings in vitro. *Cereb. Cortex* **7**, 510–522.
- Thomson, A.M., and West, D.C. (1993). Fluctuations in pyramidal-pyramidal excitatory postsynaptic potentials modified by presynaptic firing pattern and postsynaptic membrane potential using paired intracellular recordings in rat neocortex. *Neuroscience* **54**, 329–346.
- Thomson, A., Deuchars, J., and West, D. (1993). Single axon excitatory postsynaptic potentials in neocortical interneurons exhibit pronounced paired pulse facilitation. *Neuroscience* **54**, 347–360.
- Thorpe, S., Fize, D., and Marlot, C. (1996). Speed of processing in the human visual system. *Nature* **381**, 520–522.

- Tiitinen, H., Sinkkonen, J., Reinikainen, K., Alho, K., Lavikainen, J., and Naatanen, R. (1993). Selective attention enhances the auditory 40-Hz transient response in humans. *Nature* 364, 59–60.
- Tipper, S.P., Weaver, B., Jerreat, L.M., and Burak, A.L. (1994). Object-based and environment-based inhibition of return of visual attention. *J. Exp. Psychol. Hum. Percept. Perform.* 20, 478–499.
- Tipper, S.P., and Weaver, B. (1998). The medium of attention: location-based, object-based, or scene-based? In *Visual Attention*, Volume 8, R.D. Wright, ed. (Oxford: Oxford University Press).
- Tong, F., Nakayama, K., Vaughan, J.T., and Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron* 21, 753–759.
- Tononi, G., and Edelman, G.M. (1998). Consciousness and complexity. *Science* 282, 1846–1851.
- Tononi, G., Sporns, O., and Edelman, G. (1992). Reentry and the problem of integrating multiple cortical areas: simulation of dynamic integration in the visual system. *Cereb. Cortex* 2, 310–335.
- Tononi, G., Srinivasan, R., Russell, D.P., and Edelman, G.M. (1998). Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. *Proc. Natl. Acad. Sci. USA* 95, 3198–3203.
- Tootell, R.B.H., and Hamilton, S.L. (1989). Functional anatomy of the second visual area (V2) in the macaque. *J. Neurosci.* 9, 2620–2644.
- Tootell, R.B.H., and Taylor, J.B. (1995). Anatomical evidence for MT and additional cortical visual areas in humans. *Cereb. Cortex* 1, 39–55.
- Tootell, R.B.H., Dale, A.M., Sereno, M.I., and Malach, R. (1996). New images from human visual cortex. *Trends Neurosci.* 19, 481–489.
- Tovee, M., and Rolls, E. (1992a). Oscillatory activity is not evident in the primate temporal visual cortex with static stimuli. *Neuroreport* 3, 369–372.
- Tovee, M.J., and Rolls, E.T. (1992b). The functional nature of neuronal oscillations. *Trends Neurosci.* 15, 387.
- Toyama, K., Kimura, M., and Tanaka, K. (1981a). Cross-correlation analysis of interneuronal connectivity in cat visual cortex. *J. Neurophysiol.* 46, 191–201.
- Toyama, K., Kimura, M., and Tanaka, K. (1981b). Organization of cat visual cortex as investigated by cross-correlation techniques. *J. Neurophysiol.* 46, 202–214.
- Traub, R.D., Wong, R.K.S., Miles, R., and Michelson, H.B. (1991). A model of a CA3 hippocampal pyramidal neuron incorporating voltage-clamp data on intrinsic conductances. *J. Neurophysiol.* 66, 635–650.
- Traub, R.D., Whittington, M.A., Stanford, I.M., and Jefferys, J.G. (1996). A mechanism for generation of long-range synchronous fast oscillations in the cortex. *Nature* 383, 621–624.
- Treisman, A. (1982). Perceptual grouping and attention in visual search for features and for objects. *J. Exp. Psychol. Hum. Percept. Perform.* 8, 194–214.
- Treisman, A. (1988). Features and objects: the fourteenth Bartlett memorial lecture. *Quart. J. Exp. Psychol.* 40A, 201–237.
- Treisman, A. (1991). Search, similarity and the integration of features between and within dimensions. *J. Exp. Psychol. Hum. Percept. Perform.* 27, 652–676.
- Treisman, A. (1992a). Perceiving and re-perceiving objects. *Am. Psychol.* 47, 862–875.
- Treisman, A. (1992b). Spreading suppression or feature integration? A reply to Duncan and Humphreys. *J. Exp. Psychol. Hum. Percept. Perform.* 18, 589–593.
- Treisman, A. (1993). The perception of features and objects. In *Attention: Selection, Awareness and Control: A Tribute to Donald Broadbent*, A. Baddeley and L. Weiskrantz, eds. (Oxford: Clarendon Press).
- Treisman, A. (1995). Modularity and attention: is the binding problem real? *Vis. Cogn.* 2, 303–311.
- Treisman, A. (1996). The binding problem. *Curr. Opin. Neurobiol.* 6, 171–178.
- Treisman, A. (1998). Feature binding, attention and object perception. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 353, 1295–1306.
- Treisman, A., and Gelade, G. (1980). A feature-integration theory of attention. *Cogn. Psychol.* 12, 97–136.
- Treisman, A., and Gormican, S. (1988). Feature analysis in early vision: evidence from search asymmetries. *Psychol. Rev.* 95, 15–48.
- Treisman, A., and Kanwisher, N.K. (1998). Perceiving visually-presented objects: recognition, awareness, and modularity. *Curr. Opin. Neurobiol.* 8, 218–226.
- Treisman, A., and Sato, S. (1990). Conjunction search revisited. *J. Exp. Psychol. Hum. Percept. Perform.* 16, 459–478.
- Treisman, A., and Schmidt, H. (1982). Illusory conjunctions in the perception of objects. *Cogn. Psychol.* 14, 107–141.
- Treisman, A., and Souther, J. (1986). Illusory words: the roles of attention and of top-down constraints in conjoining letters to form words. *J. Exp. Psychol. Hum. Percept. Perform.* 12, 3–17.
- Treue, S., and Andersen, R.A. (1996). Neural responses to velocity gradients in macaque cortical area MT. *Vis. Neurosci.* 13, 797–804.
- Treue, S., and Maunsell, J.H.R. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* 382, 539–541.
- Triesch, J., and von der Malsburg, C. (1996). Binding—a proposed experiment and a model. In *Proceedings of the Proceedings of the International Conference on Artificial Neural Networks 1996* (New York: Springer-Verlag).
- Tsal, Y. (1989). Do illusory conjunctions support feature integration theory? A critical review of theory and findings. *J. Exp. Psychol. Hum. Percept. Perform.* 15, 394–400.
- Ts'o, D., and Gilbert, C. (1988). The organization of chromatic and spatial interactions in the primate striate cortex. *J. Neurosci.* 8, 1712–1727.
- Ts'o, D.Y., Gilbert, C.D., and Wiesel, T.N. (1986). Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis. *J. Neurosci.* 6, 1160–1170.
- Tsotsos, J.K. (1990). Analyzing vision at the complexity level. *Behav. Brain Sci.* 13, 423–445.
- Tsotsos, J.K. (1995). Toward a computational model of visual attention. In *Early Vision and Beyond*, T.V. Papathomas, ed. (Cambridge, MA: MIT Press).
- Tsotsos, J.K., Culhane, S.N., Wai, W.Y.K., Lai, Y., Davis, N., and Nuflo, F. (1995). Modeling visual attention via selective tuning. *Artif. Intell.* 78, 507–545.
- Ullman, S. (1996). *High-Level Vision* (Cambridge, MA: MIT Press).
- Ungerleider, L., and Haxby, J. (1994). “What” and “Where” in the human brain. *Curr. Opin. Neurobiol.* 4, 157–165.
- Ungerleider, L.G., and Mishkin, M. (1982). Two cortical visual systems. In *Analysis of Visual Behavior*, D.J. Ingle, M.A. Goodale, and R.J.W. Mansfield, eds. (Cambridge, MA: MIT Press).
- Ungerleider, L.G., Gaffan, D., and Pelak, V.S. (1989). Projections from inferior temporal cortex to prefrontal cortex via the uncinate fascicle in rhesus monkeys. *Exp. Brain Res.* 76, 473–484.
- Usher, M., and Donnelly, N. (1998). Visual synchrony affects binding and segmentation in perception. *Nature* 394, 179–182.
- Usrey, W.M., and Reid, R.C. (1999). Synchronous activity in the visual system. *Annu. Rev. Physiol.* 61, 435–456.
- Vaadia, E., and Aertsen, A. (1992). Coding and computation in the cortex: single-neuron activity and cooperative phenomena. In *Information Processing in the Cortex: Experiments and Theory*, A. Aertsen and V. Braitenberg, eds. (New York: Springer-Verlag).
- Vaadia, E., Ahissar, E., Bergman, H., and Lavner, Y. (1991). Correlated activity of neurons: a neural code for higher brain functions? In *Neuronal Cooperativity*, J. Kruger, ed. (Berlin: Springer-Verlag).
- Vaadia, E., Haalman, I., Abeles, M., Bergman, H., Prut, Y., Slovin, H., and Aertsen, A. (1995). Dynamics of neuronal interactions in monkey cortex in relation to behavioural events. *Nature* 373, 515–518.
- Van Essen, D.C., and Anderson, C.H. (1990). Information processing strategies and pathways in the primate retina and visual cortex. In *An Introduction to Neural and Electronic Networks*, S.F. Zornetzer, J.L. Davis, and C. Lau, eds. (New York: Academic Press).
- Van Essen, D.C., and Gallant, J.L. (1994). Neural mechanisms of form and motion processing in the primate visual system. *Neuron* 13, 1–10.

- Van Essen, D.C., and Zeki, S.M. (1978). The topographic organization of rhesus monkey prestriate cortex. *J. Physiol. (Lond.)* 277, 193–226.
- Van Essen, D.C., Anderson, C.H., and Felleman, D.J. (1992). Information processing in the primate visual system: an integrated systems perspective. *Science* 255, 419–423.
- van Vreeswijk, D., Abbott, L.F., and Ermentrout, G.B. (1994). When inhibition not excitation synchronizes neural firing. *J. Comput. Neurosci.* 7, 313–321.
- Varela, F.J. (1995). Resonant cell assemblies: a new approach to cognitive functions and neuronal synchrony. *Biol. Res.* 28, 81–95.
- Vecera, S.P., and Farah, M.J. (1994). Does visual attention select objects or locations? *J. Exp. Psychol. Gen.* 123, 146–160.
- Vogels, R., and Orban, G.A. (1994). Activity of inferior temporal neurons during orientation discrimination with successively presented gratings. *J. Neurophysiol.* 71, 1428–1451.
- Volgushev, M., Chistiakova, M., and Singer, W. (1998). Modification of discharge patterns of neocortical neurons by induced oscillations of the membrane potential. *Neuroscience* 83, 15–25.
- von der Heydt, R., and Dursteler, M.R. (1993). Visual search: monkeys detect conjunctions as fast as features. *Invest. Ophthalmol. Vis. Sci.* 34, 1288.
- von der Malsburg, C. (1981). The correlation theory of brain function. MPI Biophysical Chemistry, Internal Report 81–2. Reprinted in *Models of Neural Networks II* (1994), E. Domany, J.L. van Hemmen, and K. Schulten, eds. (Berlin: Springer).
- von der Malsburg, C. (1985). Nervous structures with dynamical links. *Ber. Bunsenges. Phys. Chem.* 89, 703–710.
- von der Malsburg, C. (1986). Am I thinking assemblies? In *Proceedings of the Trieste Meeting on Brain Theory*, G. Palm and A. Aertsen, eds. (Springer: Berlin).
- von der Malsburg, C. (1988). Pattern recognition by labeled graph matching. *Neural Networks* 1, 141–148.
- von der Malsburg, C. (1995). Binding in models of perception and brain function. *Curr. Opin. Neurobiol.* 5, 520–526.
- von der Malsburg, C. (1999). The what and why of binding: the modeler's perspective. *Neuron* 24, this issue, 95–104.
- von der Malsburg, C., and Bienenstock, E. (1987). A neural network for the retrieval of superimposed connection patterns. *Europhys. Lett.* 3, 1243–1249.
- von der Malsburg, C., and Buhmann, J. (1992). Sensory segmentation with coupled neural oscillators. *Biol. Cybern.* 67, 233–242.
- von der Malsburg, C., and Reiser, K. (1995). Pose invariant object recognition in a neural system. In *Proceedings of the International Conference on Artificial Neural Networks 1995*, F. Fogelman-Souli, J.C. Rault, P. Gallinari, and G. Dreyfus, eds. (New York: Springer-Verlag).
- von der Malsburg, C., and Schneider, W. (1986). A neural cocktail-party processor. *Biol. Cybern.* 54, 29–40.
- von der Malsburg, C., and Singer, W. (1991). Principles of cortical network organization. In *Neurobiology of Neocortex*, P. Rakic and W. Singer, eds. (New York: John Wiley).
- von Helmholtz, H.L.F. (1925). *Treatise on Physiological Optics* (New York: Dover Press).
- Wallis, G., and Rolls, E. (1997). A model of invariant object recognition in the visual system. *Prog. Neurobiol.* 51, 167–294.
- Wandell, B.A. (1999). Computational neuroimaging of human visual cortex. *Annu. Rev. Neurosci.* 22, 145–173.
- Wang, X.-J. (1999). Fast burst firing and short-term synaptic plasticity: a model of neocortical chattering neurons. *Neuroscience* 89, 347–362.
- Wang, X.-J., and Buzsaki, G. (1996). Gamma oscillation by synaptic inhibition in a hippocampal interneuronal network model. *J. Neurosci.* 16, 6402–6413.
- Wang, D.L., Buhmann, J., and von der Malsburg, C. (1990). Pattern segmentation in associative memory. *Neural Comput.* 2, 94–106.
- Wang, Q., Cavanagh, P., and Green, M. (1994). Familiarity and pop-out in visual search. *Percept. Psychophys.* 56, 495–500.
- Wehr, M., and Laurent, G. (1996). Odour encoding by temporal sequences of firing in oscillating neural assemblies. *Nature* 384, 162–166.
- Weisstein, N. (1973). Beyond the yellow Volkswagen detector and the grandmother cell: a general strategy for the exploration of operations in human pattern recognition. In *Contemporary Issues in Cognitive Psychology: The Loyola Symposium*, R.L. Solso, ed. (Washington, DC: Winston/Wiley).
- Wertheimer, M. (1923). Untersuchungen zur Lehre der Gestalt. *Psychol. Forschung* 4, 301–350.
- Wertheimer, M. (1955). Laws of organization in perceptual forms. In *A Source Book of Gestalt Psychology*, W.D. Ellis, ed. (London: Routledge and Kegan Paul).
- Wespapat, V., Tennigkeit, F., and Singer, W. (1999). Oscillations and long-term synaptic plasticity in rat visual cortex. In *From Molecular Neurobiology to Clinical Neuroscience: Proceedings of the 1st Göttingen Conference of the German Neuroscience Society, Volume 1, 27th Göttingen Neurobiology Conference*, N. Elsner and U. Eysel, eds. (Stuttgart: Thieme-Verlag).
- Whittington, M.A., Traub, R.D., and Jefferys, J.G.R. (1995). Synchronized oscillations in interneuron networks driven by metabotropic glutamate receptor activation. *Nature* 373, 612–615.
- Wickelgren, W. (1969). Context-sensitive coding, associative memory, and serial order in (speech) behavior. *Psychol. Rev.* 76, 1–15.
- Wilson, M., and Bower, J.M. (1992). Cortical oscillations and temporal interactions in a computer simulation of piriform cortex. *J. Neurophysiol.* 67, 981–995.
- Wilson, M.A., and McNaughton, B.L. (1993). Dynamics of the hippocampal ensemble code for space. *Science* 261, 1055–1058.
- Wilson, F.A., Scalaidhe, S.P., and Goldman-Rakic, P.S. (1993). Dissociation of object and spatial processing domains in primate prefrontal cortex. *Science* 260, 1955–1958.
- Wiskott, L. (1999). The role of topographical constraints in face recognition. *Pattern Recog. Lett.* 20, 89–96.
- Wiskott, L., and von der Malsburg, C. (1995). Face recognition by dynamic link matching. In *Lateral Interactions in the Cortex: Structure and Function* (electronic book), J. Sirosh, R. Miikkulainen, and Y. Choe, eds., [www.cs.utexas.edu/users/nn/web-pubs/htmlbook96](http://www.cs.utexas.edu/users/nn/web-pubs/htmlbook96).
- Wolfe, J.M. (1992). "Effortless" texture segmentation and "parallel" visual search are not the same thing. *Vision Res.* 32, 757–763.
- Wolfe, J.M. (1994a). Guided Search 2.0: a revised model of visual search. *Psychon. Bull. Rev.* 1, 202–238.
- Wolfe, J.M. (1994b). Visual search in continuous, naturalistic stimuli. *Invest. Ophthalmol. Vis. Sci.* 35, 13–28.
- Wolfe, J.M. (1996). Extending Guided Search: why Guided Search needs a preattentive "item map." In *Converging Operations in the Study of Visual Selective Attention*, A. Kramer, G.H. Cole, and G.D. Logan, eds. (Washington, DC: American Psychological Association).
- Wolfe, J.M. (1998). What do 1,000,000 trials tell us about visual search? *Psychol. Sci.* 9, 33–39.
- Wolfe, J., and Bennett, S. (1996). Preattentive object files: shapeless bundles of basic features. *Vision Res.* 37, 25–44.
- Wolfe, J.M., and Cave, K.R. (1999). The psychophysical evidence for a binding problem in human vision. *Neuron* 24, this issue, 11–17.
- Wolfe, J.M., and Gancarz, G. (1996). Guided Search 3.0: a model of visual search catches up with Jay Enoch 40 years later. In *Basic and Clinical Applications of Vision Science*, V. Lakshminarayanan, ed. (Dordrecht, Netherlands: Kluwer Academic).
- Wolfe, J.M., Cave, K.R., and Franzel, S.L. (1989). Guided Search: an alternative to the Feature Integration model for visual search. *J. Exp. Psychol. Hum. Percept. Perform.* 15, 419–433.
- Wolfe, J.M., Chun, M.M., and Friedman-Hill, S.R. (1995). Making use of text on gradients: visual search and perceptual grouping exploit the same parallel processes in different ways. In *Early Vision and Beyond*, T. Pappathomas, C. Chubb, A. Gorea, and E. Kowler, eds. (Cambridge, MA: MIT Press).
- Würtz, R. (1997). Object recognition robust under translations, deformations, and changes in background. *IEEE Trans. Pattern Anal. Machine Intell.* 19.
- Yantis, S., and Gibson, B.S. (1994). Object continuity in apparent motion and attention. *Can. J. Exp. Psychol.* 48, 182–204.
- Yen, S.-C., and Finkel, L.H. (1998). Extraction of perceptually salient contours by striate cortical networks. *Vision Res.* 38, 719–741.

- Yen, S.-C., Menschik, E.D., and Finkel, L.H. (1999). Perceptual grouping in striate cortical networks mediated by synchronization and desynchronization. *Neurocomputing*, in press.
- Yeshurun, Y., and Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature* *396*, 72–75.
- Yeshurun, Y., and Carrasco, M. (1999). Spatial attention improves performance in spatial resolution tasks. *Vision Res.* *39*, 293–306.
- Ylinen, A., Sik, A., Bragin, A., Nadasdy, Z., Jando, G., Szabo, I., and Buzsaki, G. (1995). Sharp wave-associated high-frequency oscillation (200 Hz) in the intact hippocampus: network and intracellular mechanisms. *J. Neurosci.* *15*, 30–46.
- Yoshioka, T., Blasdel, G.G., Levitt, J.B., and Lund, J.S. (1996). Relation between patterns of intrinsic lateral connectivity, ocular dominance, and cytochrome oxidase-reactive regions in macaque monkey striate cortex. *Cereb. Cortex* *6*, 297–310.
- Young, M.P., and Yamane, S. (1992). Sparse population coding of faces in the inferotemporal cortex. *Science* *256*, 1327–1331.
- Young, M.P., Tanaka, K., Yamane, S. (1992). On oscillating neuronal responses in the visual cortex of the monkey. *J. Neurophysiol.* *67*, 1464–1474.
- Yu, A.C., and Margoliash, D. (1996). Temporal hierarchical control of singing in birds. *Science* *273*, 1871–1875.
- Yuste, R., and Tank, D.W. (1996). Dendritic integration in mammalian neurons, a century after Cajal. *Neuron* *16*, 701–716.
- Zeki, S.M. (1978). Functional specialisation in the visual cortex of the rhesus monkey. *Nature* *274*, 423–428.
- Zeki, S. (1983). The distribution of wavelength and orientation selective cells in different areas of monkey visual cortex. *Proc. R. Soc. Lond. B Biol. Sci.* *217*, 449–470.
- Zeki, S., and Shipp, S. (1988). The functional logic of cortical connections. *Nature* *335*, 311–317.
- Zhang, X. (1999). Anticipatory inhibition: an intentional non-spatial mechanism revealed with the distractor previewing technique. PhD thesis, Princeton University, Princeton, NJ.
- Zhang, L.I., Tao, H.W., Holt, C.E., Harris, W.A., and Poo, M. (1998). A critical window for cooperation and competition among developing retinotectal synapses. *Nature* *395*, 37–44.
- Zipser, K., Lamme, V.A.F., and Schiller, P.H. (1996). Contextual Modulation in Primary Visual Cortex. *J. Neurosci.* *16*, 7376–7389.
- Zohary, E., and Hochstein, S. (1989). How serial is serial processing in vision? *Perception* *18*, 191–200.
- Zohary, E., Shadlen, M.N., and Newsome, W.T. (1994). Correlated neuronal discharge rate and its implications for psychophysical performance. *Nature* *370*, 140–143.