

The binding problem

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Perceptual representations depend on distributed neural codes for relaying the parts and properties of objects. Some mechanism is needed to 'bind' the information relating to each object and to distinguish it from others. Possible candidates include cells tuned to conjunctions of features, spatial attention, and synchronized firing across separate but interconnected areas of the brain. Deficits in neurological patients suggest a role for the parietal cortex in the binding process. Several current models combine these ideas.

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Abbreviations

FIT	feature integration theory
IC	illusory conjunction
IT	inferior temporal cortex
PET	positron emission tomography

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Introduction

The world that we effortlessly—and usually accurately—perceive consists of complex objects that are characterized by their shapes, colors, movements, and other properties. To identify an object, we must specify not only its parts and properties, but also how those parts and properties are combined. What mechanisms ensure that we normally see the correct conjunctions, for example, a blue shirt as blue, with gray pants as gray, and not the reverse? The binding problem comes in many different forms, which may not share the same solution. There are at least seven different types of binding:

Property binding, in which different properties (e.g. shape, color, and motion) must be bound to the objects that they characterize. The 'binding problem' arises here because different aspects of the scene are coded in specialized visual areas, with the size of visual receptive fields increasing at later levels of the coding hierarchy (see e.g. [1–3]).

Part binding, in which the parts of an object must be segregated from the background, and bound together, sometimes across discontinuities resulting from partial occlusion. This form of binding breaks down in apperceptive agnosics [4,5].

Range binding, in which particular values on a dimension (e.g. purple on the color dimension, or tilted 20° for orientation) are signalled by ratios of activity in a few distinct populations of neurons (e.g. those sensitive to blue and to red to signal purple). Any system using 'coarse coding' with just a few distinct populations of broadly tuned detectors to represent fine distinctions along a full range of properties must combine, and therefore bind, different levels of firing in cells with overlapping sensitivities to represent particular points on the dimension in question [6].

Hierarchical binding, in which the features of shape-defining boundaries (e.g. orientation, curvature, and closure) are bound to the surface-defining properties that carry them (e.g. luminance, color, texture, motion, and stereoscopic depth) [7].

Conditional binding, in which the interpretation of one property (e.g. direction of motion) often depends on another (e.g. depth, occlusion or transparency) [8,9].

Temporal binding, in which successive states of the same object must be integrated across temporal intervals, in real and apparent motion, and other transformations.

Location binding, in which objects are bound to their current locations. Objects and locations appear to be separately coded in ventral and dorsal pathways, respectively [10,11], raising what may be the most basic binding problem: linking 'what' to 'where'.

Most modeling efforts have focused on the binding of parts or properties. A number of possible mechanisms have been envisaged, including: 'grandmother cells' responding to specific conjunctions of features that uniquely identify a particular object (see e.g. [12]); local cell assemblies onto which the pathways from different feature maps converge, perhaps with adjustable connections allowing flexible routing of signals (see e.g. [13]); a serial scan of different spatial areas selected by an adjustable attention window, conjoining the features that each contains and excluding features from adjacent areas (see e.g. [14–16]); detection of temporal contiguity—parts and properties whose onset, offset or motion coincide probably belong to the same object; synchronized firing of cells responding to features of the same object, perhaps assisted by oscillatory neural activity (see e.g. [17,18,19•]). These mechanisms are not mutually exclusive.

When paying attention, we can see without difficulty any novel conjunction of properties. Although stored representations of familiar objects certainly bind their properties, matching to these 'templates' cannot provide perceptual binding for unfamiliar conjunctions. Temporary object representations must be formed to mediate perception of novel objects, and also of familiar objects in current, possibly novel instantiations. These temporary representations must be compared to previously learned representations to allow recognition or classification where possible. They must also be capable of activating any motor program to allow the flexible choice of any arbitrary response to any perceived object (in addition to 'pre-wired' connections to biologically useful actions).

Single neurons may play a role, although they are unlikely to provide a complete solution to the binding problem for complex objects. There are too few neurons to code individually the combinatorial explosion of arbitrary conjunctions that we are capable of seeing. Nevertheless, most neurons do respond best to conjunctions of properties, such as a particular orientation with a particular spatial frequency or direction of movement. Selective adaptation to conjunctions can occur, giving rise to contingent aftereffects [20], which are retinotopic and specific to the adapted eye. Many single neurons in the inferior temporal cortex (IT) respond to more complex conjunctions, such as a face or a striped patch with flanking black spots [21]. Note, however, that selectivity along more than one dimension need not imply that a neuron independently signals a particular conjunction: its role may be as part of a network coding different properties by patterns of activity in different subgroups. The neural evidence to be reviewed here suggests a distributed code for conjunctions, such as temporary cell assemblies, possibly selected through focused attention and possibly linked by synchronized activity in specialized but interconnected visual areas.

Recent reviews in this journal have discussed the neural substrate [22] and computational models [23] of binding; the present review focuses primarily on psychological and neuropsychological evidence. This evidence should constrain the neural models, and suggest possible mechanisms they might instantiate.

Psychological research

The spatial attention hypothesis has generated considerable behavioral research. The suggestion is that binding 'what' to 'where' through a serial scan of locations also binds the properties and parts of the individual 'whats'. According to feature integration theory (FIT) [14,15,24], a scalable 'window of attention' scans a 'master map' of locations, selecting the features currently active in corresponding locations of various specialized feature maps, and suppressing those in other locations to prevent erroneous binding. The selected features are assembled to form an 'object token' and are compared to stored

representations to identify the object. (See [25] for a connectionist simulation of a similar idea.)

The theory was proposed to account for the following observations. First, illusory conjunctions (ICs) are frequently seen when exposures are brief, and focused attention to each object, in turn, is prevented [26,27]. (An IC is a binding error in which a feature of one object is seen as characterizing another. For example, the presentation of a green X and a red O might yield the illusory percept of a red X or green O.) Second, directing attention in advance to the location of a target improves identification more for conjunctions than for simple features [24,28], even when overall difficulty is matched. Third, search appears to be serial (with focused attention to each item in turn) when the target is uniquely specified only by a conjunction of features (e.g. target green H among green Xs and brown Hs) [14]. Fourth, search is also serial for targets defined by the absence of a feature (e.g. O among Qs), or for less salient features among more salient features, whereas search for the presence of the same feature (Q among Os), or for more salient features among less salient features, is clearly parallel. The less salient targets may require attentional binding of features to locations [29]. A competing attention task greatly impairs performance with less salient features, leaving the more salient features intact [30•], as do V4 lesions in monkeys [31]. Finally, in dynamic displays, repetition priming across short intervals of time is object specific, where objects are defined by their spatio-temporal coordinates rather than by their properties or identity [32]. For example, an 'S' primes perception of a subsequent 'S' only if it is seen as part of the same object, whether in the same location or in a new location linked to the first by the perceived path of its motion in the interval.

Recent psychophysical evidence from both normal participants and brain-injured patients supports this account in general, but also suggests some modifications and elaborations to the theory. Experiments on binding errors in the report of brief multi-element displays, on search for visual targets, and on the perception of dynamic displays all provide relevant results.

Binding errors

High rates of ICs occur even with foveal presentation when exposures are brief and attention is overloaded [26]. Thus, when several colored shapes were flashed at fixation, flanked by two digits to be reported first, participants saw many recombinations of features that actually belonged to different objects. Contrary to earlier results, new experiments suggest that proximity increases the risk of binding errors (see e.g. [33]). The binding process is also constrained by both perceptual and conceptual grouping [34•]. More ICs are formed within than between perceptual groups [35–37], and within morphological and orthographic units in words [38]. They are also more frequent between objects with similar than dissimilar

features [39]. Whether these are direct effects on binding or an indirect result of attention being allocated to perceptual groups of elements as units is not yet clear.

The poor acuity and reduced spatial resolution of peripheral vision can also give rise to binding failures when the subject fixates centrally and stimuli are presented peripherally [40•], even with long exposures and no competing attention task. A trade-off was shown in binding accuracy between the effects of attention load and the effects of spatial uncertainty attributable to distance from the fovea. Items presented closer to fixation but with a competing attention task gave the same rate of ICs as items presented more peripherally without a competing task. Even with the competing task, the objects giving rise to ICs required responses and, therefore, presumably attracted some attention. In a task that required the relevant stimuli to be ignored completely, there was no evidence that binding was any more accurate than chance (N Lavie, personal communication). In this study, the participants classified a central colored shape, and ignored a pair of flanking stimuli. Response latencies were slowed equally when one complete flanker was associated with the competing response and when one feature from each flanker would, if conjoined, evoke the competing response. The implication is that the features of the unattended flankers were as likely to be incorrectly as correctly conjoined, supporting the idea that attention is needed for accurate binding. Although there is continuing debate on the interpretation of ICs [41•,42], the preponderance of evidence supports the claim that, at least with foveal presentation, they result from failures to focus attention.

Binding does not require synchronous presentation of the elements. ICs can occur between successive items within the same location, as well as between simultaneous items in different locations [43,44]. When time and location were pitted against each other as determinants of binding or segregation, location clearly won [45]. Spatial mis-alignments were critical determinants of parsing in an ambiguous figure, whereas substantial temporal asynchronies left binding intact [46•]. The results leave open the possibility that internally generated synchrony of neural firing acts as a binding mechanism.

Search for targets

Early results suggested that search for targets defined by a unique feature can be parallel, whereas search for a conjunction of features must be serial [14]. This conclusion has been modified by more recent research.

Some features of surfaces and depth can be detected without focusing attention: thus, parallel detection is possible for properties defined by stereoscopic depth [47], constancy scaling of brightness [48], and geometric forms seen as three-dimensional objects lit from a particular direction [49]. These properties conjoin many simple

retinal cues, in apparent conflict with the claim that serial attention is needed for binding. One resolution is that parallel search reflects not preattentive processing but global attention to the scene as a whole, with no individuation of separate elements [15]. A discrepant object is seen as a break in the global structure of the three-dimensional array. Similarly, a face can be seen as a global whole without requiring serial processing of each feature in turn.

Conjunctions of parts may create emergent features, such as closure, which also allow parallel detection [27,50]. Extensive practice may form new conjunction detectors that mediate efficient search [51,52], suggesting the possibility that 'grandmother cells' or local 'cell assemblies' may develop to solve the binding problem for familiar sets of items such as letters [53•], or for useful components of more complex shapes. Indeed, there is evidence that single units in monkey area IT change their selectivity with experience [54,55].

Search even for arbitrary conjunctions can, in certain conditions, be more efficient than was initially observed (see e.g. [16,56]). In recent versions of FIT, strategies of feature-based inhibition [57] or 'guided search' [16] supplement serial attention in solving the binding problem. When the component properties are highly discriminable, conjunction targets may emerge without binding, through the separate inhibition or activation of disjunctive sets of features. For example, a red X will stand out from a background of green Xs and red Os if areas containing green and areas containing Os are separately inhibited.

Recent evidence continues to support the idea that binding depends on attention unless one or other of these special conditions holds. Search times for conjunctions of less discriminable features increase linearly with the number of non-targets [58]. Search also remains serial for conjunctions of values within a dimension (e.g. Ts among Ls in varied orientations [59], or bi-colored squares [60]), unless the components are hierarchically organized with one color characterizing a part of another colored object [61]. Even with practice and highly discriminable features, arbitrary conjunctions cannot be rejected without attention: thus, search for any of six color-orientation-size conjunctions, defined as an 'odd one out', remained serial in displays containing mixtures of two well-learned conjunction distractors [57]. Finally, it is impossible to use three conjunction-defined objects to define a virtual triangle in a larger display, although this task is easy with feature-defined objects [62••].

An alternative account of search in terms of similarity has been proposed, in which similarity among distractors determines the strength of perceptual grouping, and similarity between target and distractors determines the ease of segregating the target from the distractors [63,64]. But similarity may itself create binding problems. Without

attention, only coarsely coded feature information is available [29,65,66]. Intermediate values—for example, a steeply tilted orientation or the color purple—may be coded as conjunctions of activity in different groups of neurons—for example, those responding to vertical with those responding to diagonal, or those responding to red with those responding to blue—and, as such, may require serial attention. Indeed, binding errors generating illusory intermediate values often occur when exposures are brief [67].

Temporal binding

Evidence exists that bound features form object tokens that are defined by their spatio-temporal continuity [32]. Up to four independently moving identical elements can be tracked, probably as a single bound token [68]. Both onsets and interruptions may disrupt the current binding and trigger a new one. For example, attention can be ‘captured’ by the sudden appearance of a new object [69•], which then takes priority in processing, or by the disappearance (for at least 75 ms to 100 ms) of the currently attended object. The same critical interval determines the organization seen in an ambiguous (Ternus) apparent motion display [69•], where the two possible percepts reflect continuity versus change of binding.

In sum, behavioral research has elaborated on the role of attention in binding in two ways: first, by showing conditions in which attentive binding can be by-passed, and second, by clarifying the factors that constrain the allocation of attention.

Parietal involvement in binding

Failures of binding related to specified brain damage may throw light on the underlying mechanisms. The finding of a correlation between performance in a spatially cued attention task and the incidence of ICs, observed among left-brain-damaged patients, has suggested a link between attentional binding and the parietal lobes [70••,71]. A patient with bilateral parietal lesions also made many ICs when asked to report the color and identity of either of two letters, even with presentations as long as 10 s [72••]. His other symptoms, typical of Balint’s syndrome, included an inability to localize objects or to see more than one or two objects at a time (simultanagnosia). The pattern of deficits suggests that the same parietal spatial map mediates explicit localization of objects, individuation of objects, and binding of features through selective attention.

Further evidence for a parietal role in spatial attention comes from a study of positron emission tomography (PET) activation [73•]. Continuous attention to motion, color or shape gave enhanced activity in different extrastriate areas, but tasks that required active shifting of attention between locations gave rise to activity in superior parietal areas. Parietal areas were also active in a task requiring feature binding (conjunction search [73•]). When participants viewed complex colored geometric designs,

PET activation was seen not only in the occipital and temporal lobes, but also in the parietal lobe [74]. The stimuli did not involve depth or motion or any explicit requirement for spatial localization, but they certainly posed a binding problem.

Recent event-related potential (ERP) studies have explored differences between feature and conjunction search. A negative (N2pc) component contralateral to the target is associated with spatial filtering and the suppression of distractors [75•]. The P1 component is reduced in response to a probe stimulus located where a non-target in conjunction search had just appeared [76••]. These event-related potential changes in search closely resemble those found in spatial cueing and sustained attention, suggesting that the same attentional mechanism is involved in conjunction search as in the overtly attentional tasks. Luck and Hillyard [75•] propose that after rapid initial processing of the search array, location information from the parietal cortex “is used to send a signal back into occipital cortex, perhaps through the pulvinar, which activates a filtering process that attenuates the flow of information from distractors surrounding the selected item.” These findings are consistent with the spatial attention account of feature integration.

Binding and synchronized firing

Most recent neuroscience research on the binding problem has focused on the hypothesis that binding is achieved by synchronized activity of cells responding to different properties of the same object, an idea earlier proposed by Milner [17] and von der Malsburg (see [77], and see [19••,23,78] for reviews). Binding by synchrony has the advantage that it is flexible and dynamic, can operate over large separations between areas, and is likely to facilitate neural transmission and learning of bound objects. Attention limits may be set by the number of clearly distinct firing rates available to code separate objects. Accidental synchronies are likely to increase with the number of objects present and could give rise to ICs, explaining why these occur mainly when the attention load is high.

The synchronized activity observed by neuroscientists is sometimes associated with oscillations around 40 Hz, especially in cats. Most importantly, it is stimulus dependent: units with spatially separate receptive fields fire synchronously in response to a single object, but not in response to two independently moving or two separately oriented objects [79,80]. Recent findings have thrown more light on this phenomenon. In strabismic animals, synchrony is reduced for activity driven by the amblyopic eye, despite normal amplitudes of firing, implying a dependency on learning and normal visual processing [81••]. Both subcortical–cortical and cortico–cortical connections appear to be involved in generating synchrony. Sillito *et al.* [82•] have demonstrated feedback effects from the cortex on thalamic relay cells, providing a source

of top-down modulation through induced synchrony. Correlated firing between single neurons in the frontal cortex of monkeys can evolve extremely rapidly in the course of a behavioral task [83•], suggesting direct as well as subcortical connections. Negative correlations also develop between more distant groups; thus, concurrently activated groups of neurons can be dissociated, allowing the representation of more than one object at a time. Oscillations are most often present when synchrony is seen across separations of more than 2 mm, perhaps because they play a role in creating the synchrony [84•]. Synchrony can be achieved even for cells that are not optimally activated, as would be required for coarse coding [85•].

These new findings increase the plausibility of binding by synchrony. There continue to be skeptical voices, however, reporting failures to find evidence for oscillations or for temporal coding, particularly in monkeys [86,87,88•]. It is not yet clear exactly how a temporal tagging code combines with the rate code by which specific neurons signal the degree to which the properties to which they are tuned are present. Moreover, the oscillations observed tend to involve large areas or relatively long periods of synchrony, whereas the binding problem arises primarily in the fine detail of differentiating local objects [89].

Models of binding

A number of models have been proposed. Some use serially scanned locations to define the features to be bound; many use temporal coding to label the features that belong together. These could be complementary rather than conflicting ideas, as the first selects which features should be bound and the second proposes a way of coding the binding. Some models combine the two.

Treisman's FIT model [15] now uses three different spatially selective mechanisms to solve the binding problem: selection by a spatial attention window, inhibition of locations from feature maps containing unwanted features, and top-down activation of the location containing the currently attended object. A neural implementation of such a model might use 'reentrant' connections to visual areas V1 or V2 [90–93]. Damasio [91] proposes that conjunctions are specified for subsequent retrieval by units in a number of 'convergence zones' that reactivate the same areas initially involved in their sensory registration. One can apply the reentry idea to the three forms of selection proposed in FIT: reentry from parietal areas, perhaps via the pulvinar, might mediate spatial attention; reentry from specialized extrastriate areas might mediate feature-based selection; and reentry from IT might mediate object-based selection. The reentry in each case would be to area V1 or V2, depending on the precision of localization needed to ensure accurate binding in a given display. Similar ideas appear in Wolfe's [94•] computer

simulation of search, which combines parallel top-down activation of feature maps containing the target features and a serial feature integration process applied to the most active locations. The hypothesis is also compatible with Olshausen *et al.*'s [13] system of 'shifter circuits', which map signals from an attention window at the level of V1 to higher visual areas by dynamically changing the efficiency of the synapses in some pathways relative to others.

Several recent models depend on temporal synchrony to label the elements to be bound perceptually. A simulation model for the perception of three-dimensional shape [95] uses synchrony to bind axes, blobs and vertices into 'geon units' (elementary volumetric components [96]), and geon units into objects. A modified version of the model adds an initial 'static' binding of features to locations [97•]. In the model proposed by Niebuhr *et al.* [98], an area within V1 is selected for attention by imposing an oscillatory modulation from subcortical structures, which also binds the information relating to the selected object at subsequent stages of processing. Schillen and König [99•] include desynchronizing connections to achieve the segregation of overlapping stimuli. Each of these ideas helps solve problems arising in earlier simpler accounts. Other models combining spatial selection and binding by synchrony have been proposed (see [100,101•,102•]).

Conclusions

The ideas reviewed here display considerable convergence. Models combining conjunction detectors, spatial selection, and synchronized firing meet many of the requirements to solve the 'binding problem' in its wide variety of guises. Multiple reentrant connections between areas could mediate the interactions between grouping and binding observed in psychological studies. Further research is needed on the links between perception, memory, and response. Some memory models use different synchronies to keep several ideas active in short-term memory [103], but long-term memory for objects and events must use more permanent traces, such as binding codes in convergence zones [91]. Some flexible means is needed of connecting the output of perception to the choice of action (see [104] for evidence of a winner-take-all mechanism in motion discrimination). The strongest evidence will come when changes in neural activity are found to coincide with perceived changes in binding, perhaps in ambiguous figures or in attentional capture. Eventually, a solution to the binding problem may also throw light on the deeper problem of the nature of conscious awareness [100].

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Van Essen DC, Felleman DJ, De Yoe EA, Olavarria J, Knerim J: **Modular and hierarchical organization of extrastriate visual cortex in the macaque monkey.** *Cold Spring Harb Symp Quant Biol* 1991, 55:679–696.
2. Gulyas B, Roland PE: **Cortical fields participating in form and colour discrimination in the human brain.** *Neuroreport* 1991, 2:585–588.
3. Silverman IE, Grossman M, Galetta SL, Liu GT, Rosenquist AC, Alavi A: **Understanding human visual cortex: the role of functional imaging.** *Neuropsychiatry Neuropsychol Behav Neurol* 1995, 8:241–254.
4. Farah MJ: *Visual Agnosia: Disorders of Object Recognition and What They Tell Us About Normal Vision.* Cambridge, Massachusetts: MIT Press; 1990.
5. Humphreys GW, Riddoch MJ, Donnelly N, Freeman T, Boucart M, Muller HM: **Intermediate visual processing and visual agnosia.** In *The Neuropsychology of High-Level Vision*. Edited by Farah MJ, Ratcliffe G. Hillsdale, New Jersey: Lawrence Erlbaum; 1993:63–101.
6. Graham N: *Visual Pattern Analyzers.* New York: Oxford University Press; 1989.
7. Cavanagh P: **Reconstructing the third dimension: interactions between color, texture, motion, binocular disparity, and shape.** *Comput Vision Graphics Image Processing* 1987, 37:171–195.
8. Nakayama K, Shimojo S, Ramachandran VS: **Transparency: relation to depth, subjective contours and color spreading.** *Perception* 1990, 19:497–513.
9. Stoner GR, Albright TD: **Image segmentation cues in motion processing: implications for modularity in vision.** *J Cogn Neurosci* 1993, 5:129–149.
10. Haxby JV, Grady CL, Horwitz B, Salerno J, Ungerleider LG, Mishkin M, Schapiro M, Rapoport SI: **Dissociation of object and spatial processing pathways in human extrastriate cortex.** In *Functional Organization of the Human Visual Cortex*. Edited by Gulyas B, Ottoson D, Roland PE. Oxford: Pergamon Press; 1993:329–340.
11. Ungerleider LG, Mishkin M: *Two Cortical Visual Systems.* Cambridge, Massachusetts: MIT Press; 1982.
12. Barlow HB: **Single units and cognition: a neuron doctrine for perceptual psychology.** *Perception* 1972, 1:371–394.
13. Olshausen BA, Anderson CH, Van Essen DC: **A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information.** *J Neurosci* 1993, 13:4700–4719.
14. Treisman A, Gelade G: **A feature integration theory of attention.** *Cogn Psychol* 1980, 12:97–136.
15. Treisman A: **The perception of features and objects.** In *Attention: Selection, Awareness and Control: A Tribute to Donald Broadbent*. Edited by Baddeley A, Weiskrantz L. Oxford: Clarendon Press; 1993:5–35.
16. Wolfe JM, Cave KR, Franzel SL: **Guided search: an alternative to the feature integration model for visual search.** *J Exp Psychol [Hum Percept Perform]* 1989, 15:419–433.
17. Milner P: **A model for visual shape recognition.** *Psychol Rev* 1974, 81:521–535.
18. Abeles M: *Local Cortical Circuits: An Electrophysiological Study.* Berlin: Springer-Verlag; 1982.
19. Singer W, Gray CM: **Visual feature integration and the temporal correlation hypothesis.** *Annu Rev Neurosci* 1995, 18:555–586.
•• An excellent detailed review of the evidence supporting the temporal correlation account of feature binding.
20. McCollough C: **Color adaptation of edge-detectors in the human visual system.** *Science* 1965, 149:1115–1116.
21. Tanaka K: **Neuronal mechanisms of object recognition.** *Science* 1993, 262:685–688.
22. König P, Engel AK: **Correlated firing in sensory-motor systems.** *Curr Opin Neurobiol* 1995, 5:511–519.
23. Von der Malsburg C: **Binding in models of perception and brain function.** *Curr Opin Neurobiol* 1995, 5:520–526.
24. Treisman A: **Features and objects: the fourteenth Bartlett Memorial Lecture.** *Q J Exp Psychol [A]* 1988, 40:201–237.
25. Mozer M: *The Perception of Multiple Objects: A Connectionist Approach.* Cambridge, Massachusetts: MIT Press; 1991.
26. Treisman A, Schmidt H: **Illusory conjunctions in the perception of objects.** *Cogn Psychol* 1982, 14:107–141.
27. Treisman A, Paterson R: **Emergent features, attention and object perception.** *J Exp Psychol [Hum Percept Perform]* 1984, 10:12–21.
28. Prinzmetal W, Presti DE, Posner MI: **Does attention affect visual feature integration?** *J Exp Psychol [Hum Percept Perform]* 1986, 12:361–369.
29. Treisman A, Gormican S: **Feature analysis in early vision: evidence from search asymmetries.** *Psychol Rev* 1988, 95:15–48.
30. Braun J: **Visual search among items of different salience: removal of visual attention mimics a lesion in extrastriate area V4.** *J Neurosci* 1994, 14:554–567.
• The author equated the difficulty of search when the target was more salient than the non-targets and when it was less salient by reducing the exposure durations for the more salient. The addition of a foveal attention task nevertheless produced a much larger reduction in performance for the less salient stimuli, suggesting that different mechanisms are involved rather than simply a difference in difficulty for a shared mechanism.
31. Schiller PH, Lee K: **The role of the primate extrastriate area V4 in vision.** *Science* 1991, 251:1251–1253.
32. Kahneman D, Treisman A, Gibbs B: **The reviewing of object files: object-specific integration of information.** *Cogn Psychol* 1992, 24:175–219.
33. Cohen A, Ivry RB: **Illusory conjunctions as a function of distance between objects inside and outside the focus of attention.** *J Exp Psychol [Hum Percept Perform]* 1990, 16:317–331.
34. Prinzmetal W: **Visual feature integration in a world of objects.**
•• *Curr Directions Psychol Sci* 1995, 4:90–94.
A review of earlier findings suggesting that binding is constrained by perceptual and conceptual grouping of elements. Illusory conjunctions occur more often, although not exclusively, within groups, suggesting a top-down component to feature integration.
35. Prinzmetal W: **Principles of feature integration in visual perception.** *Percept Psychophys* 1981, 30:330–340.
36. Prinzmetal W, Keyser B: **A functional theory of illusory conjunctions and neon colors.** *J Exp Psychol [Gen]* 1989, 118:165–190.
37. Baylis G, Driver J, McLeod P: **Movement and proximity constrain miscombinations of colour and form.** *Perception* 1992, 21:201–218.
38. Prinzmetal W, Hoffman H, Vest K: **Automatic processes in word perception: an analysis from illusory conjunctions.** *J Exp Psychol [Hum Percept Perform]* 1991, 17:902–923.
39. Ivry RB, Prinzmetal W: **Effect of feature similarity on illusory conjunctions.** *Percept Psychophys* 1991, 49:105–116.
40. Prinzmetal W, Henderson D, Ivry R: **Loosening the constraints on illusory conjunctions: assessing the roles of exposure duration and attention.** *J Exp Psychol [Hum Percept Perform]* 1995, 21:1362–1375.
Experiments showing that illusory conjunctions (ICs) can occur between peripheral colored letters even with long exposures and without a competing attention task, when subjects fixate centrally. Thus, binding errors can be caused either by divided attention or by poor spatial resolution in peripheral vision. The paper also outlines a technique for assessing the expected IC rates from the observed proportions of different types of errors, given different assumptions about the reality of the binding problem. Models that attribute ICs to guesses could not account for the data, implying the reality of binding failures.
41. Tsai Y, Meiran N, Lavie N: **The role of attention in illusory conjunctions.** *Percept Psychophys* 1994, 55:350–358.
• This paper purported to test the effect of attention on the formation of ICs, and claimed to find little support. However, the conclusions seem questionable, as the methods used depend on unlikely assumptions about the

control of attention: for example, the authors assume that attention can be selectively allotted to two separated digits within 160 ms exposures, without encompassing three items between the digits, and that the validity of a spatial cue determined attention when their results in fact show very little effect of validity.

42. Navon D, Ehrlich B: **Illusory conjunctions: does inattention really matter?** *Cogn Psychol* 1995, 29:59–83.
 43. Lawrence DH: **Two studies of visual search for word targets with controlled rates of presentation.** *Percept Psychophys* 1971, 10:85–89.
 44. Intraub H: **Illusory conjunctions of forms, objects, and scenes during RSVP search.** *J Exp Psychol [Hum Percept Perform]* 1989, 11:431–442.
 45. Keele SW, Cohen A, Ivry R, Liotti M, Yee P: **Tests of a temporal theory of attentional binding.** *J Exp Psychol [Hum Percept Perform]* 1988, 14:444–452.
 46. Fahle M, Koch C: **Spatial displacement, but not temporal asynchrony, destroys figural binding.** *Vision Res* 1995, 35:491–494.
- The authors used an ambiguous illusory contour figure to test whether dominance is determined by spatial alignment or by temporal synchrony. Spatial alignment was clearly dominant; substantial temporal asynchronies had no effect. Therefore, if binding is achieved by temporal synchrony, it must be internally generated, not externally paced.
47. Rock I, Nijhawan R, Palmer S, Tudor L: **Grouping based on phenomenal similarity of achromatic color.** *Perception* 1992, 21:779–789.
 48. He ZJ, Nakayama K: **Surfaces versus features in visual search.** *Nature* 1992, 359:231–233.
 49. Enns J, Rensink RA: **Preattentive recovery of three-dimensional orientation from line drawings.** *Psychol Rev* 1991, 98:335–351.
 50. Donnelly N, Humphreys GW, Riddoch MJ: **Parallel computation of primitive shape descriptions.** *J Exp Psychol [Hum Percept Perform]* 1991, 17:561–570.
 51. Schneider W, Shiffrin RM: **Controlled and automatic human information processing. I. Detection, search and attention.** *Psychol Rev* 1977, 84:1–66.
 52. Treisman A, Vieira A, Hayes A: **Automaticity and preattentive processing.** *Am J Psychol* 1992, 105:341–362.
 53. Wang QQ, Cavanagh P, Green M: **Familiarity and pop-out in visual search.** *Percept Psychophys* 1994, 56:495–500.
 - Search for an unfamiliar item (mirror imaged N or Z) among familiar items (N or Z) appears to be parallel whereas the reverse is serial, suggesting that a deviating item in a homogeneous field of familiar items can be detected without focusing attention. Detector templates for familiar letters may develop through extensive experience, and by-pass the binding of parts that is required for the perception of unfamiliar forms.
 54. Fujita I, Tanaka K, Ito M, Chang K: **Columns for visual features of objects in monkey inferotemporal cortex.** *Nature* 1992, 360:343–346.
 55. Miyashita Y: **Inferior temporal cortex: where visual perception meets memory.** *Annu Rev Neurosci* 1993, 16:245–263.
 56. Nakayama K, Silverman GH: **Serial and parallel processing of visual feature conjunctions.** *Nature* 1986, 320:264–265.
 57. Treisman A, Sato S: **Conjunction search revisited.** *J Exp Psychol [Hum Percept Perform]* 1990, 16:459–478.
 58. Cohen A: **Asymmetries in visual search for conjunctive targets.** *J Exp Psychol [Hum Percept Perform]* 1993, 19:775–797.
 59. Julesz B: **Towards an axiomatic theory of preattentive vision.** In *Dynamic Aspects of Neocortical Function*. Edited by Edelman GM, Gall WE, Cowan M. New York: Neurosciences Research Foundation; 1984:585–612.
 60. Wolfe JM, Yu KP, Stewart MI, Shorter AD, Friedman-Hill SR, Cave KR: **Limitations on the parallel guidance of visual search: color x color and orientation x orientation conjunctions.** *J Exp Psychol [Hum Percept Perform]* 1990, 16:879–892.
 61. Wolfe JM, Friedman-Hill SR, Bilsky AB: **Parallel processing of part-whole information in visual search tasks.** *Percept Psychophys* 1994, 55:537–550.
 62. Wolfe JM, Chun MM, Friedman-Hill S: **Making use of texton gradients: visual search and texton grouping exploit the same parallel processes in different ways.** In *Early Vision and Beyond*. Edited by Papathomas T. Cambridge, Massachusetts: MIT Press; 1994:189–198.
 - Virtual triangles were defined by three unique elements in a multi-element array. It was easy to judge the orientation of the triangle when the vertices were defined by unique colors or orientations, but impossible when they were defined only by conjunctions of color and orientation, even in displays in which any one of the three conjunctions could be detected in parallel. Apparently, we are unable to form a perceptual group from objects defined only by conjunctions of features, suggesting that grouping must precede rather than follow the binding operation.
 63. Duncan J, Humphreys GW: **Visual search and stimulus similarity.** *Psychol Rev* 1989, 96:433–458.
 64. Humphreys GW, Muller HJ: **Search via recursive rejection (SERR): a connectionist model of visual search.** *Cogn Psychol* 1993, 25:43–110.
 65. Foster DH, Ward PA: **Asymmetries in oriented-line detection indicate two orthogonal filters in early vision.** *Proc R Soc Lond [Biol]* 1991, 243:75–81.
 66. Wolfe JM, Friedman-Hill SR, Stewart MI, O'Connell KM: **The role of categorization in visual search for orientation.** *J Exp Psychol [Hum Percept Perform]* 1992, 18:34–49.
 67. Treisman A: **Search, similarity and the integration of features between and within dimensions.** *J Exp Psychol [Hum Percept Perform]* 1991, 27:652–676.
 68. Yantis S: **Multielement visual tracking: attention and perceptual organization.** *Cogn Psychol* 1992, 24:295–340.
 69. Yantis S, Gibson BS: **Object continuity in apparent motion and attention.** *Can J Exp Psychol* 1994, 48:182–204.
 - Reviews evidence for shared mechanisms in attentional capture (the involuntary allocation of attention to the onset of a new object), and in the perceptual organization of a Ternus apparent motion display. The switch in the Ternus display between seeing one object move around the other and seeing two objects moving as a group may reflect a change in binding and the initiation of a new perceptual object token.
 70. Arguin M, Cavanagh P, Joannette Y: **Visual feature integration with an attention deficit.** *Brain Cogn* 1994, 24:44–56.
 - Patients with left brain damage were divided into those who showed little benefit from a spatial cue in responding to a contralesional stimulus, and those who showed normal benefits. When tested in feature search, the two groups were equivalent, but in a conjunction search task, those with poor spatial attention reported many more ICs than those with normal spatial attention, supporting a link between feature integration and spatial attention.
 71. Cohen A, Rafal RB: **Attention and feature integration: illusory conjunctions in a patient with parietal lobe lesions.** *Psychol Sci* 1991, 2:106–110.
 72. Friedman-Hill SR, Robertson LC, Treisman A: **Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions.** *Science* 1995, 269:853–855.
 - A patient with bilateral parietal lesions made a large number of ICs between simultaneously (but not sequentially) presented objects, in addition to showing the typical loss of the ability to localize visual stimuli and the marked simultanagnosia characteristic of Balint's syndrome. The combination of deficits is consistent with the idea that feature binding and object individuation depend on an intact representation of space.
 73. Petersen SE, Corbetta M, Miezin FM, Shulman GL: **PET studies of parietal involvement in spatial attention: comparison of different task types.** *Can J Exp Psychol* 1994, 48:319–338.
 - Shows PET activation in superior parietal cortex, which is selective to shifts of spatial attention. Parietal activation accompanied a task in which subjects tracked an asterisk across a sequence of locations (either passively or under voluntary control), and one in which they searched for a conjunction target, but did not appear in maintained attention tasks that did not require spatial shifts. Supports the idea that spatial attention is involved in binding and that the parietal area is involved in its control.
 74. Roland PE, Gulyas B: **Visual memory, visual imagery, and visual recognition of large field patterns by the human brain: functional anatomy by positron emission tomography.** *Cereb Cortex* 1995, 5:79–93.
 75. Luck SJ, Hillyard SA: **Spatial filtering during visual search: evidence from human electrophysiology.** *J Exp Psychol [Hum Percept Perform]* 1994, 20:1000–1014.
 - Measured event-related potentials in search. A negative component (N2pc) at around 200–300 ms was observed over contralateral posterior scalp in conditions when distractors were present and would interfere with target processing if they were not suppressed. The N2pc seems to reflect a spatial filtering operation in extrastriate cortex, beginning around 175 ms after stimulus onset.
 76. Luck SJ, Hillyard SA: **The role of attention in feature detection and conjunction discrimination: an electrophysiological analysis.** *Int J Neurosci* 1995, 80:281–297.
 -

A reduced P1 response from extrastriate cortex was evoked by probe stimuli in locations previously occupied by distractors immediately following a conjunction but not a feature search display. Suggests that, once invoked, the spatial filter affects processing as early as 100 ms after stimulus presentation.

77. Von der Malsburg C, Schneider W: **A neural cocktail-party processor.** *Biol Cybern* 1986, 54:29–40.
78. Singer W: **Synchronization of cortical activity and its putative role in information processing and learning.** *Annu Rev Physiol* 1993, 55:349–374.
79. Gray CM, König P, Engel A, Singer W: **Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties.** *Nature* 1989, 338:334–337.
80. Engel AK, König P, Singer W: **Direct physiological evidence for scene segmentation by temporal coding.** *Proc Natl Acad Sci USA* 1991, 88:9136–9140.
81. Roelfsema PR, König P, Engel AK, Sireteanu R, Singer W:
 - **Reduced synchronization in the visual cortex of cats with strabismic amblyopia.** *Eur J Neurosci* 1994, 6:1645–1655.Synchronization (but not amplitude) of responses in striate area of strabismic cats was reduced when the amblyopic eye was driven by moving gratings and bars, compared to when the normal eye received the same stimuli. Therefore, it appears that synchrony is tied to normal visual processing.
82. Sillito AM, Jones HE, Gerstein GL, West DC: **Feature-linked synchronization of thalamic relay cell firing induced by feedback from the visual cortex.** *Nature* 1994, 369:479–482.
- Offers a new demonstration of stimulus effects on synchronization, and shows how correlated firing in response to drifting gratings is induced in thalamic relay cells by feedback from the cortex. This may be a process in which "the feedback circuit searches for correlations that support the 'hypothesis' represented by a particular pattern of cortical activity and 'locks' the ensemble onto the stimulus."
83. Vaadia E, Haalman I, Abeles M, Bergman H, Prut Y, Slovin H,
 - Aertsen A: **Dynamics of neuronal interactions in monkey cortex in relation to behavioral events.** *Nature* 1995, 373:515–518.The authors studied the detailed time structure of the cross correlations between neurons in relation to different events, showing patterns of correlation that are independent of firing rates. Both positive and negative correlations evolve rapidly in relation to stimulus and behavioral events, offering the flexibility that would be needed to code changes in binding with shifts of attention.
84. König P, Engel AK, Singer W: **Relation between oscillatory activity and long-range synchronization in cat visual cortex.** *Proc Natl Acad Sci USA* 1995, 92:290–294.
- Synchronization between cells in the same area could occur without oscillations, but synchronization between cells in separated areas or different hemispheres of cat visual cortex were always accompanied by oscillations, suggesting that oscillations may play a role in achieving synchrony across separated areas.
85. König P, Engel AK, Roelfsema PR, Singer W: **How precise is neuronal synchronization?** *Neural Computation* 1995, 7:469–485.
- Raises the question of how coarse coding by populations of differently tuned neurons can be reconciled with binding by synchronization. Shows in cats that synchronization can indeed occur for both optimally and suboptimally driven neurons, and that optimally activated neurons tend to lead in phase.
86. Bair W, Koch C, Newsome W, Britten K: **Power spectrum analysis of bursting cells in area MT in the behaving monkey.** *J Neurosci* 1994, 14:2870–2892.
87. Tovee JM, Rolls ET: **Oscillatory activity is not evident in the primate temporal visual cortex with static activity.** *Neuroreport* 1992, 3:369–372.
88. Tovee MJ, Rolls ET: **Information encoding in short firing rate epochs by single neurons in the primate temporal visual cortex.** *Visual Cognition* 1995, 2:35–58.
- An analysis of the information available in the neural response to 20 different faces in the temporal lobe of monkeys (with fixation controlled) shows that much of the discrimination is present in the first 50 ms of the response, allowing little scope for temporal coding.
89. Nelson JJ: **Binding in the visual system.** In *Handbook of Brain Theory and Neural Networks*. Edited by Arbib MA. Cambridge, Massachusetts: MIT Press; 1995:157–159.
90. Edelman GM: **Group selection and phasic re-entrant signaling: a theory of higher brain functions.** In *The Mindful Brain*. Edited by Edelman GM, Mountcastle VB. Cambridge, Massachusetts: MIT Press; 1978:51–100.
91. Damasio AR: **Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition.** *Cognition* 1989, 33:25–62.
92. Zeki S: *A Vision of the Brain*. Oxford: Blackwell Scientific Publications; 1993.
93. Tononi G, Sporns O, Edelman G: **Reentry and the problem of integrating multiple cortical areas: simulation of dynamic integration in the visual system.** *Cereb Cortex* 1992, 2:310–335.
94. Wolfe JM: **Guided search 2.0: a revised model of visual search.**
 - *Psychonomic Bull Rev* 1994, 1:202–238.A thorough review of empirical data in visual search, and an elaboration of the author's earlier model of guided search, showing how the deployment of attention in many search tasks, including some for conjunctions of highly discriminable features, can be guided by earlier parallel preattentive processes.
95. Hummel JE, Biederman I: **Dynamic binding in a neural network for shape recognition.** *Psychol Rev* 1992, 99:480–517.
96. Biederman I: **Recognition by components: a theory of human image understanding.** *Psychol Rev* 1987, 94:115–147.
97. Hummel JE, Stankiewicz BJ: **An architecture for rapid, hierarchical structural description.** In *Attention and Performance*, vol XVI. Edited by Inui T, McClelland J. Cambridge, Massachusetts: MIT Press; 1996:in press.
- A modified version of the authors' earlier simulation model for the perception of three-dimensional shape, adding a mechanism for 'static' binding of each feature to its location. This gives a viewpoint-sensitive estimate of object identity before a dynamic binding process generates a viewpoint-independent structural description through temporal synchrony. This hybrid model, though more complex than others, finds support in a number of empirical findings in human object perception.
98. Niebuhr E, Koch C, Rosin C: **An oscillation-based model for the neuronal basis of attention.** *Vision Res* 1993, 33:2789–2802.
99. Schillen TB, König P: **Binding by temporal structure in multiple feature domains of an oscillatory neuronal network.** *Biol Cybern* 1994, 70:397–405.
- A simulation of binding for overlapping stimuli across separate modules coding disparity, color and orientation, using synchronizing and desynchronizing mechanisms. The desynchronizing connections between modules can break a false grouping based on one shared property when the overlapped objects differ in another property.
100. Crick F, Koch C: **Towards a neurobiological theory of consciousness.** *Semin Neurosci* 1990, 2:263–275.
101. Sajda P, Finkel LH: **Intermediate-level visual representations and the construction of surface perception.** *J Cogn Neurosci* 1995, 7:267–291.
- Describes a model that combines low-resolution topographic grouping based on proximity and similarity, with a limited capacity, high-resolution mechanism based on temporal synchrony, which determines figure-ground relations by labeling which of two adjacent areas 'owns' the bounding contour.
102. De Carvalho LA, Roitman VL: **A computational model for the neurobiological substrates of visual attention.** *Int J Biomed Comput* 1995, 38:33–45.
- A computational model in which attentional selection is achieved by 'bursting' activity of neurons in V2, which inhibits competing pathways in V4, thus giving preference to the relevant object at later processing stages.
103. Lisman JE, Idiart MAP: **Storage of 7±2 short-term memories in oscillatory subcycles.** *Science* 1995, 267:1512–1515.
104. Salzman CD, Newsome WJ: **Neural mechanisms for forming a perceptual decision.** *Science* 1994, 264:231–237.