Binding in Models of Perception and Brain Function

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Summary The development of the issue of binding as fundamental to neural dynamics has made possible recent advances in the modeling of difficult problems of perception and brain function. Among them is perceptual segmentation, invariant pattern recognition and one-shot learning. Also, longer-term conceptual developments that have led to this success are reviewed.

Introduction

The topic of binding is central to the attempt to formulate neural dynamics on the level of *interacting groups of neurons* in analogy to the *interacting single neurons* of the classical view. This attempt is motivated by the necessity to mend a number of fundamental conceptual difficulties with the single neuron as organizing unit, a point of view most concretely formulated in the framework of Neural Networks [1]. One of the benefits of this transition would be the introduction of symbolic processing, the lack of which in Neural Networks has been repeatedly criticised [2], while preserving the capabilities for autonomous organization which are the strength of Neural Networks. As another benefit, this transition could help to break the learning time barrier of Neural Networks [3] which stands in stark contrast to the ability of animials to learn from single scenes. This barrier is created by the tremendous ambiguity faced by synaptic plasticity mechanisms that indiscriminately associate all simultaneously active neurons. The ambiguity is decisively reduced if association is an affair taking place on the level of a small number of perceptual groups that have been singled out by a potent binding mechanism.

The binding problem is most succinctly illustrated by an example introduced originally by Rosenblatt [4]. A hypothetical perceptual system consists of just four neurons, able to respond to the presence in arbitrary retinal position of (i) a triangle and (ii) a square, as well as the presence of arbitrary objects (iii) in the upper visual field and (iv) in the lower visual field. Now assume that the system is to diagnose the presence of a square in the upper visual field. In the classical Neural Networks solution, an output neuron would just have to detect simultaneous activity in cells (ii) and (iii). It would be fooled by a situation in which a triangle is in the upper visual field and a square in the lower and all four perceptual neurons active. This type of ‘conjunction error’ can be induced in humans if they are given insufficient viewing time [5]. The difficulty arises from the fact that all feature cells of several simultaneously perceived objects fuse into one indistinct whole (the ‘superposition catastrophe’ of [6]). Thus, a binding mechanism is required to group feature cells according to objects and to prevent illusory conjunctions from eliciting responses. Rosenblatt’s example is deceptively simple; in more realistic situations large numbers of elementary features have to be bound into groups. Now, the number of sets of realistic order (‘order’ being the number of neurons in a group) is astronomically large. This ‘combinatorial explosion’ precludes any exhaustive representation of groups by physical entities, like combination-coding neurons or pre-wired non-overlapping groups of neurons.

This review reports on recent advances in the modeling of important aspects of perception and brain function with the help of binding mechanisms. Being a first review of binding as a theoretical issue, it also cites earlier key papers.

Requirements for the binding mechanism.

The currently raging discussion about necessity and nature of a binding mechanism in the nervous system is often blurred by vagueness about the functional requirements to be met. Here are some of them.

1) Dynamic generation of binding. Each perceptual scene requires its own new grouping, as even a single object is reflected in an infinite variety of changing feature combinations. The binding mechanism has to pick up the relevant perceptual information to single out appropriate groups from the large background of possible combinations of active neurons, and has to physically implement these groups as functional entities.
2) Storage of newly created binding structures for future reference.
3) Retrieval of such stored binding structures.
4) Control of neural activation by binding structures (to prevent firing in response to illusory conjunctions, for instance).
5) Specific interaction of binding structures (the very essence of neural group dynamics).
6) Acceleration of learning by proper constraint of long-term synaptic plasticity by binding patterns.

Attempts to solve or avoid the binding problem.

The most common attempt to avoid the binding problem is based on combination coding cells. Whatever the intended interaction of groups of cells, these interactions can probably always be reflected back onto the level of appropriately connected single neurons. Reliance on single cells is most radically formulated in Barlow's dogma [7] according to which a decision of an animal can always be traced back to the firing decision of a single 'pontifical' cell. Although this view has been put on an experimental basis (e.g., in [8*]), it creates more problems than it solves. The most pressing of these is the question of how the organism creates and empowers these decisive neurons. Less radical versions content themselves with showing experimentally that sizeable chunks of structure are represented by single 'cardinal' cells (for examples and a review see [9]). However, the hydra cannot be slain. All neurons are combination-coding, but not all combinations can be coded by neurons, the number of combinations growing faster than the number of neurons. Ultimately, groups will have to speak for themselves. Whereas groups of neurons can be created dynamically (see below) combination-coding neurons cannot.

The classical theory of Neural Networks has no concept of group dynamics and ignores the binding problem, although it always had to deal with it implicitely. It emphasizes either the entire set of simultaneously active neurons, like Hebb's assembly or the vector of neural activities in Associative Memory, or again single neurons. The weakness of Associative Memory is the monolithic way in which it treats the set of all active neurons. This is directly responsible for its gross lack of generalization to sensory scenes that are related on the level of intermediate groups but differ in global structure.

Much effort has been spent to solve the problem of 'variable binding' [10–16]. This problem arises in the context of logic or rule-based systems and is a special case of the more general problem of binding discussed here. (In fact, the term binding is derived from this special application.) Most of the examples cited are either limited to binary binding or are based on tags that can be passed along connections (and are thus forerunners of temporal binding, see below).

In layered structures [1] statistical training methods are used to avoid the binding problem, creating appropriate combination-coding cells and suppressing connections that would cause conjunction errors. The price paid is that a network is limited to a single context and that a task can only be solved after an extended training period, which is prohibitive for many tasks of realistic size. The ultimate reason for long training periods is that in layered neural networks the grouping information that is potentially available in single stimuli is wasted (before appropriate task-adapted combination coding cells are developed) and must be tediously recovered from the statistics of many stimuli. The 'dendritic fingers' of, e.g., [17], which replace combination-coding neurons by combination-coding dendritic patches, fall under the same criticism.

The single-context constraint of neural networks has been tremendously alleviated by expert-selector networks [18] in which a stimulus is first classified according to its context (or task type) by a selector network, which then switches in the appropriate monocontextual expert network. In essence, this is a crude way of switching between different binding structures, which are implict in the expert networks as combination-coding cells.

Connector cells [19,20] are more explicitly directed at solving a binding problem (binding corresponding points in two isomorphic fields), but they have only been applied to binary binding in the correspondence problem. Also, synaptic projection patterns that are controlled presynaptically [21*], or 'three-terminal-devices' [10] have yet to be applied to higher order binding problems. All these require for their function very specific wiring patterns the ontogenesis of which may be a problem.

Binding by temporal synchrony of signals.

According to the temporal binding hypothesis, groups of cells are bound to each other by signal synchrony on the time scale of fractions of a second. The activity process of the brain is thus viewed as a rapid sequence of 'micro states,' each defined by the simultaneous activity of a set of neurons which are thereby bound together.

Appropriate neural signal fluctuations down to a millisecond range in cortex and thalamus are a familiar phenomenon. However, neural theory traditionally ignored these fluctuations, and neurophysiology interpreted them as noise to be suppressed by trial averaging. The ultimate origin of these stochastic signal fluctuations is not clear. There is evidence, however, that they are not due to unstructured noise within single cells and that cortical and subcortical circuitry is able to hand down temporal fine structure over many synaptic generations (see [22*,23*]).

Whereas dayly experience tells us that our brain sorts out different contexts on a larger scale by subdividing time and sequentially switching attention between topics, extension of this concept to a finer scale both in time and in breadth of context has met with considerable resistance in the scientific community. A systematic extension of the framework of Neural Networks by temporal binding has been proposed in [24,25,6], although earlier references to temporal binding can be identified [26,27].

It has been suggested that signal fluctuations are an insignificant epiphenomenon of brain dynamics. Although this is not very convincing — if signal fluctuations had no useful function, they could be trivially suppressed [28*], and more peripheral neurons demonstrate this by firing with exquisite regularity and precision —, only long sequences of experiments will be able to dispell doubts about the functional significance of signal correlations. The experimental evidence compiled so far (see [29*] for review) is compatible with the temporal binding hypothesis, but simultaneous neurophysiological and psychophysical experiments will be required, analogously to [8*].

There are several arguments commending the idea of binding by temporal signal correlations. Wherever required, groups of arbitrary order can be instantly formed (see the section on segmentation below), stored and retrieved, and no additional 'hardware' is required beyond appropriate adjustments in the dynamical parameters of the existing network. Signal correlations are naturally produced by common or correlated input or by direct connections between the cells concerned. Temporal correlations can be evalutated in a natural way and have strong dynamical effects in nervous tissue due to the fact that neurons are coincidence detectors, although there is some disagreement over neural integration times [30*]. Due to these facts, temporal binding can be considered as readily available and of ubiquitous functional potential.

A marked disadvantage of temporal binding arises from the limited bandwidth of neural signals. The binding structures that can be expressed within typical reaction times of fractions of a second cannot be very differentiated, since all groups to be bound have to be activated sequentially. However, reaction times are short only in stereotypical tasks, and it is commonly experienced that the flexibility required in unfamiliar situations is obtained only for the price of considerable delays. It is therefore quite conceivable that time-consuming temporal binding is used by the brain only as a bootstrapping mechanism for make-shift solutions in novel situations (some indication of this is given in [31]), and that as soon as a certain binding structure has shown its long-term value, it is frozen into less flexible but faster and more capacious special circuitry. Candidate structures for this are the combination-coding or connector cells, dendritic patches or presynaptic control structures reviewed above.

Applications.

The principal arguments for the existence of a general dynamical binding mechanism is the success of concrete models and the solution of old conceptual difficulties on its basis. Some of these results are reviewed here.

Segmentation. The process of sensory segmentation, also called figure-ground separation, takes account of the fact that our environment is composed of objects and processes that have fairly stable internal structure and are independent of each other (see [32] for an introduction to the problem). To an overwhelming extent, learning is possible due to the fact that these pieces of stable structure do recur from scene to scene. The psychophysics of the phenomenon of visual segmentation was at the focus of the Gestalt movement (for a review see [33]). On the other hand, segmentation is to this day a largely unsolved problem in computer vision [34]. By its very nature, sensory segmentation is a binding issue, and in the view of many it is just plain identical with the binding issue. The proposal that the brain solves the problem with the help of temporal synchrony was made in [27,24]. The experimental evidence in the visual cortex for oscillatory signals that might form the basis for segmentation (reviewed in [29*]) has triggered a flurry of efforts to model these oscillations [35–40], to cite but a few. Whereas these models concentrate more on the neurobiology of the creation and synchronization of signal oscillations while paying little attention to the segmentation problem as such, another set of models is more concerned with just using correlated signals, oscillatory or otherwise, to solve the segmentation problem [32, 41–50]. Unfortunately almost all of this work is based on synthetic data, but the near future will see a number of papers on the segmentation of real images (for an early example see [51*]) or auditory signals. The challenge here is to properly integrate submodalities (motion, depth, texture, color, .. for the visual modality). Segmentation by temporal binding ideally illustrates and implements the above requirements 1 (dynamic generation): each perceived object elicits its own, unique new combination of features); 4 (control of activation) and 6 (learning): neurons in different segments are not synchronized and they therefore do not cooperate in firing third neurons and are kept from being associated by synaptic plasticity.

Storage and retrieval of superimposed binding patterns is modeled in [25,52], even for the extreme case where the memory traces overlap in all their neurons and differ just in their internal binding, illustrating the above requirements 2 and 3 (storage and retrieval). This capability is an essential component in the following models of invariant recognition.

Invariant representation and recognition of objects and patterns is an important function of perception. It is required as a basis for associations that generalize over the infinite variety of sensory patterns that are created by any one external object or process. In vision, this variety is due to changes in retinal position, size, orientation, perspective, object deformation, illumination, background, partial occlusion and noise. Most theories assume that invariance is achieved with the help of a decomposition of sensory patterns into elementary features and wiring patterns that lead to the activation of central feature neurons that are unaffected by the variations to be generalized over [4]. From this principle, a binding problem arises. Since generalization is performed independently for each feature, information about neighborhood relations and relative position, size and orientation is lost. This lack of information can lead to the inability to distinguish between patterns that are composed of the same set of invariant features, though in different relative position, size or orientation. On a coarser level, the same binding problem arises whenever a stimulus is separately represented according to shape ('what') and position ('where'), each generalizing over variations in the other. If several objects are present, a binding ambiguity arises, as discussed above [4]. The conflict between generalization and unambiguous feature relations can be resolved with the help of temporal signal correlations which are created on an early level of processing — where feature relations are still explicitly available — and which is handed on to the invariant feature neurons [24,53–58,59*]. Some of these models posit the existence of rapid reversible synaptic plasticity [24] as a medium for the storage, retrieval and processing of complicated binding structures. These models comply with requirements 1 (dynamic generation): specific bindings between corresponding neurons in the primary sensory domain and the memory domain are created anew for each stimulus pattern, even for the first pattern that ever hits the system [60*]; 2 and 3 (storage and retrieval), which take place in the memory domain; 4 and 5 (control of activation and specific interaction), essential for selective activation of memory traces on the basis of their topographical binding structure; and 6 (rapid learning) in that patterns can be recognized after one-shot learning.

Rapid learning. It is a great problem for Neural Networks as a paradigm for learning in the brain that they require unrealistic numbers of examples as soon as the input domain grows beyond a few hundred neurons [3]. In contrast, the above binding models for invariant pattern recognition, e.g., [56,59*], are trained by one-shot learning. Even the generalization to whole pattern classes from single examples has been demonstrated [60*]. This inspires hope that binding can decisively alleviate the learning time problem (requirement 6 above) also in broader contexts, although much more work needs to be done.

Other applications. The applications of (temporal) binding thus far discussed are but the tip of an iceberg and many more fruitful applications to problems of brain function are to be expected if early examples are taken as an indication: the more general application of binding mechanisms to the problem of scene representation is discussed in [61,62*]; applications to the problems of logical reasoning and language processing are introduced in [63,64*]; a theory of cortex as a compositional cognitive system is presented in [65*]; and for a discussion of the relevance of binding to the consciousness issue see [66,67].

Conclusion

We are in the middle of a scientific revolution the result of which will be the establishment of binding as a fundamental aspect of the neural code, on a par with the classical rate code. If successful, this revolution will lead to fruitful experimental paradigms beyond the current focus on the single cell, to more coherent concepts of brain function and perception and to the solution of many of the remaining problems in terms of explicit models. Binding mechanisms are an integral aspect of all known symbol systems — except in our current neural brain theories! All graphical symbols, for instance, are grouped by spatial arrangement, computer data structures rely on neighborhood in address space. However, in distinction to these passive symbol systems, the binding issue is complicated for the brain, as it has to rely on autonomous organization. As reviewed, some of this has by now been demonstrated in first concrete models. Much remains to be done, though, both on the theoretical and on the experimental side.

As to the binding mechanism based on temporal signal correlations, its great advantage — being undemanding in terms of structural requirements and consequently ubiquitously available and extremely flexible — is offset by its quantitative limitations due to the limited bandwidth of neural signals. However, even if only a tiny fraction of all bindings in the nervous system are handled by temporal signal synchrony it may still play a central role for the brain's function, forming the basis for the tremendous flexibility that is one of its most puzzling aspects.

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