

Flexible cognitive resources: competitive content maps for attention and memory

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The brain has finite processing resources so that, as tasks become harder, performance degrades. Where do the limits on these resources come from? We focus on a variety of capacity-limited buffers related to attention, recognition, and memory that we claim have a two-dimensional ‘map’ architecture, where individual items compete for cortical real estate. This competitive format leads to capacity limits that are flexible, set by the nature of the content and their locations within an anatomically delimited space. We contrast this format with the standard ‘slot’ architecture and its fixed capacity. Using visual spatial attention and visual short-term memory as case studies, we suggest that competitive maps are a concrete and plausible architecture that limits cognitive capacity across many domains.

Understanding cognitive capacity limitations

When observers are asked to deal with too much information, too many tasks, or too many targets processing becomes slower or less accurate. Why? A typical answer is that the brain has only a finite ‘capacity’ for processing and, because these limited ‘resources’ are spread more thinly with increased task ‘load’, speed and accuracy must be sacrificed (e.g., [1–3]). Unfortunately, words such as ‘capacity’, ‘resources’, and ‘load’ relabel the effect without explaining why it occurs. Despite this circularity, the concept of limited resources has become central to cognitive research. So, what is the resource? Where does it reside and why is it limited? Can we get more of it?

There are a number of possible resources and we focus here on the temporary buffers that hold information for analysis and control, specifically buffers for attention and working memory, whose capacity will directly determine the complexity and quantity of processing that people can manage. Map representations (Box 1), found widely throughout many brain areas [4], are a likely format for these buffers. We suggest that competitive interactions (e.g., [5,6]) between items within these map representations provide a direct explanation of the capacity limits in cognition. In this two-dimensional ‘map’ architecture, individual items must compete for actual, bounded space.

This architecture defines a flexible resource that is physical rather than metaphorical: it is cortical real estate. Our goal is to describe this identifiable, measurable, and accessible ‘space’ as a concrete explanation for phenomena such as load and capacity. We will contrast this map

Glossary

Binding problem: independent processing of different types of information (e.g., color vs motion) requires that the information be later unified (e.g., for visual recognition). Typical solutions to this problem rely on linking features by spatial or temporal proximity.

Dorsal visual stream: a pathway of visual processing that projects primarily to the parietal lobe, associated with spatial attention and the guidance of action.

Ensemble processing: global processing of a set of objects, resulting in abstracted or statistical representations of the set.

Feature integration theory: a proposed solution to the binding problem, which suggests that visual features of an object (e.g., color, shape, motion) that are processed in spatially segregated maps are integrated when attention is directed to the object’s location [90].

Frontal eye fields: retinotopically organized maps in the primate frontal cortex, involved in the control of eye movements and attention.

Map architecture: a model of cognitive resources that proposes two-dimensional representations of globally or locally (clustered) continuous information spaces. Map capacity is flexibly determined by the number and distribution of activity ‘peaks’ within the space.

Multiple object tracking: paradigm designed by [99] that tests multifocal selection of moving objects.

Semantic identification: recognition of an object as a specific instance of a general class.

Slot architecture: a model of cognitive resources that proposes a fixed number of ‘slots’ for storing items, with an independent information limit on each slot.

Somatotopy: topographic mapping of body areas to spatially correlated locations in a cortical map.

Supramodal map: higher-level cortical map that transcends particular sensory modalities (e.g., vision, tactile, audition) of environmental stimuli

Surround inhibition: the suppressive effect of an activity ‘peak’ on a map on neighboring areas of the map.

Temporal neural synchrony: proposed temporal solution to the binding problem, in which spatially segregated brain regions synchronize activity related to a given item into a specific phase cycle.

Ventral visual stream: set of hierarchical, retinotopically organized maps from the primary visual cortex to the temporal cortex, with a strong role in object recognition.

Visual search: a perceptual task in which an observer scans a visual scene for a particular object or feature (target) among other objects and features (distractors).

Visual hemifield: half of a visual scene, usually split vertically into left and right hemifield. This partition arises from the branching of the optic nerve at the optic chiasm, such that information from the left half of a visual scene is initially processed in the right hemisphere of the brain and vice-versa.

Visual short-term memory (VSTM): capacity-limited memory that stores abstracted versions of visual sensory input for several seconds.

Visual spatial attention: selective amplification of some locations, features, or objects in the visual field.

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Box 1. Map representations

In the brain, a region can be considered a 'map' if it has a coherent spatial organization where the preferred stimuli of neurons change smoothly from one location to the adjacent one. Because of the layering of neural architecture, cortical maps are constrained to have one or two dimensions of global organization, either continuous dimensions, such as space for the FEF (a) or less systematic clusters (e.g., patches of related shape identities). Many maps also have local embedded dimensions. The retinotopic visual field map of area V1 (b) is globally spatially organized, with embedded dimensions including orientation, eye of origin, spatial frequency, and color (see [4]). A motion map (MT) differs in the embedded dimensions (motion direction, direction polarity; see [66]). A tonotopic frequency map of incoming auditory information is represented in primary auditory cortex (Heschl's Gyrus), organized by frequency ([67]), with evidence for inhibitory surrounds within that space ([68]) Figure 1.

Some maps do not show obvious continuous dimensions but do show local clusters of related values. For example, shape maps (c) are proposed in area TE of the ventral visual stream (image adapted from [69]), representing as yet unknown feature dimensions, including progressive transitions in face space [70]. There may be similar 'clustered' maps for other types of representations, including

phonemes (posterior superior temporal gyrus [57]) and principal components of odor space [71,72].

Other maps represent action plans and goals, serving not as a sensory representation but as 'source code' that underlies behavior [73]. One example is the explicitly spatial eye movement maps described in Figure 2a. There is also evidence for 'clustered' motor plan maps (d). In monkeys, precentral motor representations that are coarsely somatotopically organized (e.g., hand movement areas tend to be near finger movement areas) also contain clusters of different motor plans related to the same body area [74] and there is also evidence for inhibitory surrounds in that space [75].

Map representations offer a rich set of computational advantages ([73], but see also [76]). They allow fast parallel computation with minimized axon length between mutually relevant information [73,77]. Map addressing is error-tolerant – getting rough instructions for the carrots in a supermarket will at least get you to the vegetable section, in contrast to an almost-correct phone number which gets you nowhere. Finally, maps with shared coordinate systems benefit from straightforward cross-referencing of information, for example, for spatial representations derived from both visual and auditory information in the superior colliculus [78].

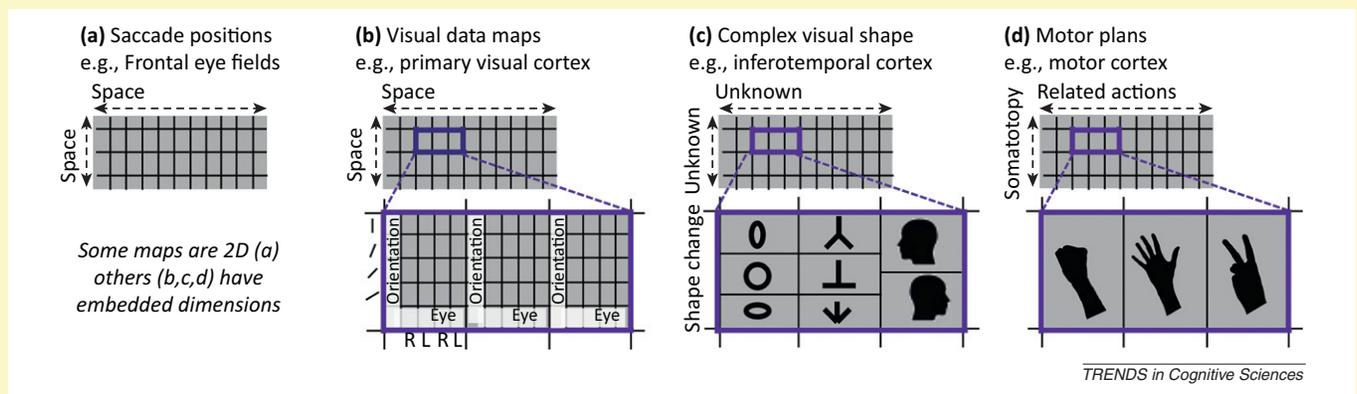


Figure 1. Examples of cortical maps.

architecture, with its focus on locations and competition within a limited space, with 'slot' architectures, which have a fixed number of places in which information can be stored.

Map vs slot architectures

In a map architecture, each position represents a value within a specific information space, such as spatial location, color, or shape. Such two-dimensional maps are widely reported in sensory and motor representations of various levels of complexity (Box 1; see [4,7], for review). The capacity of a map is flexible, limited by the space taken up by the activity profile of individual items on the map, how they interact with each other, and the spacing of the items on the map. Items interact destructively when they are close enough for their activity profiles to overlap, due to the inhibition zone that typically surrounds each activity peak [8]. These suppressive surrounds sharpen the activity profiles of single items and resolve inter-item competition – a critical step especially when unitary actions are needed (e.g., a saccade to a single location). These competitive interactions mean that map capacity is not fixed, but determined both by the number and arrangement of the items within it (Figure 1).

Previous proposals suggest that items that are cortically closer are more likely to compete with each other for representation (e.g., [5,6,8]). More recent proposals have suggested that such competitive interactions are the roots of capacity limits for tasks such as object recognition [9] and multiple object tracking [10]. Here, we suggest that these examples of inter-item competition combined with the anatomical properties underlying cortical maps provide a concrete explanation of the flexible capacity of attentional and short-term memory resources, serving as case studies for other cognitive resource limits. Representations related to more complex abilities, such as semantic identification or task control, may not be so obviously organized as a two-dimensional space (see [11–13] for discussion of alternate formats), but we will outline the capacity effects that should result if this were the case.

An alternative to the map format is a slot architecture, which stores information across a fixed number of independent locations. The location of a slot is unrelated to its contents, and serves only as an address to return to when information must be retrieved. Unlike competitive maps, the arrangement of items is irrelevant (Figure 1). Examples include characterizations of visual spatial attention (see [14], for review), as well as models of visual short-term

Box 2. The architecture of visual short-term memory

There is currently considerable debate about whether visual working memory capacity is best characterized by fixed slot or flexible resource models. Early research supported a slot architecture, in which memory was limited only by the number of objects stored, independently of the number of features stored per object [79,80]. The strong version of this claim has been challenged by a variety of empirical findings [81,82], with the current debate centered on the discovery of a tradeoff between the number of items stored and the precision of each item [38,83]. Flexible resource models predict this tradeoff, but are too flexible to firmly predict how many items can be stored and the precision with which they will be stored. Most find their support by fitting the data to a continuous function relating number of items to precision (e.g., [83–85]).

Slot models cannot account for the quantity-precision tradeoff without significant upgrades. The most straightforward modification is to construct a hybrid model, where the number of slots limits the number of objects that can be stored and the amount of some other cognitive resource determines the precision with which they can be stored [16,86]. Alternatively, the slots themselves can be treated as discrete chunks of resources, where memory can store multiple copies of objects in separate slots and then average those copies to increase the precision of a subset of item representations [15].

Although these models compete to explain the quantity-precision tradeoff function, recent research is converging on a wide range of findings that are not yet addressed by either class of model. In particular, working memory representations appear to be hierarchical and structured [87,88], contrasting with standard models that focus only on individual item capacity (which may be impossible to define even in simple displays). Such structured representations may be accommodated by a system in which the contents of memory are integrated across multiple competitive maps. An important direction for future research is to determine how multiple maps would accommodate these structured memory representations and what constraints this would impose.

memory [15,16] (Box 2). The capacity of the slot architecture is set by the number of items that can be held (typically one per slot), with an independent information limit for each item. Slot models often cite temporal neural synchrony limitations as the root of the slot limitation (e.g., [17]), but the item limit is typically set by fiat – there are as many slots as the behavioral data warrant.

We suggest that the map architecture is the better alternative because it best explains why capacity varies across different kinds of information and different tasks. We illustrate this point with two case studies: the capacity of spatial attention and the capacity of visual short-term memory (VSTM). We then suggest new examples of cognitive limitations that we believe could be explained in a similar way.

Case study I: map representations for eye movements and visual selection

A vast field of research has explored the properties of the spatially localized ‘spotlight’ [3] of visual attention. These attention hotspots appear to be controlled by the locations of target-related activity on two-dimensional maps, such as the frontal eye fields (FEF), which were initially thought to be solely for control of eye movements (see [18,19]). A localized current delivered to the retinotopic map triggers an eye movement to the corresponding spatial location. However, a weaker stimulation that does not trigger a saccade still affects visual processing at the corresponding retinotopic location. For example, stimulating the FEF enhances responses at corresponding locations in V4 [20]. Another study [21] showed related results for stimulation of the superior colliculus, a subcortical saccade/attention map. When not actively directing saccades, these maps, therefore, serve a second function: an attention map that acts through downward connections to visual cortex.

Activity peaks in saccade areas also engage large suppressive surrounds that allow stronger targets to suppress weaker ones in the competition to be the single, executed saccade. Attentional foci also come with suppressive surrounds [22–27] that may be directly related to those of the saccade areas. The suppression is beneficial for the selection of the saccade target, but also fills a critical role when these areas serve as attention maps, by preventing the selection of nearby distractors that would compete for target identification (Figure 2a). However, this competitive suppression also limits the number of locations that can be

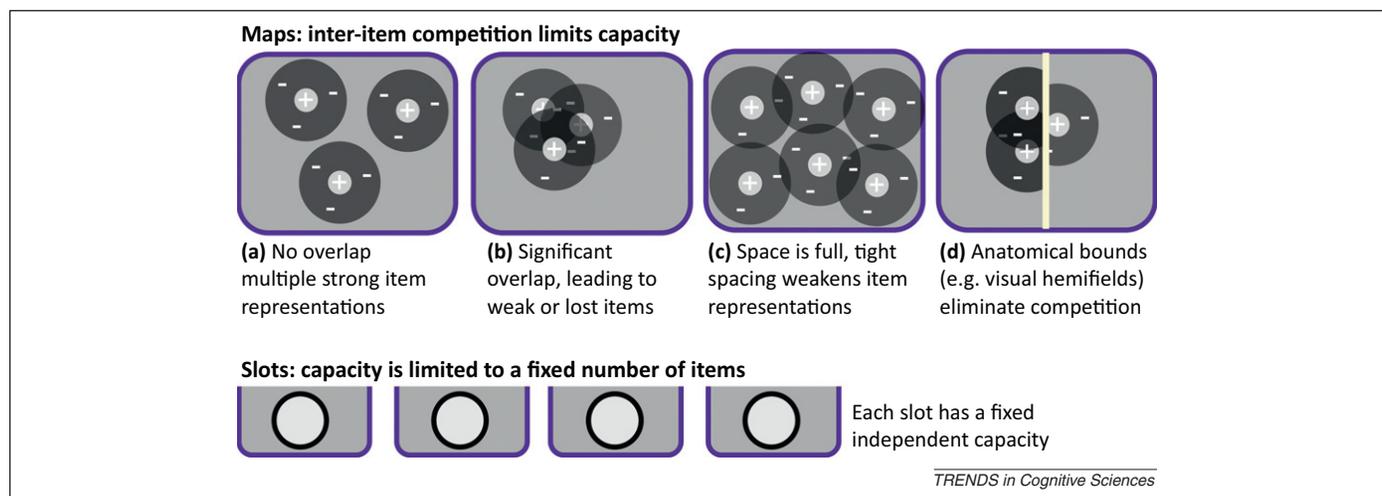


Figure 1. Map vs slot architectures. At top, a competitive map representation within a bounded, two-dimensional space. (a) This panel depicts how each location represents value in the space, with items represented by peaks of activation. Each peak also suppresses surrounding space, inhibiting nearby competitors [8]. This surround suppression will limit the number of items that can be simultaneously maintained. If the item spacing is dense, as in (b), the space will be inefficiently used. If the spacing is sparse, as in (c), the space is efficiently used and capacity is maximized, though still limited (by approximately six items in this case). (d) This panel shows that anatomical boundaries (e.g., the visual hemifield divisions of V1) can mimic spacing effects by eliminating mutual inhibition. At bottom, a slot representation limited to four independent items.

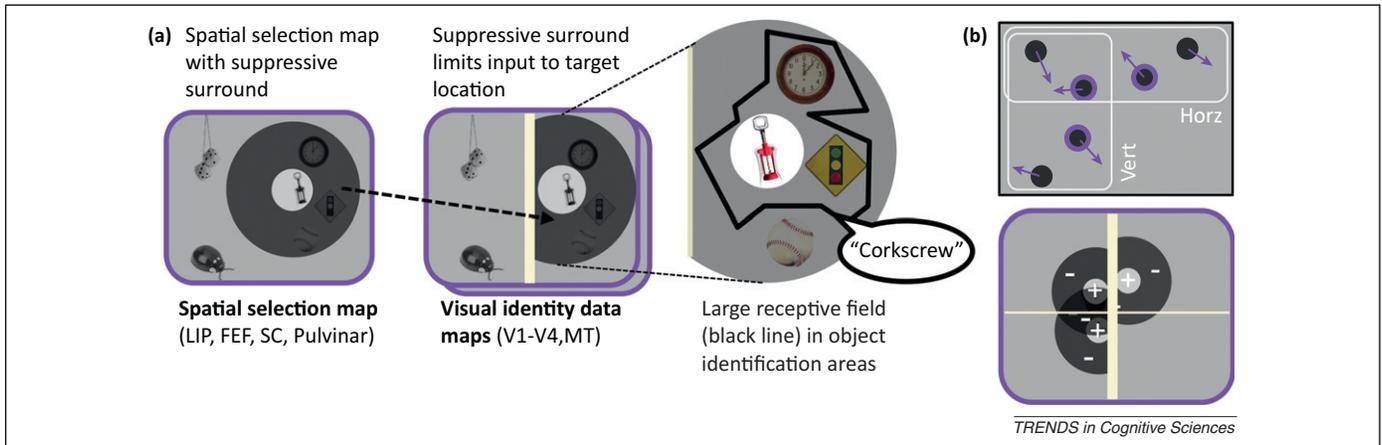


Figure 2. Maps as limits on spatial attention capacity. (a) Architecture of spatial attention (adapted from [19]). A network of areas form a competitive target map that subserves spatial attention, as well as eye movements. Peaks of activity specify retinotopic coordinates of feature data in earlier visual areas which are shown, highly simplified, as a stack of aligned areas divided into right and left hemifields with the fovea in the center. In object recognition areas, cells have large receptive fields shown here as a heavy black outline for the receptive field of one cell that specializes in identifying corkscrews. These cells must rely on attention to bias input in favor of the target and suppress surrounding distractors, so that only a single item falls in the receptive field at any one time. The surround suppression must be imposed in early retinotopic areas, because the large fields in object recognition cannot locally modulate sensitivity. (b) Resource limits in multiple object tracking (MOT) tasks. In MOT, a participant is asked to track multiple moving objects (marked here in red for illustration only) among visually identical distractors, which requires constant spatial selection of those objects. When concurrent MOT displays are arranged within visual quadrants, tracking within two vertically arranged displays leads to ‘resource drains’, where performance drops. However, when arranged horizontally, resources are ‘independent’, because performance is virtually unaffected [33]. At bottom, the flexible map account predicts this effect, because the visual hemifield boundary strongly blocks inhibition horizontally, but only weakly blocks it vertically [28]. A strong competitive map account of such effects predicts that almost all performance limitations in this task can be ascribed to competition within a spatial map representing target positions [10].

simultaneously attended. This is a major component of the resource limit for competitive maps, as well as the source of the flexibility in this limit.

Such competition may impose the performance limit on both static multifocal selection tasks [10] and dynamic multiple object tracking tasks [10,28–30]. Despite frequent claims that such abilities are limited to three–four locations or objects (see [14], for review), recent work shows that these limits are malleable in the ways that a map-based explanation predicts [31]. Moving the selected locations closer can reduce the limit to one or two, whereas moving them farther apart can increase the limit to eight or nine [14,32]. Figure 2b depicts how these limits depend on the distribution of items in the visual field [9,33–35], suggesting that they arise from competition within lower level visual areas, where each hemifield is represented by a separate map [36]. The layout and interactions within a map are likely malleable with training. Extensive practice with video games has been shown to improve performance on multiple object tracking tasks [37] and this effect may be due to a reduction in the spatial extent of the suppressive surround of each item, allowing more objects to be tracked.

Case study II: capacity limitations on visual short-term memory

Slots are limited to a set number of independent items. Maps are limited by the types of information and its layout, and, thus, predict flexible capacities depending on task parameters. This distinction parallels recent debates in the visual memory literature over whether capacity is limited by fixed slots or flexible resources (Box 2). Here, we focus on the properties of a competitive-content map that can explain flexible memory limits. In particular, the degree of inter-item competition on such a map, and, therefore, its carrying capacity, will depend on the amount

of space required to represent an item on a map, the spacing between items, the extent of surround inhibition, and the reduction of suppressive surrounds that cross the vertical midline. As an example of the change in overall space taken by an item, Figure 3 depicts the tradeoff between the difficulty of recognizing an object’s identity and the number that can be stored [38].

Examples of the effects of physical spacing are seen in a number of studies on simultaneous visual identification. For example, increased spacing among items within spatially organized visual data maps increases the speed and accuracy of visual identification tasks [35,39] and visual search tasks [40–42], and may be a key constraint on our ability to identify multiple items in parallel [9]. The reduction of inter-item suppression with greater spacing would affect both identification and retention in memory.

Brain imaging also suggests that nearby items decrease the representational strength of a target item through some form of surround suppression [9,43,44] and this inhibitory effect should influence not just visual identification, but also visual memory retention [45]. Such inter-item competition during identification can be reduced by separating items across the visual hemifield boundary for both identification [35,46] and memory retention [45], which suggests again that the hemifield boundary reduces competition across otherwise adjacent areas of a map (Figure 1).

One way to reduce this local competition may be to process a single item at a time on a map. When items are presented in isolation as a sequence over time, the quality of visual representations improves for both recognition [9] and visual memory [45,47–49]. This temporal isolation can be mimicked by isolating a subset of objects with selective attention, suppressing other items in the map and preventing them from competing. This can

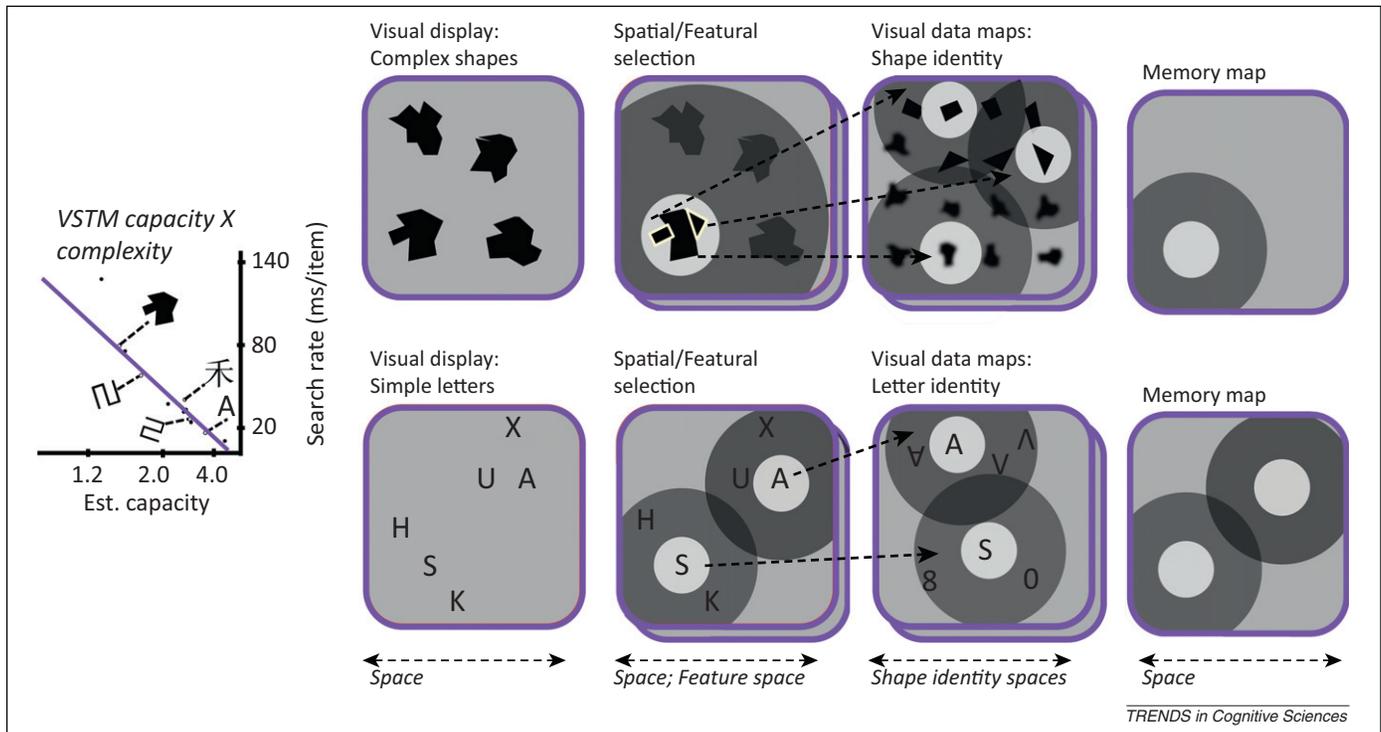


Figure 3. Maps as limits on visual memory capacity. At left, data from [38], showing that VSTM can hold fewer objects as they become more complex, with an ultimate limit of approximately four total objects that can be held. The remaining boxes present a series of maps that might create visual short-term memory limitations. The first set shows two types of visual displays, complex shapes and simple letters. The next column depicts spatial selection maps (though feature selection, e.g., by color, is equally likely). In this case, one or two locations are selected, biasing competition within multiple hierarchical levels of visual data maps (V1-V4, MT, IT) relevant to recognition of those objects. Critically, because the space for complex shapes is more densely packed and/or requires simultaneous activation of more locations to encode the complex shape information, few shapes can be represented concurrently without their representations degrading, and therefore only one shape should be attended at once in the selection maps. Letters, by contrast, have a well-spaced map of high-level identities created by vast experience, and, therefore, multiple letter identities can be reliably encoded at once, allowing multiple locations to be attended at once in the selection maps. On the right, a hypothetical ‘spatial’ memory map that holds pointers to previously seen visual data (or more likely, pointers to selection maps that point to those data). These could be subserved by connections between activation maintenance structures in frontal cortex and parietal selection maps.

improve the quality of visual representations in recognition [9,44] and visual memory tasks [50].

Competitive interactions within strictly visual maps are not likely to be the only limiting factor on visual memory performance. For example, the function that relates information load to capacity shows that, even for items with minimal competition at the recognition stage (as measured by visual search performance), the storage limit is still at most approximately 4 or 5 objects (though this interpretation of this limit is debated, see Box 2). Therefore, in addition to competition between the objects within visual maps (e.g. as described in Case Study I), there is likely more competition within frontal or parietal structures during later memory maintenance [51,52]. These parietal and frontal structures may also be organized as rough spatial maps, becoming activated primarily when storing information from particular spatial positions (see [53], for review; see also [54] for evidence of multiple overlapping maps in frontal cortex). Lesions of portions of these frontal maps can even create ‘memory scotomas’, where memory representations (but not online perceptual representations) for spatial positions are impaired within particular regions of the visual field [55].

We take the map architecture for memory as a plausible assumption: an implementation of a cognitive ‘resource’ that has been otherwise vaguely specified.

Maps as limitations for broader cognitive resources

Our case studies of maps within the perceptual system can be extrapolated to maps of broader information spaces across cognition, from task scheduling to social reasoning. There is evidence that many cortical areas are locally specialized for high-level representations, such as faces, bodies, or places [56]. Map architectures likely underlie even such high-level functions, given the planar structure of the neuronal layers of the cortex (as well as many subcortical areas). It is easy to imagine ‘clustered’ maps for many high-level spaces and indeed they have been suggested for ‘phonemic maps’ (posterior superior temporal gyrus; [57]), specialized ‘letter maps’ in the visual word form area (left fusiform gyrus; see [7]), supramodal maps of ‘emotional expression’ with separate subregions for representing variations in anger, disgust, fear, happiness, and sadness (MPFC and STS, [58]), or even maps of abstract ‘semantic knowledge’, such as vegetables and tools (e.g., [59]). And like the ‘source code’ maps for ‘action plans’ organized by body part or action goal (Box 1), one might imagine a ‘task buffer’ that stores the type and state of current tasks within a clustered space of possibilities. Suppressive surrounds have been demonstrated for memory representations in many such high-level spaces, including inhibition of items that are semantically [60,61] and orthographically [62] similar to items in memory.

Box 3. Competitive maps and the binding problem

A dinner party presents strong demands on cognitive resources. The limitations on encoding and remembering new faces and new names might be explained through competition within maps for various properties. However, what about matching those new faces, which are stored in one set of maps, to those new names, stored in another set of maps? This ‘binding problem’ challenges all models of perception, attention, and memory, and there are several classes of proposed mechanisms that might link separate representations together (e.g., [89–91]). It is likely that the strength of these links, as well as the competition for space that we are discussing here, both affect the limit in the number of items that can be attended, planned, or remembered. Nonetheless, there are aspects of the map architecture that are particularly relevant to the binding problem.

In some ways, maps are especially prone to binding difficulties, because their maximum of two dimensions limits the scope of what they can represent. Thus, strongly hierarchical representations must be linked across many maps, for instance, across the levels of the ventral object recognition hierarchy. Maintaining binding across such maps might be particularly demanding and recent evidence suggests that items are not actually stored as bound units in working memory [92,93].

However, in other ways, maps have properties that might help address these binding difficulties. First, note that some maps contain embedded dimensions (e.g., orientation or color for primary visual cortex; Box 1) arrayed in fine-scale local topologies. Embedded dimensions exist in early visual representations, such as V1, and are proposed in other disciplines (e.g., string theory; [94]). Second, in many cases, maps that share a common format allow simple cross-referencing. For example, target-related activity peaks in the retinotopic saccade and attention maps indicate the locations of the targets, but they do not carry information about their features or identity. Nevertheless, those locations point to features that can be found within other retinotopically organized visual areas [20,95]. Indeed, the classic feature integration theory binding model proposed location as the common property that links features across separate maps [90].

Although such maps are easy to imagine, we focus on what such structures imply about the nature of cognitive capacity limitations. Across all of these examples, the carrying capacity in each of these spaces would be flexible, determined by the spacing and suppressive surrounds of items being represented. Even if these higher-level maps are only roughly hinted at by brain imaging and multiunit recordings, a competitive map format implies a common set of properties for their capacity limitations. Computational modeling of these maps could lead to new insights and predictions about the roots and connections among the limitations of each map type [63,64] (Box 3). As more is learned about the layout, resolution, and surround suppression properties of each map (see Box 4 for examples of open questions), including how such properties change with experience [65], a competitive map account predicts how cognitive capacity should vary based on moment-to-moment content.

Concluding remarks

The human brain depends on a variety of temporary buffers to retain information of current interest. We propose that the commonly found map organizations seen throughout the brain can give a concrete explanation of their capacity limits.

Maps are 2D spaces of potential sensory and motor representations, such as spatial location, visual features, or motor plans. Unlike slot architectures, where capacity

Box 4. Outstanding questions

- Do some maps act as ‘pointers’ to other maps? Attentional pointers may index the features of a target by specifying its coordinates [19]. A task planning map may need to cross reference maps of object features to specify the task target, perhaps by specifying the color of the object to be picked up.
- Could variation in surround suppression be used to change the ‘computation’ occurring on a map? For example, if surround suppression is disabled, individual items lose their isolated peaks and activity is aggregated across several items. This ‘ensemble’ mode could provide a substrate for summary representations of a space, such as the histograms required to generate perception of featural ‘averages’ of dimensions, such as size, orientation, location, or higher-level identities, such as facial emotions (see [96], for review).
- What would be the consequence of local competition in ‘clustered’ information spaces with less systematic dimensions of organization? Would arbitrary clustering lead to idiosyncratic capacity constraints and idiosyncratic inter-item interference? For example, on somatosensory maps, the hand representation is adjacent to the face and the genitals next to the feet, resulting in unusual transfer of sensation for individuals with phantom limbs (see [97]). Would there be similar idiosyncratic adjacencies and interference patterns for semantic or shape maps?
- Can studies exploring maps of functional selectivity (e.g., physiological recordings, functional MRI) reveal consistent and stable map architectures within individuals for more abstract information spaces (e.g., executive planning, semantic processing, social reasoning) in a manner akin to mapping the large scale organization in the visual stream (e.g., [98]), leading to specific predictions regarding processing limits for more abstract cognitive tasks?

limits are fit to the data, the 2D representations proposed here predict that capacity limits are flexible, constrained by competition for space within the bounded size of each map. Competition decreases with distance and sufficient distance (or an anatomical boundary) eliminates competition, creating an ‘independent cognitive resource’. We propose that capacity limits across the cognitive system may be best understood as competition within 2D maps, from attention and memory to motor control and executive planning.

The bottleneck in determining the roots of cognitive capacity limits is not a lack of effort, but instead a lack of concrete suggestions for how these mental resource limits might arise from properties of neural organization of information storage in the brain. We hope that the principle of the competition-limited cognitive map will serve as a concrete suggestion to guide future research into the nature of cognitive capacity limits.

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