

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Issue: *The Year in Cognitive Neuroscience***A new perspective on the perceptual selectivity of attention under load**Barry Giesbrecht,¹ Jocelyn Sy,² Claus Bundesen,³ and Søren Kyllingsbæk³¹Department of Psychological and Brain Sciences and The Institute for Collaborative Biotechnologies, University of California, Santa Barbara, Santa Barbara, California. ²Department of Psychological Sciences, Vanderbilt University, Nashville, Tennessee. ³Center for Visual Cognition and Department of Psychology, University of Copenhagen, Copenhagen, DenmarkAddress for correspondence: Barry Giesbrecht, Ph.D., Department of Psychological and Brain Sciences, University of California, Santa Barbara, Santa Barbara, CA 93106. barry.giesbrecht@psych.ucsb.edu

The human attention system helps us cope with a complex environment by supporting the selective processing of information relevant to our current goals. Understanding the perceptual, cognitive, and neural mechanisms that mediate selective attention is a core issue in cognitive neuroscience. One prominent model of selective attention, known as load theory, offers an account of how task demands determine when information is selected and an account of the efficiency of the selection process. However, load theory has several critical weaknesses that suggest that it is time for a new perspective. Here we review the strengths and weaknesses of load theory and offer an alternative biologically plausible computational account that is based on the neural theory of visual attention. We argue that this new perspective provides a detailed computational account of how bottom-up and top-down information is integrated to provide efficient attentional selection and allocation of perceptual processing resources.

Keywords: selective attention; visual attention; load theory; theory of visual attention; perceptual selectivity; distraction

Introduction

The day-to-day environment is extremely complex and contains much more information than an individual can process at once. Coherent and adaptive behavior in this environment is therefore dependent on a mechanism that affords the selective processing of a subset of the information most pertinent for current behavioral goals, while ignoring distracting information that is largely irrelevant. This mechanism is *selective attention*. And, while the need for a robust selective attention mechanism has not been debated—rather, it often is considered to be self-evident^{1–9}—the nature of the selection mechanism has been. For the better part of 40 years (from the late 1950s to the mid-1990s), one of the most prominent debates in the literature on selective information processing was focused on determining the locus in the information processing stream at which

attention operated to select information to be acted upon or to be stored in memory^{a, 3,7,10–14}

The year 2014 marks the 20th anniversary of a significant turning point in the locus of selection debate. This turning point, based on a theoretical perspective proposed by Lavie and Tsal,¹⁵ was focused on identifying the conditions under which early (or late) selection *could* occur, rather than determining whether selective attention is *either* early *or* late. According to Lavie and Tsal,¹⁵ perceptual load was a

^aThere were, and continue to be, other prominent debates in the attention literature, including debates about the units of selection (space, objects, or features), serial versus parallel information processing models, spotlight versus zoom-lens models, contrast gain or response gain models of the effect of attention on neuronal responses, and the number of attentional foci.

key factor in determining whether or not selective attention acted at an early stage of processing. This theoretical perspective, which is often referred to as *load theory* (LT; also *perceptual load theory*), was supported empirically when Lavie¹⁶ demonstrated that the amount of behavioral interference caused by task-irrelevant information decreased when the perceptual processing demands imposed by task-relevant information were high.

The LT framework, which will be described in more detail later in this review, has been influential for two important reasons. First, LT provided a relatively straightforward descriptive framework within which both early and late selection could occur. This framework was grounded on the basic premise that selectivity depends on task demands. As a result, LT effectively rendered the locus of selection debate moot.¹⁵ Furthermore, the basic notion that selection is not fixed at one stage or another—sometimes referred to as *flexible selection*—has been incorporated into a number of accounts of attentional phenomena in the cognitive psychology and cognitive neuroscience literatures.^{17–20} Second, and perhaps more important, is that LT provides an account of the factors that determine the efficiency of selective attention, particularly at early perceptual stages of information processing. This aspect of LT has made it relevant for understanding the basic mechanisms of attention, and it has implications for research on a variety of issues in a number of areas, including distractibility, awareness, aging, clinical disorders, individual differences in personality, spontaneous fluctuations in attention, and classroom performance^{b, 22,24}

^bAnother way to estimate the impact of LT on the cognitive psychology and cognitive neuroscience literature is by citations. While there are certainly pitfalls with putting too much emphasis on citation counts, they can provide a rough gauge of where LT fits within the context of the literature. One recent analysis of citations from 1956–2004 using the *Web of Science* reported that both Lavie and Lavie *et al.* are in the top 500 articles in the cognitive psychology literature published between 1950 and 2004.²¹ We conducted a separate *Web of Science* citation analysis of the four core LT articles.^{15,16,22,23} Between 1994 and 2013 these articles have collectively been cited 1825 times, equaling a combined annual citation rate of 92.95 citations/year (total citations/20 years). The

Despite the simplicity of the LT framework—or perhaps because of it—the explanation of perceptual selectivity it provides presents some significant impediments for a complete understanding of selective attention. Indeed, the results of a number of recent studies have suggested that it is time for a different perspective on the effects of task demands on the perceptual selectivity of attention.^{25–31} The purpose of this review is to evaluate several key LT assumptions and to present an alternative perspective on the mechanisms by which task demands affect attention. Specifically, the remainder of this review is divided into three sections.

In the first section, we provide a concise review of the core assumptions of LT. The goal of the review is not to be exhaustive—because others have done so eloquently^{22,24,32}—but rather to be targeted, highlighting LT in a historical context, the strengths and weaknesses of LT, and recent challenges to several of its core assumptions. Importantly, this review emphasizes the LT account of the perceptual selectivity of attention. The allocation of perceptual processing capacity is the core aspect of the original model and it has remained unchanged in more recent versions of LT that have been proposed to also explain the effects of task demands at later stages of cognitive control.²³

In the second section, we propose an alternative framework that addresses the weaknesses of LT. As an example, we describe a computational approach that fits within this framework; the approach is based on the theory of visual attention (TVA)⁴ and its neural implementation (NTVA).³³

In the third section, we discuss the implications that this framework has for understanding how the selectivity of attention changes with task demands, how this framework and the NTVA implementation relates to other prominent accounts of attention, caveats, and shortcomings of our alternative, and novel predictions.

Perceptual selectivity and task demands

Historical context for LT

A natural component of scientific discourse is debate. In the attention literature one would be

annual citation rates for these articles from the time of publication are 17.1 (Ref. 15), 36.3 (Ref. 16), 41.4 (Ref. 23), and 53.3 (Ref. 22) citations/year.

hard-pressed to find a theoretical debate that lasted as long as the locus of selection debate. Indeed, the locus of selection debate effectively began at the dawn of the cognitive revolution in the 1950s. Empirically, this debate was rooted in the discrepancy between Cherry's¹¹ evidence for filtering in the dichotic listening paradigm and Moray's¹³ evidence that subjectively important information (i.e., personal names) can break through the filter. Theoretically, this debate was rooted in the distinction between Broadbent's filter theory³ and Deutsch and Deutsch's late selection account.¹² Forty years of behavioral evidence from a variety of paradigms, time and again, demonstrated that task-irrelevant information could be effectively filtered out at early perceptual stages of processing.^{11,13,34–41} This debate was one of the first in the cognitive psychology literature in which *in vivo* human neural recordings were used to provide some insight.^{42–44} However, like the range of behavioral evidence, the neural evidence also provided support to both sides of the debate.⁴⁵

In the late 1980s and early 1990s a small number of investigators argued for a change in perspective. For instance, Allport,^{1,2,46} along with Kahneman and Treisman,⁷ suggested that the debate between early and late selection was misplaced. Instead, they proposed that both early and late selection could occur. Consistent with this notion, a number of lines of behavioral evidence suggested that the availability of postperceptual information was influenced by the extent that relevant and irrelevant items are spatially or configurally distinguishable,⁴⁷ the perceptual complexity of the display,^{48,49} and the extent to which attention is spatially focused.^{50,51} Moreover, multiple accounts offered plausible explanations, suggesting that postperceptual processing of unattended information could arise because of information-processing leakage from perceptual stages of processing to postperceptual stages, either because of an early selection failure or because of the lower processing demands of some types of information.^{14,50} Lavie and Tsai¹⁵ used these proposals as inspiration and provided a strong argument, along with a straightforward framework, explaining how both early and late selection could occur. From this new perspective, Lavie and Tsai¹⁵ emphasized that the key issue was not determining whether selection was only early or only late but rather was identifying the conditions under which early and late selection occurred.

According to Lavie and Tsai,¹⁵ a key factor in determining selective stimulus processing was task demands. The notion that task demands could influence selective processing of goal-relevant information was not new. For instance, William James proposed that increasing the demands on lessons would reduce distraction (i.e., increase selectivity) in the classroom;⁵² Treisman suggested that filtering may only be needed if there was competition across multiple input channels;¹⁴ Hillyard *et al.* suggested that attention-related modulations of neural activity may be modulated by the difficulty of the task;⁴² and Yantis and Johnston suggested that the perceptual load of a task influenced the spatial selectivity of attention.⁵⁰ Lavie and Tsai built on these suggestions and developed a task difficulty–based framework that provided an explanation of the conditions under which selection occurred in early and late stages.¹⁵

LT is a central component of the change in perspective on the locus of selection debate, offering an avenue to reconciliation between the opposing views. Perhaps even more important, LT also provided a framework for understanding the efficiency of perceptual selectivity. From this perspective, LT is perhaps even more important in the context of the attention literature because it offers an account of the conditions under which task-irrelevant information is processed at early stages of the information-processing pathway and, as a consequence, is brought to bear on several fundamental issues relating to attention, including distractibility,⁵³ clinical populations,^{54,55} aging,⁵⁶ mind wandering,⁵⁷ and awareness.^{58–60}

The LT kernel of perceptual selectivity

The LT framework is well rooted in traditional cognitive models of dual-task information processing, demonstrating behavioral costs when attention is divided among relevant stimuli.^{61–64} LT is an extension of many of these ideas to task-irrelevant information processing. Based on these classic frameworks, Lavie and Tsai¹⁵ assumed that the upper limit on the resources that could be allocated was determined by the current availability of resources or the internal demand, which ever was less. LT included three other assumptions. First, an additional constraint was placed on the allocation of attentional resources such that perceptual processing resources are allocated exhaustively. Second, the

exhaustive allocation of resources is automatic and thus proceeds until no processing capacity is available. A key aspect of this automaticity assumption is that task demands are inherently driven by the bottom-up perceptual characteristics of the display or by external constraints of the task. This aspect of the perceptual processing scheme is captured by Lavie:¹⁶ “Whether selective processing will occur is at the mercy of the perceptual load imposed by external events.” (p. 466). Third, to the extent that there is some physical distinctiveness between the task-relevant and task-irrelevant information (e.g., spatial location, color), the allocation of perceptual processing capacity first occurs to task-relevant information and then, if capacity remains, it “spills over” to task-irrelevant information. In other words, the allocation of perceptual resources occurs in two steps, first to relevant information and then to irrelevant information.

With these assumptions in place, LT could account for what appeared to be patterns of behavioral performance that supported both early and late selection. Easy tasks, in which the target discrimination does not require all available resources, were more likely to provide patterns of behavioral performance consistent with late selection because the excess resources would spill over to facilitate the perception of task-irrelevant information. Difficult tasks in which the target discrimination requires all (or most) of the available resources are more likely to provide patterns of behavioral performance consistent with early selection, because no excess resources spill over, effectively filtering out task-irrelevant information.

Empirical support

Behavioral performance. The bulk of the behavioral evidence that has been used to support the basic tenets of LT comes from a task that is a hybrid between a visual search task⁶⁵ and a flanker task.⁶⁶ For example, Lavie (Ref. 16, Exp. 1) asked participants to make a speeded discrimination about whether a target presented on the horizontal meridian of a search display was *x* or *z*. The target was either presented alone (i.e., search set size 1) or with five other letters (set size 6). Examples of the high- and low-load displays are illustrated in Figure 1A. The assumption in this experiment was that the increase in the number of items increased the perceptual load of the task.

In addition to the task-relevant search items (target plus distractors), one additional item was presented in the upper or lower visual field. The participants were instructed that a target would never appear off of the meridian and, as such, the additional letters were completely task irrelevant. Importantly, like in the classic flanker task, the identity of this task-irrelevant letter was the same as the target, was the alternative, or was neutral. Selectivity in this task was measured by the amount of interference caused by the irrelevant flanker. The key finding, shown in Figure 1B, was that the amount of interference caused by the task-irrelevant flanker was significantly smaller under high load relative to low load. Subsequent behavioral evidence has come from similar tasks that control the number of items and the eccentricity of the stimuli and that manipulate load by manipulating the visual similarity between the targets and distractors in the search display.⁶⁷ Again, even with the changes in the search display, when the search task is more difficult (high target–distractor similarity), the amount of interference caused by the task-irrelevant flanker is reduced.

Neural evidence. In addition to the LT predictions that behavioral interference caused by task-irrelevant information should be reduced under high load, LT also makes the prediction that neural responses evoked by task-irrelevant information should be reduced by high load. Several lines of evidence from the cognitive neuroscience literature are often cited as supporting this prediction. For example, in an fMRI study, Rees *et al.*⁶⁸ asked participants to make judgments either about the case of a word presented at fixation (low load) or about the number of syllables in the word (high load). In addition to the word on the screen, task-irrelevant motion fields were also presented. The key result, shown in Figure 2A, was that blood oxygen level–dependent (BOLD) responses in motion-sensitive area MT evoked by the task-irrelevant stimulus were reduced under conditions of high load. Similarly, other work has shown that the magnitude of the visual P1 event-related potential (ERP) evoked by a peripheral task-irrelevant stimulus is reduced when a foveal letter-discrimination task was made difficult by noise (Fig. 2C).⁶⁹ Analogous reductions in BOLD responses in retinotopically organized visual areas that represent task-irrelevant locations, in areas that

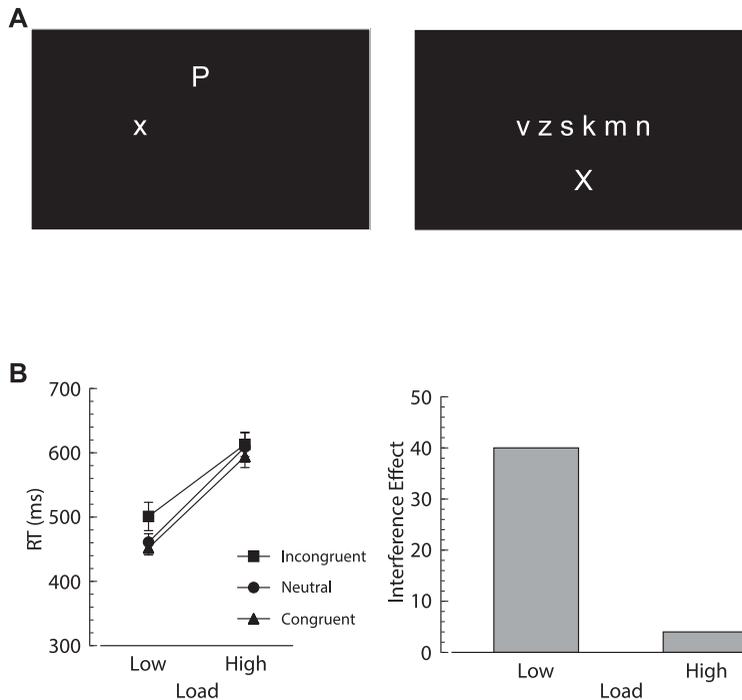


Figure 1. Sample displays and key behavioral results from Lavie.¹⁶ (A) Two sample displays used in the experiment. The task-relevant search display was presented on the horizontal meridian and consisted of lowercase letters. The target was either an “x” or a “z.” Task-irrelevant flankers were presented above or below fixation and were uppercase letters that were congruent, incongruent, or neutral with respect to the target (X, Z, P). The example on the left shows a low-load display in which the target is “x” and the flanker is neutral (“P”). The example on the right shows a high-load display in which the target is “z” and the flanker is incongruent (“X”). Displays were constructed based on the information provided in the Experiment 1 Methods section.¹⁶ (B) Sample results. Left panel shows the response time (and standard error of the mean) to indicate whether the task-relevant target was an x or z as a function of load and flanker congruency. Right panel shows the distractor interference effect that served as the basis for the key conclusions in Lavie,¹⁶ computed as the difference between the incongruent and neutral conditions (i.e., incongruent–neutral). Only the effect in the low-load condition was significant. The response times and interference effect data were taken from Table 1 of Ref. 16.

represent objects (e.g., faces), and in areas outside of the visual cortex (e.g., the amygdala) have been observed when performing high-load tasks.^{70–73}

Evidence for reduced neural responses evoked by task-irrelevant information under high load is not restricted to the human brain. For instance, responses evoked by unlikely targets measured in macaque V4 neurons can be suppressed under high task difficulty, compared with low task difficulty.⁷³ Similarly, when attention is directed outside the receptive field (RF) of macaque V1 neurons, the response evoked by the neuron’s preferred stimulus is lower when the task demands are high, compared with when the task demands are low (Fig. 2C).⁷⁴

A critical reexamination of perceptual selectivity in LT

Given that the LT framework is simple, has empirical support from a number of sources, provides a reconciliation of a longstanding debate, and has been generalized beyond the confines of the traditional research on selective attention, one may ask, Why take a second look? We argue here that there is a wealth of evidence in the literature that raises significant questions about each of LT’s cornerstone assumptions, and thus LT’s explanation of perceptual selectivity.^{25–31} Here, we focus on three specific issues: the definition of perceptual load, the automaticity of the allocation scheme, and the two-step allocation process.

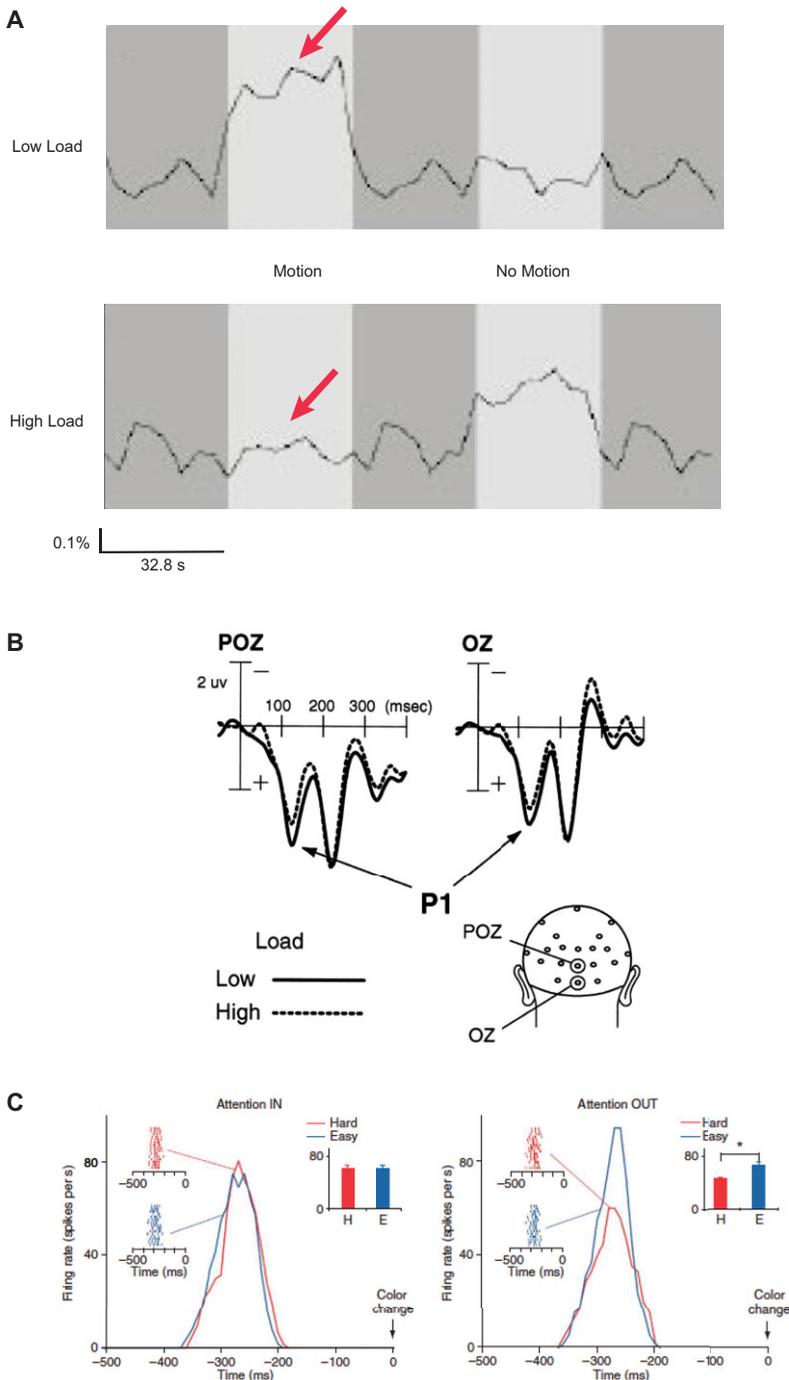


Figure 2. Examples of neural evidence that is consistent with LT. (A) Results showing reduced BOLD signal evoked by task-irrelevant motion in area MT under high-load conditions. Adapted from Rees *et al.*⁶⁸ and reprinted with permission from AAAS (arrows, labels, and scale added). (B) Visual event-related potentials (ERP) evoked by task-irrelevant stimuli under conditions of low and high load. The mean amplitude of the P1 ERP component is reduced under high load. Adapted from Handy *et al.*⁶⁹ with permission. (C) The response of a single macaque V1 cell showing a larger response to a task-irrelevant stimulus when attention is directed outside the receptive field and the task is easy (blue lines and bars) compared to when the task is hard. Adapted from Chen *et al.*⁷⁴ with permission from Macmillan Publishers Ltd.

Definition of perceptual load. Despite the centrality of the concept of load to LT, the definition is vague. Load was originally explained as follows:

Obviously, the concept of perceptual load is difficult to operationalize. It necessarily includes two components that are not easily defined – the number of units in the display and the nature of processing required for each unit. In the present discussion we consider units as those items appearing in the display with different identities . . . Note that by the term *unit* we do not refer to the basic perceptual units, but rather to items that serve as different alternatives for the relevant response in the task. Consequently, a string of letters, for example, can serve as one unit (word) or as several units (letters). The number of units, so defined, provides the level of perceptual load. . . . However, perceptual load also correlates to the amount of information required to process each unit in order to produce the required response.¹⁵ (p. 185)

Perhaps even more unfortunate, more recent versions of the model have not provided a more precise definition:

Increased perceptual load means that either the number of different-identity items that need to be perceived is increased, or that for the same number of items perceptual identification is more demanding on attention
Reduced distractor interference under conditions of high perceptual load is not simply the result of the general increase in task difficulty with load and the associated slowing of performance. Manipulations of extreme sensory degradation (e.g., reducing the target size or contrast so much that it is barely seen) that cannot be compensated for by applying more attention – in other words subjecting target identification to sensory ‘data limits’ rather than attention ‘resource limits’ – increase the general task difficulty . . . but do not reduce distractor interference.²² (p. 75)

The lack of a precise definition of *perceptual load* is, not surprisingly, problematic. A vague definition makes the theory hard to test and introduces the potential for circular reasoning about the

nature of load and its resulting effects. We are not the first to raise this issue.³² A vague definition of load also makes it much more difficult to completely understand the fundamental mechanisms of perceptual resource allocation, because it is unclear which aspects of information processing are being affected. At best, the vague definition has resulted in inconsistent labeling of load as “perceptual load” or “attentional load.”^{68,69,72,75} At worst, the vague definition has resulted in some empirical findings being marshaled in support of LT when they are expressly inconsistent with the assumptions of the theory. For example, several fMRI and ERP studies have provided strong evidence that increased task difficulty causes reduced neural responses to task-irrelevant information.^{68,69,71} On the surface, the notion that increasing task demands reduces neural responses to task-irrelevant information is exactly what LT would predict, and these results have been cited as evidence in favor of LT.^{22,24} However, in several of these instances, the manipulation of difficulty does not align well with the perceptual constraints outlined in LT. For instance, the load manipulation used by Rees *et al.* was, in their own words, a linguistic manipulation (letter case (low load) versus number of syllables (high load)). In other cases, the manipulation of load was achieved with noise masking (lines or dots).^{69,71} Noise masking is generally considered to be a sensory or data-limited manipulation,⁷⁶ which, according to LT, should not increase perceptual selectivity.^{22,77}

Automaticity of allocation. LT rests on the assumption that the allocation of resources is determined exhaustively and automatically by the inherent bottom-up processing demands imposed by the task-relevant information. However, several studies have provided evidence suggesting that reduced distraction is not determined by increased perceptual load alone. For example, spatial cues predictive of the target location can reduce interference typically observed under low load,²⁷ and expectancies created by intertrial repetitions of low- and high-demand displays can also modulate the magnitude of behavioral distraction.²⁸ Top-down expectancies about task-irrelevant information also challenge the automaticity assumption. For example, during visual search, if observers are provided a cue about the likelihood of distractors at specific locations, retinotopic regions of visual cortex that represent

the distractor locations exhibit suppressed BOLD responses time locked to the cue and in the absence of the distractor.⁷⁸ Moreover, even the single unit evidence from monkey neurophysiology that has been used to support LT also suggests that top-down expectations play a key role in perceptual selectivity as a function of load. Specifically, in the Boudreau *et al.* study described earlier (see section Neural evidence), three monkeys were tested and the only one to exhibit suppressed V4 responses to unlikely targets was the monkey that had previous experience with distractor rejection tasks (>100,000 trials). This result suggests that top-down strategies are critically important in mediating perceptual selectivity. Together, these studies suggest that perceptual load may not be the only determinant in modulating distraction, but that voluntary control may dynamically interact with load to modulate the efficiency of selective attention.

Two-step allocation scheme. While LT critiques typically focus on either the definition of load or the automaticity components of the model,^{27,32} little attention has been paid to another problematic assumption: the two-step resource allocation scheme. Under conditions when the distinction between task-relevant and task-irrelevant information is clear (e.g., differing spatial locations or colors), perceptual processing capacity is first allocated to task-relevant information, and then any remaining capacity should spill over to the task-irrelevant information. This two-step allocation scheme makes the strong prediction that there should be no effect of the type, number, or presence of task-irrelevant objects on performance. In contrast, the presence of the distractor can influence performance. For example, we recently conducted a behavioral and computational modeling study using stimuli that closely matched those used in previous LT papers.³¹ These results, which will be discussed in detail later, revealed that there are clear effects of distractor number, type, and presence (see also Ref. 79). Thus, as with the other key aspects of LT, the two-stage allocation scheme is not a viable explanation of how perceptual selectivity changes with task demands.

An alternative

General framework

TVA⁴ appears to have been the first theory of attention based on the principle that Desimone and

Duncan⁹ referred to as biased competition (BC) in a later, highly influential article.^{80–82} In TVA, all possible visual categorizations ascribing features to objects “compete” (race) to become encoded into visual short-term memory (VSTM) before it is filled up. Each possible categorization is supported by the sensory evidence that the categorization is true. However, the competition is biased by attentional weights and perceptual biases, so that particular objects and categorizations have higher probabilities of being encoded into VSTM. The way in which sensory evidence and attentional biases interact is specified in two basic equations: the rate and weight equations of TVA. Hence TVA may be regarded as a mathematical formalization of the BC principle.

Several recent computational models of visual attention may be viewed as special instantiations of the general BC framework. This includes the normalization model of attention by Reynolds and Heeger⁸³ as well as the NTVA.^{33,84} Perhaps even more important within the present context, BC has recently been proposed as a potential basis for a new, more biologically precise definition of perceptual load.^{85,86} In the following, we will describe NTVA in detail, how it may explain attentional allocation of visual processing resources, and the nature of visual processing capacity in general.

A neural theory of visual attention

NTVA was proposed as a neurophysiological interpretation of TVA.^{33,84} NTVA is a combined theory of recognition and selection that instantiates the two processes in a unified mechanism implemented as a race of categorizations having the form “object *x* has feature *i*.” The unification of selection and recognition tries to resolve the long-standing debate of early versus late selection. The rate of processing $v(x, i)$ of a categorization “object *x* has feature *i*” in the race is given by two equations.

The first is the *rate equation*:

$$v(x, i) = \eta(x, i)\beta_i \frac{w_x}{\sum_{j \in S} w_j}, \tag{1}$$

where $\eta(x, i)$ is the strength of the sensory evidence that element *x* belongs to category *i*, β_i is the perceptual bias associated with *i*, *S* is the set of elements in the visual field, and w_x and w_z are attentional weights for elements *x* and *z*. Thus the rate of processing is determined by the strength of the sensory evidence that object *x* is of category *i*, weighted by

the bias toward making categorizations of type i , and by the relative attentional weight of object x (given by the ratio of w_x over the sum of the attentional weights of all objects in the visual field). Second, the attentional weights are in turn given by the *weight equation*:

$$w_x = \sum_{j \in R} \eta(x, j) \pi_j, \quad (2)$$

where R is the set of perceptual categories, $\eta(x, j)$ is the strength of the sensory evidence that element x belongs to category j , and π_j is the pertinence (priority) value associated with category j . The distribution of pertinence values defines the selection criteria at any given point in time (filtering). By Eq. (2), the attentional weight of object x is a weighted sum of pertinence values, where each pertinence value π_j is weighted by the degree of evidence that object x is actually a member of category j (see also Ref. 87).

The first wave of unselective processing

In NTVA, a typical neuron in the visual system is assumed to be a specialized representation of a single feature that responds to the properties of only one object at any given time. Thus, a neuron can represent different objects at different times, but—learning and development aside—it always represents the same feature i .

Visual processing starts with a massive parallel comparison (matching) between objects in the visual field and visual representations in long-term memory. Visual neurons are distributed at random among the objects in the visual field and the process has unlimited capacity and results in the computation of sensory evidence values, $\eta(x, i)$, each measuring the degree of a match between a given object x in the RF of the neuron and a long-term memory representation (category) i .

At the end of the first wave, an attentional weight is computed for each object in the visual field. The weights are found as levels of activation in a priority map, which may be located in the pulvinar of the thalamus (for a summary of the supporting evidence see Bundesen *et al.*,³³ p. 300). The weights are used for redistribution of cortical processing capacity across the objects in the visual field by dynamic remapping of RFs, so that the expected number of cells allocated to a particular object becomes proportional to the attentional weight of the object.

The second wave of selective processing

Different categorizations “object x has feature i ” of the objects in the visual field compete for entrance into VSTM in a stochastic race process. The capacity of VSTM is limited to K elements, typically around four. Categorizations of the first K visual objects to finish processing are stored in VSTM (the first K winners of the race). Categorizations from other elements are lost.

The object selection of the neuron occurs by dynamic remapping of the cell’s RF so that the functional RF contracts around the selected object.^{88–91} The remapping is done in such a way that the probability that the neuron represents a particular object equals the attentional weight of the object divided by the sum of the attentional weights of all objects in the classical RF. Thus, for neurons with RF that only covers a subset of the stimuli in the visual field, the set S in the rate equation reduces to only the objects within the classical RF of the neuron (see Eq. (1)).

Though the total activation representing the categorization depends on the number of neurons representing the categorization, it also depends on the level of activation of the individual neurons representing the categorization. The bias parameter β_i is a scale factor that multiplies activations of all individual feature- i neurons, so the total activation representing the categorization “object x has feature i ” is also directly proportional to β_i .^{92,93} By scaling up or down the general processing rate in a population of neurons specifically responsive to certain visual features, the general processing rate of the features for all objects in the visual field will be scaled up or down.

Thus, in the neural interpretation of the rate equation (see Eq. (1)), the total activation representing the categorization “object x has feature i ” is directly proportional to both the number of neurons representing the categorization, and the level of activation of the individual neurons representing the categorization. The number of neurons is controlled by $w_x / \sum w_z$ (filtering), whereas the activation of the individual neurons is controlled by β_i (pigeonholing).¹⁰

Processing capacity in NTVA

NTVA assumes that the total activation representing the categorization “object x has feature i ” is directly proportional to both the number of neurons representing the categorization and the level of

activation of the individual neurons representing the categorization. The definition of the total processing capacity in NTVA naturally follows as the total activation representing all categorizations of all objects in the visual field:

$$C = \sum_{x \in S} \sum_{i \in R} v(x, i), \quad (3)$$

where S is the set of all visual stimuli and R is the set of all visual categories/features. Referring back to the rate equation (see Eq. (1)), the processing capacity depends on both sensory evidence and perceptual bias. Vangkilde *et al.*⁹⁴ explored how temporal expectancy may modulate processing capacity in a single-stimulus identification experiment. They found strong evidence for an increased processing rate with higher expectancy of the stimulus and suggested that an increase in perceptual bias was the most plausible explanation for their results.

Because RF varies between populations of visual neurons at different levels of the visual system, it also becomes essential to relate processing capacity to variation in RF size. In low-level visual areas such as V1 or V2, RFs are small, and so only a single or at most two objects will be present within the RF of the cells. Competition for representation within the cell will thus be minimally effective, leading to unlimited processing capacity. To see this, compare the situation when one, two, three, or four objects are presented each in a separate quadrant of the visual field at an eccentricity of about 10 visual degrees. In this case, all cells in V1 will have at most one object within their RF due to the large spatial separation compared to the size of the RFs. In accordance with NTVA, let the processing capacity at this level of the visual system be defined as the total activity in the population of V1 cells. Looking at the V1 processing capacity, as the number of presented stimuli increases from one to four, it is straightforward to see that the activity will increase linearly with the number of stimuli, so that the processing capacity when two stimuli are presented is twice as large as when only a single object is presented, and half of the processing capacity, compared to the situation when four stimuli are presented, that is, with unlimited processing capacity. Now, consider the processing capacity at the level of the inferior temporal (IT) cortex: here many cells will have all four stimuli within their RF, leading to strong competition for representation between the objects. At

this level in the visual system the processing capacity will only increase minimally when several stimuli are presented, compared to the condition with only a single stimulus within the visual field, that is, limited processing capacity. Finally, consider processing at the level of V4: some neurons will have only one stimulus in their RF, but several cells will have two and even three stimuli within their RF. Thus, competition will vary across the population of cells in V4 and, consequently, visual processing capacity will neither be unlimited as at the level of V1 nor strongly limited as in IT.

Kyllingsbæk *et al.*⁹⁵ found support for the relationship between processing capacity and RF size by manipulating the spatial separation between several stimulus letters in a whole report, while keeping the eccentricity of the stimuli constant. The proportion of correctly identified letters was a strictly increasing decelerating function of the spatial separation of the stimuli, indicating increased processing capacity when the spatial separation between the stimuli was increased. To explain the results, a computational model of visual crowding was developed based on the assumption in NTVA of dynamic remapping of RFs of neurons in the visual cortex. Using the model, Kyllingsbæk *et al.*⁹⁵ estimated the size of the RFs involved in the processing of the letter stimuli. The estimated radius of the RFs was 29° of visual angle, which corresponded well with neurophysiological findings by recordings in the inferotemporal cortical visual area of macaque monkeys.^{96,97}

Is processing capacity allocated in one or two stages?

Though LT and NTVA are common in their focus on limits in overall processing capacity, the two theories differ strongly in how processing capacity is allocated. According to LT, allocation of perceptual processing resources happens in two stages. To understand the distinction between the two stages, it is important to understand the distinction made by LT between *task-relevant* and *task-irrelevant* objects, both defined in terms of location. Task-relevant objects are located at positions in the visual field that *may* contain a target (e.g., the positions may otherwise contain a distractor or be empty). In contrast, task-irrelevant items are presented at positions in the visual field where a target will *never* appear during the task. In the first stage, LT assumes that processing resources are exclusively allocated to

stimuli at task-relevant locations. Only in the second stage, spare processing resources left over from the first stage may spill over to task-irrelevant objects, which will then also be processed.

In contrast to LT, NTVA assumes that allocation of processing resources happens in a single step: once attentional weights have been computed, all available processing resources are distributed across the objects in the visual field in direct proportion to the attentional weights of the objects (see Eq. (1)). Thus, in contrast to LT, processing resources to distractors at task-irrelevant positions are allocated at the same time as processing resources to targets and distractors at task-relevant positions.

In two partial-report experiments, Kyllingsbæk *et al.*³¹ tested the predictions of LT and NTVA against each other. In the first experiment, four target letters were presented at four out of six possible task-relevant locations. In the periphery, zero, one, or two neutral distracting flankers were shown at two task-irrelevant locations. The flankers were neutral in the sense that they had no relation to the targets in terms of response selection. The color of the flanking distractors was either the same (blue) as the targets or different (red). The exposure duration of the stimulus display was manipulated systematically and terminated by pattern masks. The task of the participants was to report correctly on as many of the four target letters as possible. If allocation of processing resources happens in two stages, as conjectured by LT, allocation to the four targets should happen in the first stage and be independent of both the number of flanking stimuli and their color. However, strong effects of both manipulations were found. The number of correctly reported targets *decreased* with the number of flanking stimuli and *increased* when the flankers were colored in a different color than the targets, thus enabling the participants to ignore them more efficiently. All these effects were modeled very well when fitting the data with NTVA, thus favoring the simpler assumption of a single stage of allocation of processing resources.

In the second experiment, the perceptual load was manipulated by varying the number of targets to be reported between two and eight letters. The flankers were shown in the same color as the targets (blue) and the number of flankers again varied between one and two. Again, NTVA fitted the data well, assuming a single allocation stage.

In addition, Kyllingsbæk *et al.*³¹ explored the interaction between VSTM capacity and the perceptual load (the number of targets) of the task. They found that the effect of the number of flankers was strongest when the perceptual load was close to the estimated capacity of VSTM and weaker for perceptual loads below and above VSTM capacity. This prediction follows naturally from NTVA: when the perceptual load is close to VSTM capacity, relatively high attentional weights, and thus processing capacity, are assigned to flankers. In addition, when the limit of VSTM is reached, a flanker entering VSTM before it is filled up will prevent a subsequent target from entering. These two combined effects lead to a stronger decrement in overall performance compared to when the perceptual load is below the capacity of VSTM.

Implications

Couching the alternative account of perceptual selectivity within the general BC framework and more specifically on NTVA has several important implications.

First, we argue that the approach gives a more parsimonious explanation of the nature of allocation of visual processing capacity than LT and one that addresses LT's weaknesses. For instance, NTVA makes no arbitrary dichotomized definition of task-relevant versus task-irrelevant stimuli and describes how allocation of attention happens in a single step. This account provides a nice fit with published empirical findings,³¹ whereas LT does not. Additionally, whereas the link between task difficulty and resources that is central to two-stage models like LT has been criticized,^{98,99} NTVA offers a more clear explanation. Indeed, the specificity of our approach, especially Eq. (1), makes it much clearer what constitutes a manipulation of perceptual load: factors that serve to change the rate of processing, ν , change load. Finally, whereas LT has difficulty accounting for evidence showing that top-down expectations about the search task (e.g., target location and load) modulate the perceptual selectivity of attention, our approach does not because top-down expectations are explicitly captured within the NTVA framework by both Eqs. (1) and (2).³³

Second, the NTVA framework can be used to test novel predictions and competing models. For instance, an implicit assumption in LT follows from the sharp distinction between task-relevant and

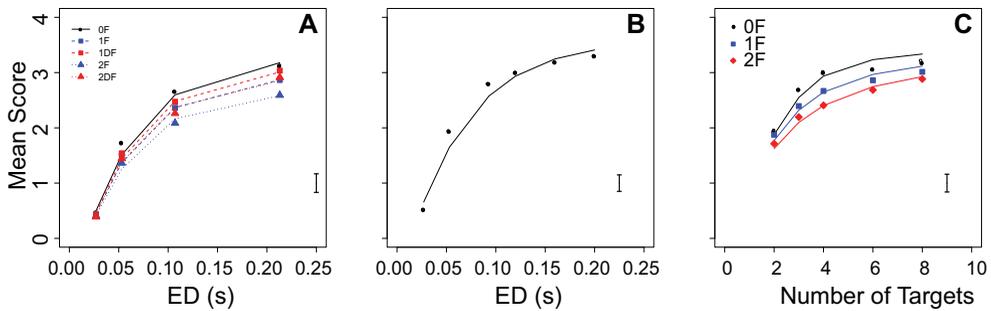


Figure 3. Results from Experiments 1 and 2 in Kyllingsbæk *et al.*³¹ (A) The mean scores as a function of exposure duration and the number and color of the task-irrelevant flankers in Experiment 1. Symbols indicate observed values and lines indicate predicted values derived from TVA. Black filled circles and black solid lines represent trials without any flankers present. Blue symbols and lines represent trials where the task-irrelevant flankers were presented in the same color as the targets. Filled squares and dashed lines represent trials with only one flanker. Filled triangles and dotted lines represent trials with two flankers present. The error bar in the lower right corner of each plot indicates the average standard error of the observed mean scores across participants. (B) The mean score as a function of exposure duration in Experiment 2. Solid black circles represent observed values and solid lines represent predicted values of NTVA. (C) The mean score as a function of the number of targets to be reported in Experiment 2. Black circles represent trials with no flankers presented, blue squares represent trials with a single flanker present, and red diamonds represent trials with two flankers in the display. Solid lines represent predicted values derived from NTVA. The error bars in the lower right corners of the plots representing all participants indicate the average standard error of the observed mean scores across participants. Adapted from Ref. 31 with permission.

task-irrelevant display locations. This implies that the processing of information about the locations of the stimuli is accurate and computed rapidly before the two-stage allocation of processing resources takes place. NTVA makes no such assumption. Importantly, these competing views could be tested by creating two alternative models in NTVA, one based on LT in which location information is available immediately and one in which location information is processed in parallel with the processing of stimulus identity.

Third, the NTVA framework provides a different perspective on recent LT alternatives. Specifically, in the recent literature, LT has been criticized on the grounds that in experiments that manipulate load by manipulating set size, the reduction in task-irrelevant flanker interference observed for larger set sizes (i.e., high load) is not due to increased perceptual load but rather to the processing of the features of the other distractors in the search display.^{25,26,29,32} This so-called *dilution theory* has been supported by a series of behavioral experiments showing that when the number of items are appropriately controlled for in low-load displays, one can still observe reduced distractor interference. However, dilution theory has difficulty explaining reduced interference when display set size is controlled,^{31,67}

as well as difficulty explaining the nonlinear effect of set size we observed in our previous work (Fig. 3).³¹ Moreover, dilution theory also has difficulty accounting for reduced neural responses evoked by task-irrelevant information in high-load single element displays.⁷² It is important to point out that LT can account for these findings, and thus it could be correct for those situations in which load is not manipulated by set size. However, adopting this premise severely limits the explanatory power of LT, and the limitations are compounded when considering the other shortcomings of the model. In contrast, the NTVA framework provides an overarching account of both the effect of dilution when the number of items in the display varies and the reduced distractor interference when the number of items does not.

Fourth, one of the core principles of the NTVA framework is the notion that items compete (race) for representation in VSTM. We argue that this principle plays a key role in determining how the selectivity of attention changes with task demands; and the evidence from our computational work supports this argument.³¹ Others have also reported behavioral evidence consistent with the competition principle by showing that the amount of flanker interference is reduced when targets and

distractors are presented within a single visual hemifield, a condition in which multiple items are likely to be processed by a single cortical representation.⁸⁶ This finding, along with convergent neuroimaging evidence,¹⁰⁰ has led to the proposal that the effects of perceptual load and dilution are mediated by the BC principle.^{85,86} Importantly, this proposal is also consistent with the NTVA framework.

Finally, because NTVA is a computational framework that is based on the underlying physiological properties of the visual system, our account of the perceptual selectivity of attention can both be brought to bear on, and be constrained by, evidence from cognitive psychology, cognitive neuroscience, neuropsychology, and neurophysiology. Importantly, NTVA can be viewed as a part of a larger class of models of attention that also includes the BC model,⁹ the normalization model of attention,⁸³ the selective tuning model,¹⁰¹ the visual attention model,¹⁰² and the ambiguity resolution model.¹⁰³ Thus, future work will need to do detailed comparisons with these other theories to determine which offers the most accurate account of the perceptual selectivity of attention under load.

Conclusion

Understanding the nature of the perceptual selectivity of human attention is a core issue in cognitive neuroscience. The importance of the change in perspective that LT solidified in the literature cannot be underestimated: putting emphasis on identifying the conditions determining (early or late) selection of perceptual information pulled a good portion of the field out of the rut created by the locus of selection debate. The fact that LT also provided an account of the efficiency of perceptual selectivity was also an important contribution. However, based on the recent literature and a close examination of LT, we argue it is time for a new perspective. We have offered one potential new perspective that is rooted in both cognitive psychology and neuroscience and provides a detailed computational account of how bottom-up and top-down information is integrated to provide efficient attentional selection and allocation of perceptual processing resources.

Acknowledgments

The authors thank Hannah Bartlebaugh for her help with the *Web of Science* searches reported in Footnote b. The authors are also grateful to Werner X.

Schneider and one anonymous reviewer for their constructive suggestions on an earlier version of this manuscript. This research was generously supported by the Institute for Collaborative Biotechnologies through Grant W911NF-09-0001 from the U.S. Army Research Office (the content of the information does not necessarily reflect the position or the policy of the U.S. Government and no official endorsement should be inferred), The University of Copenhagen Programme of Excellence, The Danish Agency for Independent Research, Sapere Aude program, and a grant from the University of Copenhagen Excellence Programme for Interdisciplinary Research.

Conflict of interest

The authors declare no conflicts of interest.

References

- Allport, A. 1989. Visual attention. In *Foundations of Cognitive Science*. M.I. Posner Ed.: 631–682. MIT Press: Cambridge, MA.
- Allport, A. 1993. Attention and control: Have we been asking the wrong questions? A critical review of twenty-five years. In *Attention and Performance XIV: Synergies in Experimental Psychology, Artificial Intelligence, and Cognitive Neuroscience*. D.E. Meyer & S. Kornblum Eds.: 183–218. MIT Press: Cambridge, MA.
- Broadbent, D.E. 1958. *Perception and Communication*. Pergamon: London.
- Bundesen, C.A. 1990. Theory of visual attention. *Psychol. Rev.* **97**: 523–547.
- Corbetta, M., G. Patel & G.L. Shulman. 2008. The reorienting system of the human brain: from environment to theory of mind. *Neuron* **58**: 306–324.
- Duncan, J. 1984. Selective attention and the organization of visual information. *J. Exp. Psychol.: Gen.* **113**: 501–517.
- Kahneman, D. & A. Treisman. 1984. *Varieties of Attention*. R. Parasuraman & D.R. Davies Eds. Academic Press: New York.
- Pashler, H. 1998. *The Psychology of Attention*. MIT Press (A Bradford Book): Cambridge, MA.
- Desimone, R. & J. Duncan. 1995. Neural mechanisms of selective visual attention. *Ann. Rev. Neurosci.* **18**: 193–222.
- Broadbent, D.E. 1971. *Decision and Stress*. Academic Press: London.
- Cherry, E.C. 1953. Experiments on the recognition of speech with one and two ears. *J. Acoust. Soc. Am.* **25**: 975–979.
- Deutsch, J.A. & D. Deutsch. 1963. Attention: some theoretical considerations. *Psychol. Rev.* **70**: 80–90.
- Moray, N. 1959. Attention in dichotic listening: affective cues and the influence of instructions. *Quart. J. Exp. Psychol.* **11**: 56–60.
- Treisman, A.M. 1964. Selective attention in man. *Br. Med. Bull.* **20**: 12–16.

15. Lavie, N. & Y. Tsal. 1994. Perceptual load as a major determinant of the locus of selection in visual attention. *Percept. Psychophys.* **56**: 183–197.
16. Lavie, N. 1995. Perceptual load as a necessary condition for selective attention. *J. Exp. Psychol.: Human Percept. Perform.* **23**: 451–468.
17. Giesbrecht, B., J.L. Sy & J.E. Elliott. 2007. Electrophysiological evidence for both perceptual and post-perceptual selection during the attentional blink. *J. Cogn. Neurosci.* **19**: 2005–2018.
18. Giesbrecht, B., J.L. Sy & M.K. Lewis. 2009. Personal names do not always survive the attentional blink: behavioral evidence for a flexible locus of selection. *Vision Res.* **49**: 1378–1388.
19. Kastner, S. & M.A. Pinsk. 2004. Visual attention as a multilevel selection process. *Cogn. Affect. Behav. Neurosci.* **4**: 483–500.
20. Vogel, E.K., G.F. Woodman & S.J. Luck. 2005. Pushing around the locus of selection: evidence for the flexible-selection hypothesis. *J. Cogn. Neurosci.* **17**: 1907–1922.
21. Cho, K.W., C.-S. Tse & J.H. Neely. 2012. Citation rates for experimental psychology articles published between 1950 and 2004: top-cited articles in behavioral cognitive psychology. *Memory Cogn.* **40**: 1132–1161.
22. Lavie, N. 2005. Distracted and confused? Selective attention under load. *Trends Cogn. Sci.* **9**: 75–82.
23. Lavie, N., A. Hirst, J.W. de Fockert & E. Viding. 2004. Load theory of selective attention and cognitive control. *J. Exp. Psychol.: General* **133**: 339–354.
24. Lavie, N. 2010. Attention, distraction, and cognitive control under load. *Curr. Directions Psychol. Sci.* **19**: 143–148.
25. Benoni, H. & Y. Tsal. 2010. Where have we gone wrong? Perceptual load does not affect selective attention. *Vision Res.* **50**: 1292–1298.
26. Benoni, H. & Y. Tsal. 2012. Controlling for dilution effects while manipulating load: perceptual and sensory limitations are just two aspects of task difficulty. *Psychon. Bull. Rev.* **19**: 631–638.
27. Johnson, D.N., A. McGrath & C. McNeil. 2002. Cuing interacts with perceptual load in visual search. *Psychol. Sci.* **13**: 284–287.
28. Theeuwes, J., A.F. Kramer & A.V. Belopolsky. 2004. Attentional set interacts with perceptual load in visual search. *Psychon. Bull. Rev.* **11**: 697–702.
29. Tsal, Y. & H. Benoni. 2010. Diluting the burden of load: perceptual load effects are simply dilution effects. *J. Exp. Psychol.: Human Percept. Perform.* **36**: 1645–1656.
30. Wilson, D.E., M. Muroi & C.M. MacLeod. 2011. Dilution, not load, affects distractor processing. *J. Exp. Psychol.: Human Percept. Perform.* **37**: 319–335.
31. Kyllingsbæk, S., J.L. Sy & B. Giesbrecht. 2011. Understanding the allocation of attention when faced with varying perceptual load in partial report: a computational approach. *Neuropsychologia* **49**: 1487–1497.
32. Benoni, H. & Y. Tsal. 2013. Conceptual and methodological concerns in the theory of perceptual load. *Front. Psychol.* **4**: 522.
33. Bundesen, C., T. Habekost & S. Kyllingsbæk. 2005. A neural theory of visual attention: bridging cognition and neurophysiology. *Psychol. Rev.* **112**: 291–328.
34. Eriksen, C.W. 1966. Temporal luminance summation effects in backward and forward masking. *Percept. Psychophys.* **1**: 87–92.
35. Jonides, J. & S. Yantis. 1988. Uniqueness of abrupt visual onset in capturing attention. *Percept. Psychophys.* **43**: 346–354.
36. Kahneman, D. 1968. Method, findings, and theory in studies of visual masking. *Psychol. Rev.* **70**: 404–425.
37. Schneider, W. & Shiffrin, R.M. 1977. Controlled and automatic human information processing: I. Detection, search, and attention. *Psychol. Rev.* **84**: 1–66.
38. Serences, J.T. *et al.* 2005. Coordination of voluntary and stimulus-driven attentional control in human cortex. *Psychol. Sci.* **16**: 114–122.
39. Serences, J.T. & S. Yantis. Spatially selective representations of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. *Cereb. Cortex*, In press.
40. Wolford, G. & S. Hollingsworth. 1974. Retinal location and string position as important variables in visual information processing. *Percept. Psychophys.* **16**: 437–442.
41. Johnston, W.A. & V.J. Dark. 1986. Selective attention. *Ann. Rev. Psychol.* **37**: 43–75.
42. Hillyard, S.A., R.F. Hink, V.L. Schwent & T.W. Picton. 1973. Electrical signs of selective attention in the human brain. *Science* **182**: 177–180.
43. Luck, S.J. *et al.* 1994. Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection. *J. Exp. Psychol.: Human Percept. Perform.* **20**: 887–904.
44. Van Voorhis, S.T. & S.A. Hillyard. 1977. Visual evoked potentials and selective attention to points in space. *Percept. Psychophys.* **22**: 54–62.
45. Luck, S.J., E.K. Vogel & K.L. Shapiro. 1996. Word meanings can be accessed but not reported during the attentional blink. *Nature* **383**: 616–618.
46. Allport, A. 1987. Selection for action: Some behavioral and neurophysiological considerations of attention and action. In *Perspectives on Perception and Action*. H. Heuer & A.F. Sanders Eds.: 395–420. Lawrence Erlbaum Associates, Inc.: Hillsdale, NJ.
47. Gatti, S.W. & H.E. Egeth. 1978. Failure of spatial selectivity in vision. *Bull. Psychon. Soc.* **11**: 181–184.
48. Dark, V.J., W.A. Johnston, M. Myles-Worsley & M.J. Farah. 1985. Levels of selection and capacity limits. *J. Exp. Psychol.: General* **114**: 472–497.
49. Kahneman, D. & D. Chajczyk. 1983. Tests of the automaticity of reading: dilution of Stroop effects by color-irrelevant stimuli. *J. Exp. Psychol.: Human Percept. Perform.* **9**: 497–509.
50. Yantis, S. & J.C. Johnston. 1990. On the locus of visual selection: evidence from focused attention tasks. *J. Exp. Psychol.: Human Percept. Perform.* **16**: 135–149.
51. Eriksen, C.W. & Y. Yeh. 1985. Allocation of attention in the visual field. *J. Exp. Psychol.: Human Percept. Perform.* **11**: 583–597.

52. James, W. 1890. *The Principles of Psychology*. Henry Holt & Co.: New York.
53. Forster, S. & N. Lavie. 2007. High perceptual load makes everybody equal: eliminating individual differences in distractibility with load. *Psychol. Sci.* **18**: 377–381.
54. Remington, A.M., J.G. Swettenham & N. Lavie. 2012. Lightening the load: perceptual load impairs visual detection in typical adults but not in autism. *J. Abnormal Psychol.* **121**: 544–551.
55. Lavie, N. & I. Robertson. 2001. The role of perceptual load in visual neglect: rejection of ipsilesional distractors is facilitated with higher central load. *J. Cogn. Neurosci.* **13**: 867–876.
56. Maylor, E.A. & N. Lavie. 1998. The influence of perceptual load on age differences in selective attention. *Psychol. Aging* **13**: 563–573.
57. Forster, S. & N. Lavie. 2009. Harnessing the wandering mind: the role of perceptual load. *Cognition* **111**: 345–355.
58. Beck, D.M., G. Rees, C.D. Frith & N. Lavie. 2001. Neural correlates of change detection and change blindness. *Nature Neurosci.* **4**: 645–650.
59. Cartwright-Finch, U. & N. Lavie. 2007. The role of perceptual load in inattention blindness. *Cognition* **102**: 321–340.
60. Lavie, N. 2006. The role of perceptual load in visual awareness. *Brain Res.* **1080**: 91–100.
61. Kahneman, D. 1973. *Attention and Effort*. Prentice-Hall: Englewood Cliffs, NJ.
62. Navon, D. & D. Gopher. 1979. On the economy of the human processing system. *Psychol. Rev.* **80**: 214–255.
63. Norman, D.A. & D.G. Bobrow. 1975. On data-limited and resource-limited processes. *Cogn. Psychol.* **7**: 44–64.
64. Wickens, C.D. 1980. The structure of attentional resources. In *Attention and Performance VIII*. R. Nickerson Ed.: 239–257. Erlbaum: Hillsdale, NJ.
65. Treisman, A.M. & G.A. Gelade. 1980. Feature-integration theory of attention. *Cogn. Psychol.* **12**: 97–136.
66. Eriksen, B.A. & C.W. Eriksen. 1974. Effects of noise letters upon the identification of a target letter in a nonsearch task. *Percept. Psychophys.* **16**: 143–149.
67. Lavie, N. & S. Cox. 1997. On the efficiency of attentional selection: efficient visual search results in inefficient rejection of distraction. *Psychol. Sci.* **8**: 395–398.
68. Rees, G., C.D. Frith & N. Lavie. 1997. Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science* **278**: 1616–1619.
69. Handy, T.C., M. Soltani & G.R. Mangun. 2001. Perceptual load and visuo-cortical processing: event-related potentials reveal sensory-level selection. *Psychol. Sci.* **12**: 213–218.
70. Pessoa, L., M. McKenna, E. Guitierrez & L.G. Ungerleider. 2002. Neural processing of emotional faces requires attention. *Proc. Natl. Acad. Sci. U. S. A.* **99**: 11458–11463.
71. Yi, D.-J., G.F. Woodman, D. Widders, *et al.* 2004. Neural fate of ignored stimuli: dissociable effects of perceptual and working memory load. *Nature Neurosci.* **7**: 992–996.
72. Schwartz, S. *et al.* 2005. Attentional load and sensory competition in human vision: modulation of fMRI responses by load at fixation during task-irrelevant stimulation in the peripheral visual field. *Cereb. Cortex* **15**: 770–786.
73. Boudreau, C.E., T.H. Williford & J.H.R. Maunsell. 2006. Effects of task difficulty and target likelihood in Area V4 of macaque monkeys. *J. Neurophysiol.* **96**: 2377–2387.
74. Chen, Y. *et al.* 2008. Task difficulty modulates the activity of specific neuronal populations in primary visual cortex. *Nature Neurosci.* **11**: 974–982.
75. Carmel, D., J.D. Thorne, G. Rees & N. Lavie. 2011. Perceptual load alters visual excitability. *J. Exp. Psychol.: Human Percept. Perform.* **37**: 1550–1560.
76. Breitmeyer, B.G. 1984. *Visual Masking: An Integrative Approach*. Oxford University Press: New York.
77. Lavie, N. & J.W. de Fockert. 2003. Contrasting effects of sensory limits and capacity limits in visual selective attention. *Percept. Psychophys.* **65**: 202–212.
78. Serences, J.T., S. Yantis, A. Culbertson & E. Awh. 2004. Preparatory activity in visual cortex indexes distractor suppression during covert spatial orienting. *J. Neurophysiol.* **92**: 3538–3545.
79. Forster, S. & N. Lavie. 2011. Entirely irrelevant distractors can capture and captivate attention. *Psychon. Bull. Rev.* **18**: 1064–1070.
80. Desimone, R. 1996. Neural mechanisms for visual memory and their role in attention. *Proc. Natl. Acad. Sci. U. S. A.* **93**: 13494–13499.
81. Desimone, R. 1998. Visual attention mediated by biased competition in extrastriate visual cortex. *Phil. Trans. R. Soc. Lond. B. Biol. Sci.* **353**: 1245–1255.
82. Duncan, J. 1996. Cooperating brain systems in selective perception and attention. In *Attention and Performance XVI: Information Integration in Perception and Communication*. T. Inui & J.L. McClelland Eds.: 549–578. MIT Press: Cambridge, MA.
83. Reynolds, J.H. & D.J. Heeger. 2009. The normalization model of attention. *Neuron* **61**: 168–185.
84. Bundesen, C., T. Habekost & S. Kyllingsbæk. 2011. A neural theory of visual attention and short-term memory (NTVA). *Neuropsychologia* **49**: 1446–1457.
85. Scalf, P.E., A. Torralbo, E. Tapia & D.M. Beck. 2013. Competition explains limited attention and perceptual resources: implications for perceptual load and dilution theories. *Front. Psychol.* **4**: 243.
86. Torralbo, A. & D.M. Beck. 2008. Perceptual-load-induced selection as a result of local competitive interactions in visual cortex. *Psychol. Sci.* **19**: 1045–1050.
87. Nordfang, M., Dyrholm, M., & Bundesen, C. 2013. Identifying bottom-up and top-down components of attentional weight by experimental analysis and computational modeling. *J. Exp. Psychol.: Gen.* **142**: 510–535.
88. Chelazzi, L., J. Duncan, E.K. Miller & R. Desimone. 1998. Responses of neurons in inferior temporal cortex during memory-guided visual search. *J. Neurophysiol.* **80**: 2918–2940.
89. Chelazzi, L., E.K. Miller, J. Duncan & R. Desimone. 1993. A neural basis for visual search in inferior temporal cortex. *Nature* **363**: 345–347.

90. Moran, J. & R. Desimone. 1985. Selective attention gates visual processing in extrastriate cortex. *Science* **229**: 782–783.
91. Reynolds, J.H., L. Chelazzi & R. Desimone. 1999. Competitive mechanisms subserve attention in macaque areas V2 and V4. *J. Neurosci.* **19**: 1736–1753.
92. McAdams, C.J. & J.H.R. Maunsell. 1999. Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *J. Neurosci.* **19**: 431–441.
93. Martinez-Trujillo, J.C. & S. Treue. 2004. Feature-based attention increases the selectivity of population responses in primate visual cortex. *Curr. Biol.* **14**: 744–751.
94. Vangkilde, S., J.T. Coull & C. Bundesen. 2012. Great expectations: temporal expectation modulates perceptual processing speed. *J. Exp. Psychol.: Human Percept. Perform.* **38**: 1183–1191.
95. Kyllingsbæk, S., C. Valla, J. Vanrie & C. Bundesen. 2007. Effects of spatial separation between stimuli in whole report from brief visual displays. *Percept. Psychophys.* **69**: 1040–1050.
96. Desimone, R. & Ungerleider, L.G. 1989. Neural mechanisms of visual processing in monkeys. *Handbook of Neuropsychology*. Vol. 2. Boller & J. Grafman Eds.: 267–299. Elsevier Science Publishers: Amsterdam.
97. Desimone, R. & C.G. Gross. 1979. Visual areas in the temporal cortex of the macaque. *Brain Res.* **14**: 363–380.
98. Neumann, O. 1984. Automatic processing: A review of recent findings and a plea for an old theory. *Cognition and Motor Processes*. W. Prinz & A.F. Sanders Eds.: 255–293. Springer: Berlin.
99. Neumann, O. 1987. Beyond capacity: A functional view of attention. *Perspectives on Perception and Action*. H. Heuer & A.F. Sanders Eds.: 361–394. Lawrence Erlbaum Associates, Inc.: Hillsdale, NJ.
100. Scaf, P.E. & D.M. Beck. 2010. Competition in visual cortex impedes attention to multiple items. *J. Neurosci.* **30**: 161–169.
101. Tsotsos, J. *et al.* 1995. Modelling visual attention via selective tuning. *Art. Intell.* **78**: 507–547.
102. Schneider, W.X. 1995. VAM: a neuro-cognitive model for visual attention control of segmentation, object recognition, and space-based motor action. *Vis. Cogn.* **2**: 331–375.
103. Luck, S.J., M. Girelli, M.T. McDermott & M.A. Ford. 1997. Bridging the gap between monkey neurophysiology and human perception: an ambiguity resolution theory of visual selective attention. *Cogn. Psychol.* **33**: 64–87.