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Perceptual load-induced selection as a result of local competitive interactions in visual cortex

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Abstract

There is a growing literature which suggests that the degree to which distracting information can be ignored depends on the *perceptual load* of the task, or the extent to which the task exhausts perceptual capacity. However, there is currently no a priori definition of what constitutes high or low perceptual load. Here we propose that local spatial interactions among stimuli in visual cortex determine the perceptual load of a task, and thus manipulations designed to reduce those spatial interactions should modulate distractor processing. We found that either spatially separating the task-relevant items in a display or placing them in different visual fields resulted in greater distractor interference. These data are consistent with the idea that our ability to ignore distracting information is the result of the need to actively resolve competitive interactions in visual cortex, and not the consequence of an exhausted capacity *per se*.

The extent to which distracting information can be ignored has been debated for decades, with some researchers suggesting that ignored information is filtered early in the system such that it is essentially blocked from perception (i.e. early selection; e.g. Broadbent, 1958) and others suggesting the unattended information is processed to a fairly high level and thus can still influence behavior (i.e. late selection; Deutsch and Deutsch, 1963). A more recent theory, however, proposes that attentional selection can be either early or late, depending on the perceptual demands of the relevant task (Lavie, 1995). When the perceptual demands, or *perceptual load*, of the task is high, then few resources are available for processing the distractor and the distractor is excluded *early* in processing. However, when the perceptual load of the task is low and consequently does not exhaust perceptual capacity, then the remaining resources spill over on to the distractors and processing proceeds past the early stages resulting in the need for *late* selection. Although this theory has received considerable support from both behavioral and neuroimaging experiments (Lavie, 1995; Lavie & Cox, 1997; Rees, Frith & Lavie, 1997; Beck & Lavie, 2005; Handy, Soltani & Mangun, 2001), it remains unsatisfying for two reasons. First, a clear definition of perceptual load has yet to emerge. Second, the concept of an exhausted capacity is difficult to accord with mechanisms in the brain. We propose a definition of perceptual load that is both neurally plausible and generates two novel predictions that are supported by the data.

There exist a number of phenomena whereby the detectability, discriminability or the neural representation of a target stimulus is diminished by the presence of nearby items (Andriessen & Bouma, 1976; Polat & Sagi, 1993; Kastner, de Weerd, Desimone, Ungerleider, 1998; Reynolds, Chelazzi & Desimone, 1999; Intriligator & Cavanagh, 2001; Petrov, Carandini, & McKee, 2005) and many of these phenomena are thought to occur due to local spatial interactions among cells in early to intermediate areas in visual cortex (eg. striate and extrastriate cortex; Kastner et al, 1998; Reynolds et al, 1999; Blakemore & Tobin, 1972; DeAngelis, Robson, Ohzawa & Freeman, 1992; Polat, Mizobe, Pettet,

Kasamatsu & Norcia, 1998; Bair, Cavanaugh & Movshon, 2003; Reynolds & Desimone, 2003). For example, stimuli presented simultaneously in the visual field are not processed independently, but instead interact in a mutually suppressive way that suggests a competition for neural representation (Desimone & Duncan, 1995; Kastner et al, 1998; Reynolds et al, 1999; Beck & Kastner, 2005). Moreover, evidence suggests that selective attention can bias this competition in favor of the attended stimulus; that is, suppressive interactions among stimuli decrease or disappear when the subject attends to a single item (Kastner et al, 1998; Reynolds et al, 1999).

We propose that these competitive interactions in visual cortex and the resulting biasing mechanisms needed to resolve the competition in favor of the target may be the neural mechanisms underlying perceptual load. In particular, we suggest that the degree to which items within a display compete for representation in visual cortex determines the strength of the biasing mechanisms necessary to resolve the competition, which will, in turn, determine the degree to which unattended information is processed. Stimuli that induce strong competitive interactions among items should require a strong top-down bias in order to overcome the competition and select the target, and can thus be characterized as high perceptual load. Whereas tasks in which minimal competition is induced among the task-relevant items will require little top-down bias in order to select the target and can thus be characterized as low perceptual load.

Such a characterization of perceptual load fits well with the two most common manipulations of load in the literature, increments in the number of items in a display (i.e. set size) and the similarity of target and non-targets. Increments in set size are said to increase the perceptual demands of the task, and have been shown to result in diminished interference from a distractor, as predicted by perceptual load theory (Lavie & Cox, 1997). However, increments in the number of items in a display will also increase the likelihood of suppressive interactions in visual cortex (i.e. there are more items to interact), thus resulting in a greater need for top-down biasing in order to identify the target.

In a second common manipulation of perceptual load, set size is kept constant and the similarity of the target and the non-target items is manipulated (Lavie & Cox, 1997; Beck & Lavie, 2005). In low load, the target and non-targets are perceptually dissimilar making the target salient and easy to detect (i.e. the target is an X or N embedded in a field of O's). Such a manipulation is also consistent with data showing that suppressive interactions among stimuli in visual cortex are reduced when one of the items is made salient (Reynolds et al, 2003; Beck & Kastner, 2005). In high load, however, the same targets are embedded among other angular letters that share many of the features with the target (i.e. Y, Z, H). Therefore, the target does not benefit from increased saliency and thus a strong top-down bias will be needed to bias the competition in favor of the target.

Experiment 1

This conception of perceptual load as determined by competitive interactions in visual cortex, not only can account for previous perceptual load manipulations, but it also suggests two novel and previously untested perceptual manipulations which should modulate distractor processing. First, because these spatial interactions are thought to occur locally, the distance between potential target items should impact the degree to which these interactions occur. Indeed, the distance between stimuli has been shown to modulate suppressive interactions in visual cortex (Kastner, de Weerd, Pinsk, Elizondo, Desimone & Ungerleider, 2001; Bles, Schwarzbach, de Weerd, Goebel & Jasma, 2006). Thus, if perceptual load is determined by local interactions among stimuli, as we have been arguing, then manipulations of display density should modulate the degree to which subjects are able

to ignore a distractor. Specifically, we should find that as the distance between the target and non-target stimuli decreases, the bias needed to resolve the competition should increase, resulting in the diminished processing of the distractor. Because set size, target and non-target similarity, and the distance between the target and distractor are kept constant across our density conditions, there would be no reason to expect on the basis of previous perceptual load manipulations that the density of the search display should impact distractor processing. It is reasonable to suspect, however, that finding a target in higher density displays would be more difficult, and thus may be considered high perceptual load. However, we stress that our manipulation was derived in a principled way from our theory regarding local interactions, not, as many perceptual load manipulations before it, based on an appeal to task difficulty. Such appeals are not wholly satisfying as they beg the question of why the task is more difficult in the first place.

Method

Sixteen volunteers recruited from the University of Illinois, Urbana-Champaign participated for course credit or monetary reward.

Subjects' task was to search an array of four letters for a target letter (X or Z) arranged in an arc (radius of 3.7° of visual angle) around a central fixation point (Fig. 1a). The density of the display was manipulated by either placing small circles ($0.2^\circ \times 0.2^\circ$) between each letter resulting in a center-to-center distance of 2.57° between adjacent letters (low density) or placing the four letters immediately adjacent to each other, separated by 1.29° with the circles on either side of the letters (high density). Stimuli were presented for 100 ms immediately following a fixation cross that appeared in the center of the screen for 500 ms. Trials terminated following a response, or after 2 seconds if there was no response. At a viewing distance of 40 cm (stabilized by a chin rest), each letter in the search array subtended $0.7^\circ \times 1^\circ$ of visual angle and the distractor, which was fixated, subtended $0.8^\circ \times 1.1^\circ$.

Targets appeared equally in one of the two inner positions of the array, and the search array appeared randomly and equally in one of the four quadrants. Within a block, the distractor was equally likely (i.e. 33.3%) to be compatible (e.g. Z when target was Z), incompatible (e.g. Z when target was X) or neutral (R when the target is X or Z) with respect to the target. Half of the participants started with a low-density block and half began with a high-density block, and then alternated between block types. They completed a practice block of 48 trials and six experimental blocks of 96 trials at each density condition. Participants were instructed to answer as quickly as possible once they identified the target by pressing one of the two keys (counterbalanced across participants) on the keyboard with their right and left index fingers. They completed 24 trials of each density by compatibility by target position by array location condition.

Results and Discussion

Mean RTs and error rates were computed for each participant as a function of compatibility (compatible, incompatible) and density (low, high) and entered into a two-way within-subject ANOVA. Error trials were not included in any RT analyses. RTs faster or slower than 2.5SD above or below the mean of each condition, computed separately for each subject, were considered outliers and excluded from the RT analyses. This affected 3% of the correct responses.

There was a main effect of density, such that RTs to high density displays were slower than to low density, $F(1,15)=8.48$, $p<.01$; (666 ms and 648 ms respectively). The degree to which

subjects processed a distractor placed at fixation was assessed by comparing reaction times (RTs) to the target as a function of whether the distractor was compatible or incompatible with the target response. There was a main effect of compatibility ($F(2,30)=28.54$, $p<.0001$), such that mean RTs in the presence of an incompatible distractor (679 ms) were significantly slower than in the presence of a compatible distractor (647 ms; $t(15)=5.09$, $p<.0001$) or neutral distractor (646 ms; $t(15)=7.55$, $p<.0001$), indicating that the distractor was in fact processed despite instructions to ignore it because it was irrelevant to the task. Importantly, however, this distractor effect was modulated by the density manipulation ($F(2,30)=4.32$, $p<.022$), such that the high density displays produced much smaller distractor effects (Fig. 1b). Distractor compatibility effects were significant for both low density (40 ms; $t(15)=5.42$, $p<.0001$, two-tailed paired t-test) and high density (24 ms; $t(15)=4.21$, $p<.001$), but were significantly reduced in the high density condition. A similar pattern was seen in the error rates (Table 1), but only the main effect of compatibility was significant, $F(2,30)=6.26$, $p<.005$. Thus, in accordance with our hypothesis that local competitive interactions in visual cortex underlie manipulations of perceptual load, more closely spaced letters actually resulted in less interference from a distractor than a less dense letter display.

Experiment 2

The conception of perceptual load as reflecting local suppressive interactions in visual cortex makes another and more surprising prediction. Local suppressive interactions have primarily been seen in early to intermediate levels of visual cortex (i.e. V1–V4) in which the representation of a visual hemifield (right or left) is confined to the contralateral hemisphere. If perceptual load is determined by local interactions in these areas, then placing multiple items within the same hemifield should result in greater perceptual load and reduced distractor processing than when the target item appears alone within a hemifield, and thus is not subject to the same local interactions. This hemifield manipulation was achieved by placing the peripheral search display (the target and three non-target letters arranged in a diamond configuration) such that only one of the four items crossed the vertical midline (Fig. 2a). In half of the trials the target was the item that crossed the midline, and thus appeared alone in the hemifield, and in the other half of the trials, the target shared a hemifield with the two non-target items.

Method

Twenty volunteers recruited from the University of Illinois, Urbana-Champaign participated in this study for course credit or monetary reward.

Subjects' task was to identify a target letter (X or Z) in a peripheral search display arranged in a diamond configuration. The sides of the diamond subtended 1.57° and the two target positions (right or left vertices of the diamond) were located 5.3° from fixation (see Fig 2a). The minor and major axes of the diamond subtended 1.40° and 2.80° respectively. The edge of targets was 0.28° or 1.76° from the midline and non-targets were 0.28° , 0.50° and 1.76° from the midline. Distractors were equally likely to be compatible or incompatible. As in the first experiment, the distractor was located at fixation, and thus represented in both hemifields. Participants completed a practice block of 32 trials and 6 experimental blocks of 64 trials each. They completed 24 trials of each target location by compatibility by array location condition, which were randomly intermixed within blocks. Because local interactions should occur within and not between visual hemifields, we predict greater competition among target and non-target letters, and thus reduced distractor processing, when the target and non-targets appear in the same hemifield than when they appear in different hemifields.

Results and Discussion

As in Experiment 1, mean RTs and error rates were computed for each participant as a function of compatibility (compatible, incompatible) and hemifield (target in *same* hemifield as non-targets, or target in *different* hemifield than non-targets) and submitted to a two-way within-subject ANOVA. Using the same procedure as in Experiment 1, 2.8% of correct responses were excluded as RT outliers. There was a main effect of compatibility; RTs to incompatible trials were slower than to compatible trials, $F(1,19)=13.27$, $p<.002$; (691 ms and 674 ms respectively). However, as predicted, trials in which the target appeared in a different hemifield than the non-targets produced greater distractor effects than trials in which the target appeared in the same hemifield as the non-targets ($F(1,19)=6.97$, $p<.016$; see Fig 2b, and Table 1 for error rates). Distractor compatibility effects were significant when the target was presented alone in the hemifield (27 ms; $t(19)=4.75$, $p<.0001$, two-tailed paired t-test) but not when the target and non-target appeared in the same hemifield (8 ms; $p>.2$). It should be pointed out that, because observers are generally unaware of the division between their left and right hemifields, from the subjects' perspective the task was the same throughout the experiment, yet the hemifield manipulation had a dramatic effect on distractor effects. These results further support our proposal that perceptual load is determined by local interactions in early to intermediate levels of visual cortex, because it is in these areas that the right and left visual field are processed in separate hemispheres.

Interestingly, these results not only support the hypothesis that local suppressive interactions among the target set dictate the extent to which a distractor can be ignored, but they also suggest that the attentional bias is determined independently in the two visual cortices. Despite the fact that the target set forms a single perceptual group, the degree to which the distractor was processed depended on the location of the target within that group. By our theory, a strong bias was produced when the target appeared in the same hemifield as the non-targets, whereas a weak, or non-existent, bias was produced when the target appeared in a different hemifield than the non-targets.

This result is in accordance with evidence of parallel attentional processing by the two hemispheres in split-brain patients (Luck, Hillyard, Mangun & Gazzaniga, 1989) and more recently in neurologically intact subjects (Alvarez & Cavanagh, 2005; Sclaf, Banich, Kramer, Narechania & Simon, 2007). Moreover, our theory suggests why attentional biases may be determined independently in the two hemispheres, despite the fact that information in the two hemispheres is integrated across visual fields in higher visual areas. If the task is such that targets must be resolved in early to intermediate levels of visual cortex (i.e. local suppressive interactions in those areas must be counteracted in order to resolve the target), then different top-down biases may develop to resolve competition in the two visual cortices.

General Discussion

The data presented here suggest that competition for representation in visual cortex may underlie perceptual load, and thus determine the degree to which unattended information is processed. Stimuli that should produce greater competition in visual cortex resulted in distractor effects akin to high perceptual load. Moreover, these experiments implicate local interactions in early to intermediate levels of visual cortex in which the representation of the visual fields is both spatiotopic (Experiment 1) and in which right and left visual field are represented in separate hemispheres (Experiment 2). Higher visual areas, such as inferotemporal cortex, have large receptive fields that encompass both visual hemifields and therefore, they are less probable candidates for effects found here (Gross, Rocha-Miranda & Bender, 1972).

We should note that some researchers have manipulated perceptual load in ways that cannot be explained by appealing to local competitive interactions because the manipulations do not involve changes to the stimuli, but changes to the task itself (eg. discriminate colors versus discriminate color and orientation conjunctions; Lavie, 1995; Handy et al, 2001). Thus, we are not suggesting that the only way in which to manipulate the perceptual load of the task is to manipulate local competitive interactions in visual cortex. However, it is possible that the same biasing mechanisms needed to resolve local competitive interactions may be involved in binding features, such as orientation and color, into a single object in a conjunction task (Duncan, Humphreys & Ward, 1997; Schoenfeld et al, 2003). In other words, the smaller distractor effects found in conjunction versus feature task may also reflect the need for a stronger top-down biasing mechanism in the conjunction than the feature task.

Finally, these data and our theory suggest a neurally plausible description of perceptual resources. Many researchers have taken issue with the concept of a resource as it is not clear what this means in terms of the brain. We suggest that the so-called limited resource that stimuli are competing for is the response of local regions of visual cortex. However, it is also clear from our description of local suppression and the ensuing bias that although the concept of resources provides a convenient description of the data, we are proposing very different underlying neural mechanisms. It is not the case that perceptual resources are exhausted per se, but rather that in order to overcome local suppressive interactions, a strong bias is necessary to isolate and improve the representation of the target.

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Figure 1. Displays and results of density experiment

a, Examples of displays with stimuli appearing in the upper left quadrant. **b**, Mean reaction time of correct responses plotted against array density and distractor compatibility. Error bars denote standard error of the mean.

Figure 2. Displays and results of visual field experiment

a, Examples of targets appearing in the same or different hemifields as the non-targets (target in left hemifield not shown). Gray circle, lines and distance in upper left panel were not shown in the actual experiment. **b,** Mean reaction time of correct responses plotted against visual field and compatibility. Error bars denote standard error of the mean.

Table 1

Mean error rates for as a function of compatibility in Experiments 1 (Density) and 2 (Hemifield).

Density		
	Low	High
Compatible	5 (0.0094)	5 (0.0076)
Neutral	4 (0.0089)	4 (0.0087)
Incompatible	6 (0.0114)	5 (0.0085)
Hemifield		
	Different	Same
Compatible	9 (0.0118)	10 (0.0135)
Incompatible	9 (0.0122)	9 (0.0129)

Standard error of the mean in parentheses.