CORTICAL COMPETITION: A NEURALLY PLAUSIBLE ACCOUNT OF HEMISPHERE-SPECIFIC PROCESSING RESOURCES?

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THESIS
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ABSTRACT

Recent studies have shown performance advantages in visual tasks when task-relevant stimuli are presented in different visual hemifields as opposed to a single hemifield. A common interpretation of these findings is that each cortical hemisphere has an independent tank of processing resources and that overloading a single hemisphere leads to performance degradation. However, it is not clear what such processing resources might be. We explore three ways of interpreting processing resources and their relationship to hemifield independence: resources as a kind of neural fuel, as a limitation on the coordination of attentional deployment, and as competition (interference) between representations in visual cortex. We report three experiments centered on hemifield independence that provide constraints on each of the three models. Experiments 1 and 2 show that, while fixing hemifield-level display density, local display density seems to drive hemifield independence. We argue that the competition model a priori predicts this effect and offer suggestions for how the other models can be adapted to account for it. Experiment 3 shows that hemifield independence can be modulated by attention: when the location of target is validly cued hemifield independence disappears. Once again, this effect is predicted by the competition model but is not inconsistent with the other two models. Taken as a whole, we argue that these three experiments provide constraints on any successful explanation of hemifield independence and suggest that the competition model naturally satisfies these constraints.
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1. Introduction

A number of studies have shown surprising and significant performance advantages when task-relevant stimuli are spread across both the left and right visual hemifields as opposed to when the same stimuli appear within a single hemifield (Sereno & Kosslyn, 1991; Awh & Pashler, 2000; Alvarez & Cavanagh, 2005; Delvenne, 2005; Scalf et al., 2007). One study (Alvarez & Cavanagh, 2005), for instance, found that spreading objects into both hemifields effectively doubled the number of objects that participants could track. This dramatic asymmetry in processing capacity due to hemifield placement (which has been called hemifield independence) has important implications for models of attention and working memory, as well as practical applications (e.g., how to represent information to improve processing capacity). Understanding the cognitive and neural underpinnings of hemifield independence can thus inform both theory and application.

However, despite a wealth of data demonstrating hemifield independence as a behavioral phenomenon, tractable cognitive and neural explanations remain elusive. There is general agreement that hemifield independence arises due to independent processing resources in each cortical hemisphere (e.g., Alvarez & Cavanagh, 2005; Franconeri & Alvarez, 2007; Alvarez, Gill, & Cavanagh, 2012). Since the left and right visual hemifields project to contralateral cortical hemispheres, displaying items across hemifields thus spreads the visual load across two hemispheres (and two processors). Conversely, putting items into a single visual hemifield concentrates the visual load onto a single processor, increasing the difficulty of the task. While this hemifield-specific processing resources account seems to fit much of the behavioral data well, the cognitive and neural mechanisms that underlie it remain relatively unspecified. Our
goal here is to outline a neural mechanism that we believe can inform and constrain cognitive-
level explanations of hemifield independence.

In what follows we compare three explanations of hemifield independence: a resource
model, an attentional-control model, and a competition model. Each of these models explains
hemifield independence by reference to different processing bottlenecks. The resource model
conceptualizes attention as a kind of processing fuel (Kahneman 1973; Lavie, 1995; Franconeri
& Alvarez, 2007) and explains capacity limits as due to the depletion of attention. The
attentional-control model explains hemifield independence as the result of capacity limits in the
coordination of attentional deployment (Alvarez, Gill, & Cavanagh, 2012). The competition
model claims that within-hemifield processing limitations may result from local interference
between representations in visual cortex (Sereno & Kosslyn, 1991; Scalf & Beck, 2010; Scalf,

1.1 The Resource Model

Attention is often conceptualized as a capacity limited fuel or resource that is necessary
for the visual system to construct the objects of experience (Treisman & Gelade, 1980). Visual
processing bottlenecks thus arise when the processing requirements (load) of a task exceed the
amount of available attentional resources. Lavie and colleagues have crystallized this logic into a
theory of attention (Lavie, 1995; Lavie, 2005) that explains both early and late selection as a
result of the availability of attentional resources: when perceptual load is low, all stimuli are fully
processed because attentional resources are available, however when perceptual load is high
attention is depleted and some stimuli are filtered out at an early stage. Because Lavie’s theory
conceptualizes attention as a global processing resource, hemifield independence appears to be
incompatible with it. However, others have argued for something like a hemifield-specific
version of this theory where each hemisphere possesses its own finite pool of resources that are
necessary to process stimuli (Friedman & Polson, 1981; Friedman, Polson, Dafoe, & Gaskill,
1982; LaBerge & Brown, 1989; Sereno & Kosslyn, 1991; Alvarez & Cavanagh, 2005; Delvenne
& Holt, 2012). When the processing load of some task exceeds a hemisphere’s available
resources, that hemisphere becomes overtaxed and processing capacity suffers. Spreading a task
across two hemispheres in such cases can reduce the load on any single hemisphere, thus
alleviating processing bottlenecks and improving capacity. This model thereby provides a natural
and intuitive explanation for hemifield independence in terms of the independent availability of
processing resources across hemispheres.

However, it is not entirely clear what the resource model is supposed to be a model of. If
taken literally, as a model of the implementational details of attention, it does not accord with the
extant neuroscience literature. The resource model as implementation appears to posit something
like neural fuel: actual, physical resources in the brain that are produced, distributed, and
depleted. Currently, however, there are no plausible neural candidates for such fuel. As Scalf et
al. (2013) note, while depletion of metabolites like glucose and oxygen may, in cases of extreme
deficiency, explain some cognitive limitations, there is not much evidence that the capacity
limits observed in normal conditions are caused by resource exhaustion. Without evidence for a
plausible neural mechanism, the resource model as implementation is purely speculative.
Further, the explanatory work that the resource model as implementation can do is quite limited
without either a plausible mechanism or some way to measure resource-demand independently
of behavioral costs. While the model does provide a potential explanation for why, in general,
adding more stuff for people to simultaneously process degrades behavioral performance, it does
not explain why this is not always true. In some cases, like pop-out visual search or displays in which stimuli can be grouped in meaningful ways, adding more stuff does not seem to degrade behavior much at all (Treisman & Gelade, 1980). These examples are exceptions to normal behavioral patterns, of course, and while the resource model can be made consistent with them it does not offer theoretical machinery rich enough to predict them. The concern is that if we cannot make substantive predictions about where and when capacity limits due to resource exhaustion will occur, our resource becomes just a synonym for difficulty.

Despite this, as noted, we are not suggesting that the resource model is devoid of value. We instead argue that resources are better (and perhaps typically) understood as a description of general behavioral regularities, a functional-level explanation, rather than a story of implementation. However, the resource model as functional explanation suffers from the same explanatory limitations just mentioned. Since the model is really just a description of behavioral regularities (an empirical generalization) it does not provide any theoretical machinery to predict deviations from those regularities (e.g., hemifield independence). Partly because it is agnostic to implementational details, the resource model as functional explanation can be made consistent with any of the three models here under consideration (what it sacrifices in prediction it makes up for in pliability). As such, we do not consider the functional interpretation of the resources model in depth in this paper. Rather, we consider whether the resource model could be a model of implementation.

1.2 The Attentional-Control Model

In contrast to the resource model, the attentional-control model explains hemifield independence as arising from capacity restrictions on the deployment of attention to multiple
locations within a hemifield (Alvarez et al., 2012). This explanation is based on the observation that the parietal and frontal areas that subserve the deployment of spatial attention to visual cortex primarily respond to a single hemifield (Bruce & Goldberg, 1985). Because of this, the thinking goes, it might be possible that these attentional-control areas have independent capacities for deploying attention into the separate hemispheres. When multiple stimuli project to two hemifields these areas can coordinate the deployment of attention to each hemisphere more efficiently than if the same stimuli shared a hemifield. Importantly, especially in contrast to the competition model below, the attentional-control model places the processing bottleneck explaining hemifield independence at the level of the control processes that deploy and coordinate attention. This implies that hemifield-independence arises because of our inability to efficiently deploy attention where it is needed. This is similar to the resource model explanation where capacity limits arise because of a lack, or absence, of attention. In both cases, if enough attention were available and/or able to be efficiently deployed, processing bottlenecks (capacity limits) would be alleviated. However, as discussed below, previous work (Scalf & Beck, 2010) has shown that processing bottlenecks can arise even when attention is fully engaged on the to be processed stimuli.

Despite this, the attentional-control model is an attractive theoretical refinement of the resource model insofar as it provides a falsifiable neural locus for the processing bottlenecks that lead to hemifield independence. There is also data showing that activity in the posterior parietal cortex (PPC) appears to track attentional load (Mitchell & Cusak, 2008; Xu & Chun, 2009; Scalf & Beck, 2010). However, we are not aware of any data showing that hemispheric asymmetries in the parietal cortex might actually explain hemifield independence. Scalf and Beck, 2010, investigated parietal contributions to hemifield independence and failed to find any differences in
PPC activity between unilateral and bilateral deployments of attention. It is therefore still an open question how, if at all, attentional-control areas contribute to hemifield independence.

1.3 The Competition Model

Lastly, we suggest that there might already be a neurally plausible explanation for hemifield independence in the literature: competition (interference) between representations in adjacent areas of cortex. Competition between representations in cortex is known to be an important bandwidth limitation on our ability to process visual input. When multiple objects project to similar areas of the brain they interact in a mutually suppressive way, degrading each other’s neural representations (Moran & Desimone, 1985; Desimone & Duncan, 1995; Luck et al., 1997; Kastner et al., 1998). This can occur when multiple objects fall into the receptive field of the same neuron; in such cases the neuron appears to respond with a weighted average of the responses evoked by each item in isolation (Reynolds et al., 1999; Zoccolan et al., 2005), resulting in a response that signals neither item clearly. Degradation can also occur when multiple objects fall into the non-overlapping receptive fields of separate, but cortically adjacent, neurons (Reynolds & Heeger, 2009; Carandini & Heeger, 2012). Neurons in visual cortex are densely connected to their neighbors, and those connections may form a suppressive field: an area of the visual field in which the presence of other objects suppresses a neuron’s firing. This is thought to occur because an individual neuron’s response to an object is dependent upon (normalized to) the responses of its neighboring neurons (Reynolds & Heeger, 2009; Carandini & Heeger, 2012). This means that a neuron’s response to a single object can be dramatically degraded when that object appears close to, and is suppressed by, other stimuli (Rolls, Aggelopoulos, & Zheng, 2003; Bles, Schwarzbach, De Weerd, Goebel, & Jansma, 2006;
This increases processing difficulty and reduces performance for tasks like detection, recognition, and tracking (Andriessen & Bouma, 1976; Polat & Sagi, 1993; Kastner, de Weerd, Desimone, Ungerleider, 1998; Reynolds, Chelazzi & Desimone, 1999; Petrov, Carandini, & McKee, 2005). We suggest that this simple and well-researched neural mechanism might provide a neural explanation for the behavioral evidence of hemifield independence.

Because of the anatomical separation of the hemispheres, neurons in one hemisphere are not locally connected to neurons in the other hemisphere (Schmidt, 2013). Together with the contralateral organization of visual cortex (Golomb & Kanwisher, 2011), these facts mean that multiple objects falling close together within a visual hemifield strongly compete with one another, mutually suppressing one another’s representations. However, when multiple objects fall across hemifields they are cortically isolated from one another, at least in early to intermediate visual areas, and do not strongly compete. So the idea is that separating stimuli into different hemifields reduces task difficulty and improves processing capacity, but it does so by reducing competitive interactions (interference) between representations resulting in a clearer representation of the stimuli. According to this account, hemifield independence might result not from depletion of resources or constrained attentional deployment, but from greater competition in unilateral as opposed to bilateral presentations.

The competition model suggests a different account of processing bottlenecks and capacity limits than either the resource or attentional-control models. As mentioned above, these models explain processing bottlenecks as arising from a lack of attention, either because attention has been physically used up or because control systems cannot efficiently coordinate its deployment. In contrast, the competition model suggests that processing bottlenecks arise when
representations actively interfere with one another. Thus, these processing bottlenecks are not the product of top-down attention, per se, but of the “wiring” of the brain (however as we will see below attention does interact with these mechanisms in important ways). This account of processing bottlenecks is conceptually different from the “lack of attention” accounts of the resource and attentional-control models. It also makes an interesting prediction: if multiple stimuli are represented in an area of the brain where they strongly interact, attending equally to both stimuli may not improve their representations because attention has not reduced the ability of the stimuli to interfere with each other (Scalf & Beck, 2010). Adding attention, then, does not alleviate the bottleneck because the bottleneck is not caused by a lack of attention. This is discussed more in the general discussion.

In short, the competition model of hemifield independence has a number of advantages over both the resource and attentional-control models. First, it is a neurally plausible mechanism for which researchers have accumulated a vast array of evidence across a number of methodologies (e.g., single cell recordings, ERP, fMRI, behavioral). Second, the model does explanatory work. It integrates the behavioral data with a well-understood neural mechanism, producing clear, novel predictions about when the effect should occur that conflict with the predictions of the other two models under consideration. The experiments we discuss below tested two of these predictions.

In Experiment 1, we had participants search a briefly-displayed array for one of two targets. The display was asymmetrically organized such that three objects always appeared in one visual hemifield and a single object always appeared in the other (as in Torralbo & Beck, 2008) (see Figure 1). We varied whether the target was the sole object in a hemifield or whether it shared a hemifield with non-targets. We operationalized hemifield independence as the extent
to which performance was better when the target was alone in a hemifield relative to when it shared a hemifield with non-targets. We crossed the hemifield manipulation with an overall display-density manipulation, where the target appeared either near to or far from the non-targets. Critically, the competition model predicts that hemifield independence should only occur when items are close enough to strongly compete with one another. Importantly, both the resource and attentional-control models predict no differences in hemifield independence between density conditions because the total number of objects per hemifield is held constant. We note that both the resource and the attentional-control models could be made consistent with a display-density effect by either theoretical augmentation or by positing a theoretically-external mechanism like crowding (though it is not clear whether crowding, a behavioral regularity, and competition, a neural mechanism, are independent). However, the competition model a priori predicts a display-density effect.

In Experiment 3, we tested an implication of the competition model concerning the effect of attentional cueing on hemifield independence. Attending to an object has been shown to increase the fidelity of its representation and to reduce the suppressive influences of its competitors (Luck, Chelazzi, Hillyard, & Desimone, 1997; Kastner & Ungerleider, 2001; Reynolds & Heeger, 2009; Yeshurun & Rashal, 2010). Attention thus biases the competition between targets and non-targets, causing the target to become well-represented and the non-targets to be suppressed. In other words, attention appears to alter neural computations such that neurons switch from computing an average representation of multiple objects to computing a winner-take-all representation of the attended object (Reynolds et al., 1999; Carandini & Heeger, 2012). According to the competition model, then, when multiple objects are densely arranged within a hemifield, attending to one of them should reduce or eliminate the suppressive
influences of the others, thereby reducing or eliminating any performance benefit for spreading
the objects over two hemifields. Importantly, the same prediction should not be made by a basic
resource model in which the term resource is used synonymously with attention. Cueing
attention to one of multiple objects in one hemifield should have little effect on an independent
resource in the other hemisphere. Thus, whether it is cued or not, the visual system should have a
greater capacity to represent information in two separate hemifields than in a single hemifield.
Similarly, the attentional-control model should also predict no cue-based differences in hemifield
independence; regardless of whether a location is cued, the number of within- and between-
hemifield objects to be selected remains the same.
2. Experiment 1

In Experiment 1, we had participants complete a visual search task while we varied both the number of objects with which a target shared a hemifield and overall display-density. When objects are densely arranged and fall within the same hemifield they can strongly compete with one another (Kastner et al., 1998), but densely arranged objects that fall into different hemifields are cortically isolated and so are not subject to same competitive interactions (Torralbo & Beck, 2008). The competition model thus predicts greater hemifield independence when display-density is high and less when display-density is low. When multiple objects within a hemifield are sparsely arranged, it is less likely that a neuron’s response to an object will be suppressed by the other objects in that hemifield (Kastner, De Weerd, Pinsk, Elizondo, Desimone, & Ungerleider, 2001; Bles, et al., 2006). This is because neurons are densely connected to their nearest neighbors and more sparsely connected to cortically distant neurons (Schmidt 2013). The competition model thus predicts that separating densely-arranged objects within a hemifield should have a similar effect as separating objects across hemifields: both manipulations should increase the cortical distance between objects and reduce competition between them. It is less clear what the resource and attentional-control models would predict here. As specified, neither model provides the theoretical apparatus to predict that display-density should have an impact on hemifield independence. However, it is possible that both models could be augmented to account for such effects (as discussed below).
2.1 Methods

Participants

Sample size was determined by emulating a pilot experiment that we conducted that had a similar manipulation and post hoc power of .8. Twelve participants were recruited from the University of Illinois at Urbana-Champaign in exchange for course credit. All twelve gave informed consent and reported normal or corrected-to-normal vision. Participants were comfortably seated 57 cm (chinrest enforced) from a 24-inch LCD monitor set to a refresh rate of 100 Hz.

Apparatus, Stimuli, and Procedure

The stimuli consisted of seven images of animals on white backgrounds (Konkle, Brady, Alvarez, & Oliva, 2010) that subtended 1.1° x 1.1° of visual angle. Two of the images were dogs, two were birds, one a horse, one a butterfly, and one a turtle. On each trial, participants saw a black dot at fixation on a white screen for 300 - 500 ms. Four images were then displayed in the periphery, briefly (200 ms) to control for eye-movements. One of the four images (the target) was always either a bird or a dog, whereas the other three images (the non-targets) were a horse, a butterfly, and a turtle. Participants were told that each trial contained a single target image: either a bird or a dog. They were told to covertly search the display and indicate as quickly as possible via keypress which target category was present. Trials without responses were terminated after 2500 ms and marked incorrect. Participants completed 64 practice trials and 4 blocks of 64 experimental trials.

On each trial, four items were arranged in a configuration such that one of the two lateral positions appeared in a different visual hemifield than the other three images (Figure 1). Targets could appear in one of these two lateral positions, and both positions were equidistant (4.2°)
from fixation and from the non-targets. The orientation of the configuration was counterbalanced such that each hemifield condition could appear in both the left and right hemifields and the location was also counterbalanced such that the entire configuration could appear in both the upper and lower visual fields. In half of the trials, the target appeared alone in a visual hemifield and in the other half of the trials the target shared a hemifield with non-targets. Since neurons in early-to-intermediate visual areas are densely connected within cortical hemispheres and not across hemispheres (Schmidt 2013), we expected this hemifield manipulation to modulate competition between the target and non-targets when the items were close enough to compete with one another (Torralbo & Beck, 2008; Liu, Jiang, Sun, & He, 2009; Scalf & Beck, 2010).

We crossed the hemifield manipulation with a display-density manipulation. In half of the trials, the target was centered close enough (2.2°) to the two adjacent non-targets that we expected strong competition in early-to-intermediate visual cortex when the items shared a hemifield (Kastner et al, 1998; Kastner, De Weerd, Pinsk, Elizondo, Desimone, & Ungerleider, 2001). In the other half of trials, the target was centered far enough away (4.4°) from the non-targets that we expected relatively little competition in early-to-intermediate visual areas (Kastner, De Weerd, Pinsk, Elizondo, Desimone, & Ungerleider, 2001, Bles, et al., 2006).

2.2 Results and Discussion

Mean reaction times (RTs) and error rates were calculated for each participant in each combination of hemifield and density conditions (Figure 2). We designed the experiment to test RTs (participants were told to prioritize RTs) so were restricted our statistical tests to RTs. However, the error rates show no evidence of a speed-accuracy tradeoff (Table 1). We had one main prediction: that we would find hemifield independence when the objects were close enough
to strongly compete with one another (when density was high) and not when the objects were far enough apart that they would not strongly compete with one another (when density was low). We investigated this prediction with three tests that directly tested our prediction. We did not conduct a 2-way ANOVA followed by t-tests, as is often done in 2 x 2 factorial designs, because we were not interested in two of the three tests that constitute an ANOVA and did not want to unnecessarily increase our false positive rate (Cramer, Ravenzwaaij, Matzke, Steingroever, Wetzels, Grasman, Waldorp, & Wagenmakers, 2015). Instead, we directly tested our prediction with three two-tailed, within-subjects t-tests, and used a sequential Bonferroni to correct for multiple comparisons (see Cramer et al., 2015 for the corrected thresholds mentioned below).

All three models predict hemifield independence in the high density displays, such that RTs should be faster when the target is presented alone in the hemifield than when the target shares a hemifield with non-targets; in the parlance of the resource model, when there are fewer (alone) as opposed to more items in a hemifield (shared). When density was high, performance was indeed worse (participants were slower to find the target) when the target shared a hemifield with non-targets (M = 652.92 ms, SD = 142.89 ms) than when the target was alone in a hemifield (M = 629.28, SD = 118.64 ms), \( t(11) = 3.71, p = .003, 95\% \text{ CI } [11.312, 44.363], \text{ Cohen’s } dz = 1.070. \) This result is significant at the corrected alpha threshold of .05.

Importantly, as predicted by the competition model, we found greater hemifield independence (here operationalized as the difference in RTs between when the target was isolated in a hemifield and RTs when the target shared a hemifield with non-targets) when density was high (M = 23.64 ms, SD = 29.11 ms) than when density was low (M = -8.7 ms, SD = 19.22 ms), \( t(11) = 3.16, p = .009, 95\% \text{ CI } [9.81, 54.87], \text{ Cohen’s } dz = .912. \) This result is significant at the corrected alpha threshold of .025. As mentioned above, it is not entirely clear
what the resource and attentional-control models predict here. Taken at face value, neither model
predicts that display-density should matter for hemifield independence, but that may be because
the models are underspecified or that there is some theoretically-external mechanism at play.
This suggests that the models could be augmented to account for this data (though importantly
the competition model predicts this data a priori). For example, the resource model could posit
localized resources that are differentially exhausted when too many stimuli occupy a localized
set of neurons. Similarly, the attentional-control model could be modified to place another
bottleneck in attentional coordination at a level lower than the hemifield (e.g., the receptive
field). It would therefore be able to account for display-density effects and would move
theoretically closer to the competition model. These options will be discussed more in the
general discussion.

Finally, the competition model does not predict hemifield independence when density is
low, and we found no evidence of hemifield independence. When density was low, performance
was not worse when the target shared a hemifield with non-targets (M = 616.38 ms, SD = 121.40
ms) than when the target appeared alone in a hemifield (M = 625.08, SD = 123.95 ms), t(11) = -
1.29, p = .223, 95% CI [-34.903, 9.103], Cohen’s dz = -.373. This result was not significant at
the corrected alpha threshold of .017.

In sum, our data are consistent with the predictions of the competition model: reducing
the number of objects in a hemifield improved performance only when those objects were close
enough to strongly compete with one another. When objects were spread farther apart it did not
matter how many appeared in the same hemifield. In other words, hemifield independence
occurred only when competition between objects was strong and disappeared when competition
was minimal.
3. Experiment 2

In Experiment 1, we found evidence for the competition model in terms of increased search times. The idea is that a target is subject to more competition when it shares a hemifield with non-targets than when it is alone in a hemifield. More competition means a degraded representation, increasing search difficulty and thus reaction times. In Experiments 2 and 3, we wanted to replicate and extend this finding, while addressing potential concerns with Experiment 1. One concern about Experiment 1 is that the objects used are irregularly shaped, and thus the distances between objects vary slightly across trials. In Experiments 2 and 3, we addressed this concern by using uniformly-sized objects. We also switched from the discrimination task used in Experiment 1 to a difficult target present/absent detection task. One of the key predictions of the competition model is that differential performance in hemifield conditions is due to differential amounts of target information and not to differences in response thresholds or biases. While the increased search times found in Experiment 1 are consistent with this prediction, we more directly tested this prediction in Experiments 2 and 3 by reporting d’. The present/absent task was used to accommodate a d’ measure. In particular, the task, which we adapted from VanRullen, Reddy, & Fei-Fei (2005), was to detect an upright face among inverted faces.

Experiment 2 is a replication of the high density condition of Experiment 1. Using the same hemifield conditions, we asked whether the target would be less detectable when it shared a hemifield with non-targets.
3.1 Methods

Participants

We used the same sample size as Experiment 1 since the key test, whether there was greater hemifield independence when density was high, had high post-hoc power (.82). Twelve volunteers were recruited from the University of Illinois at Urbana-Champaign. All twelve gave informed consent and reported normal or corrected-to-normal vision.

Apparatus, Stimuli, and Procedure

The same apparatus was used as in Experiment 1. Only one image was used as a stimulus and was taken from a publically available database (Minear & Park, 2004). The image was a square cutout of a grayscale Caucasian female face subtending 1.5° x 1.5° of visual angle. Participants saw a black dot at fixation on a middle gray screen for 300 - 500 ms. Four copies of the image were then displayed for 120 ms, followed by a 500 ms display of phase-scrambled versions of the image that were used as masks. On half of the trials, all four faces appeared upside down. On the other half of trials, three faces appeared upside down and a single face, the target, was upright. Participants were instructed to indicate via keypress whether or not an upright face appeared on the trial, and to prioritize accuracy. Trials without responses were terminated after 2500 ms and marked incorrect. Participants completed 4 blocks of 32 trials.

The stimuli placement was identical to Experiment 1 with the following exceptions: the target was centered 5° from fixation and 2° from the non-targets. As in Experiment 1, the images were positioned close enough together that we expected the target to strongly compete with the non-targets when it shared a hemifield with them. In Experiment 1, we saw evidence that competition increased the time needed to identify a target. We think this occurred because participants needed time to deploy attention to bias the competition and successfully recover
information about the target (Desimone & Duncan, 1995; Torralbo & Beck, 2008). By reducing exposure time and including a mask in this experiment, we limited participants’ ability to deploy attention and recover target information. We therefore expected the hemifield manipulation to cause differences in detection sensitivity (d’), with participants better able to detect the upright face when it appeared alone in a hemifield than when it shared a hemifield with non-targets.

3.2 Results and Discussion

Detection sensitivity rates (d’) were calculated for each participant in both hemifield conditions (Figure 4). Since the display was identical on target absent trials, we used participant-level false alarm rates to compute sensitivity. A two-tailed, paired-samples t-test revealed that performance was better when targets appeared alone in a hemifield (M = .967, SD = .726) than when targets shared a hemifield with non-targets (M = .611, SD = .508), t(11) = 3.413, p = .006, 95% CI [.127, .586], Cohen’s dz = .985. This result replicates the high-density hemifield independence found in Experiment 1, and is consistent with our claim that differential target information might be the underlying cause.

Experiment 2 replicates and extends the finding in Experiment 1 of improved performance when targets appear alone in a hemifield relative to when they share a hemifield with non-targets (hemifield independence). Importantly, the improved performance in Experiment 2 comes in the form of detection sensitivity, consistent with the idea that differential target information is the crucial difference.
4. Experiment 3

In Experiment 3, we tested an implication of the competition model concerning the effect of exogenous spatial cues on hemifield independence. Exogenous spatial cues direct attention to the cued location, thereby enhancing processing for stimuli that appear in that location for a short time afterward (Vecera & Rizzo, 2003). Thus, we predicted that cueing a target among non-target competitors would enhance processing for the target and reduce the competitive effects that the non-targets would have on the target absent such a cue. If competition is an important cause of hemifield independence, cueing should therefore reduce or eliminate hemifield independence. Specifically, we predicted that valid spatial pre-cues would increase processing at target locations, boosting the representation of the target when it appeared. This should bias the competition between targets and non-targets such that the target “wins out” and the suppressive effects of the non-targets are reduced or eliminated. In contrast, invalid spatial-cues direct attention away from the target location and thus do not give targets the boost they need to avoid suppression by non-targets. According to the competition model, we should only find hemifield independence when the target is invalidly cued because valid cues reduce or eliminate the differences in competition between hemifield conditions. As in Experiment 1, neither the resource model nor the attentional-control model provide theoretically-based reasons to predict a reduction in hemifield independence due to valid cues, they can both be made consistent with such an effect (as will be discussed below).
4.1 Methods

Participants

After completing Experiment 2, the same twelve subjects completed Experiment 3.

Apparatus, Stimuli, & Procedure

The same apparatus was used as in the prior experiments. The stimuli and procedure were identical to Experiment 1 except for the inclusion of a spatial pre-cue between the fixation and the stimuli displays. The pre-cue was a black outline of a square that subtended 2.1° x 2.1°. The cue appeared for 100 ms after the offset of fixation (fixation appeared for between 200 ms and 500 ms), disappearing as the stimulus screen appeared. Participants completed 8 blocks of 32 trials. On 70% of trials, the cue was centered exactly where the target would be centered on the stimulus screen (validly cued trials). On the remaining 30% of trials, the cue appeared in the visual field (upper or lower) opposite to where the target would appear on that trial (invalidly cued trials). The cue appeared equally often in the left and right visual fields. The invalid cues always appeared in a location where targets could appear.

4.2 Results and Discussion

Sensitivity rates (d’) were calculated for each participant in each combination of hemifield and cue conditions (Figure 5). We again operationalized hemifield independence by calculating the benefit in performance due to a target appearing alone in a hemifield versus it sharing a hemifield with non-targets. We had one main prediction: we should find greater hemifield independence in the invalid condition than in the valid condition. We again investigated this prediction with three two-tailed, within-subjects t-tests, using a sequential Bonferroni correction for multiple comparisons.
Both the competition and the attentional-control models predict that we should find hemifield independence when attention is invalidly cued, such that targets that appear alone in a hemifield are more detectable than targets that share a hemifield with non-targets. When attention was invalidly cued, performance was indeed better when the target was alone in a hemifield (M = 1.399, SD = .809) than when it shared a hemifield with non-targets (M = .959, SD = .805), t(11) = 4.415, p = .001, 95% CI [.221, .659], Cohen’s dz = 1.274. This result was significant at the corrected alpha threshold of .05. Sensitivity rates were in general higher in Experiment 3 than in Experiment 2, likely due to the fact that participants completed Experiment 2 before completing Experiment 3.

The competition model predicts greater hemifield independence when attention is invalidly cued than when it is validly cued. In line with this, we found greater hemifield independence when participants were invalidly cued (M = .440, SD = .345) than when they were validly cued (M = -.013, SD = .431), t(11) = 3.107, p = .01, 95% CI [.132, .773], Cohen’s dz = .897. This result was significant at the corrected alpha threshold of .025.

Lastly, we did not find any evidence of hemifield independence in the valid condition. Performance was not better when the target was alone in a hemifield (M = 1.616, SD = .613) than when it shared a hemifield with non-targets (M = 1.629, SD = .969 ms), t(11) = -.104, p = .919, 95% CI [-.287, .261], Cohen’s dz = -.03. This result was not significant at the corrected alpha threshold of .017.

These results are consistent with the competition model: we only found hemifield independence when attention was unable to ameliorate the suppressive effects of the non-targets. When attention was invalidly cued, the within-hemifield non-targets interfered with the target,
rendering it less detectable. However, hemifield independence was eliminated when attention was directed to the target location and able to reduce the suppressive effects of the non-targets.

While the competition model predicts these results a priori, it is also possible to augment both the resource and attentional-control models to account for these results. It might be possible that cueing a location prioritizes the allocation of resources, and thus the processing of stimuli, at that location. If a target at a cued location is processed before non-targets at uncued locations, this might explain a reduction of interference from non-targets. However, it is difficult to square this possibility with the claim of some resource models (e.g., Lavie, 1995) that selective processing occurs only because of capacity exhaustion (that capacity exhaustion explains selection). Alternatively, cueing a location might increase either the amount of resources deployed to that location or the ease of deploying such resources, thus reducing the amount of leftover resources available to process non-targets. While this might explain why cueing reduces the deleterious effects of non-targets on performance, it does not explain why separating targets and non-targets into different hemifields also improves performance.

The attentional-control model might also be able to account for these results. When a target in a certain hemifield is validly cued the control processes that deploy attention to that hemifield could prioritize processing of the target, thus reducing the effects of non-targets on performance. This would explain why cueing the target reduces hemifield independence. Further, since these control processes are thought to be lateralized, the attentional-control model can also explain why we find evidence of hemifield independence when targets are invalidly cued.
5. General Discussion

The above results provide evidence that hemifield independence may be a special case of a well-known cortical mechanism: competition between representations in visual cortex. In Experiment 1, we used a visual search task to show that separating task-relevant objects within a hemifield improved performance similarly to separating them across hemifields. Performance improved when the cortical distance between objects was sufficient to alleviate competition, regardless of whether the separation was within or between hemifields. Thus, the factor limiting behavioral performance here might be competition between object representations and not hemifield-level availability of processing resources or limitations in the ability to coordinate within-hemifield deployment of attention.

However, it is possible for both the resource as implementation model and the attentional-control model to account for this data. If resources are conceptualized as localized to a scale smaller than the entire brain or a single hemifield, then local display density could interact with resources. Specifically, behavioral performance should be worse when multiple stimuli fall within a section of the brain where neurons all share resources than when the same stimuli are spread across sections of the brain where neurons do not share resources. A similar argument could be made for the attentional-control model: performance will suffer when stimuli fall inside a section of the brain where the coordination of attentional deployment for a single stimulus is not independent of the coordination for the other items. Experiment 1 (as well as Experiment 2) thus suggests that the locus of the attentional bottleneck in hemifield independence may not be at the level of the hemifield, but rather at the level of more localized processes.

In Experiment 2, we extended the hemifield independence effect from Experiment 1 to a detection task to show, as predicted by the competition model, that sensitivity to the target (and
not simply response bias) is responsible for hemifield independence. A similar prediction could also be made by a resource model if one assumes that the resource in question facilitates the processing of perceptual information and not just the facilitation of response selection. Similarly, the attentional control model could also make this prediction provided that attention is necessary to extract/construct perceptual information.

In Experiment 3, we used exogenous spatial cues to manipulate the ability of attention to resolve competition. Exogenous spatial cues have been shown to increase both the P1 ERP component (Doalla, Lorenzo-Lopez, Vizoso, Holguín, Amenedo, Bara, & Cadaveira, 2004) and behaviorally-measured contrast sensitivity (Reynolds & Chelazzi, 2004; Pestilli & Carrasco, 2005) at cued locations. These results indicate that exogenous spatial cues improve the representation of a target at the cued location, making the target more likely to “win” when it competes with non-targets (Carandini & Heeger, 2004, Reynolds & Heeger, 2009). When targets were invalidly cued, attention seemed unable to effectively bias the competition between the target and non-targets. As predicted by the competition model, we found hemifield independence in this case: performance was better when objects appeared alone in a hemifield than when they shared a hemifield with non-targets. However, when validly cued, attention could effectively bias the competition, reducing the suppressive influences of the non-targets. In accord with the competition model, we did not find hemifield independence in this case.

We think Experiment 3 also suggests a reinterpretation of past data. While Alvarez & Cavanagh (2005) consider perceptual interference (competition) as an explanation for hemifield independence, one of the reasons they reject an interference account is that they find large performance differences across physically identical displays by simply manipulating the number of objects that people needed to track. For instance, when two objects are placed in a single
hemifield, participants are better at tracking a single object than they are at tracking two objects. Since the two tracking conditions are physically identical, they conclude that perceptual interference must also be identical across them and so cannot explain the differences in performance. We have a different interpretation. As in Experiment 3, and the neural work referenced above, when attention is directed to a target among non-targets, the suppressive influence of the non-targets is reduced and the representation of the target is improved, thus improving performance. Said differently, top-down attentional processes feedback into early visual cortex, select the target, and alter the perceptual interference between objects such that the target representation improves and its competitors’ representations are suppressed. Thus, even though two conditions may contain physically identical displays, attentional manipulations can alter the perceptual interference (competition) between objects.

This last point is one of general importance for cognitive theories of attention. If resolving perceptual competition is of the main functions of attention, as researchers have argued (Desimone & Duncan, 1995; Kastner et al., 1998; Kastner & Ungerleider, 2001), it is possible that many bottlenecks which appear to be attentional (because they are modulated by attentional manipulations) are actually perceptual. This means that some capacity limits may not be due to lack of attention (as both the resource and attentional-control models claim about hemifield independence), but rather due to an inability to successfully boost a target from the suppressive effects of its competitors. For instance, Scalf & Beck (2010) had participants in an fMRI view displays containing a group of three densely-arranged objects. Participants either attended one of the objects, all three of them, or an entirely separate group of objects (attending away). Measuring from a contralateral ROI in V4 corresponding to the location of the object in the attend one condition, they found that attending to just that one object increased BOLD activity
relative to both attending away and attending to all three objects. Importantly this was observed in a visual area, as opposed to an attention control region, consistent with the idea that attention changes perceptual information and reduces competition.

Interestingly, Scalf & Beck also found that attending to all three items actually led to slightly less BOLD activity than when attention was directed away from the objects, implying that attending to a number of competing objects did not improve their representations in cortex relative to when those items were unattended. In a separate but similar study, Scalf & Beck (2011) also found that attention only reduces the amount of suppression an object receives from its competitors (relative to when attention is diverted away) when it is the only object attended. Taken together, these findings imply that attention is not a cure all for capacity limits: if multiple objects are suppressing one another, attending to them all may simply boost their ability to suppress one another rather than improve their representations. Crucially, even though the target (along with its competitors) is now being attended, its representation may be just as poor as when it was unattended.

While we have been talking about the competition and resources as implementation models as though they are mutually exclusive, the same is not true for the competition model and resources as functional explanation. As mentioned, resources can be understood as something like a functional explanation of behavioral regularities: performance, in general, drops when people have to simultaneously process multiple stimuli. While we have argued against understanding resources as an implementational story, there is a real sense in which we think of competition as the neural implementation of something like a functional level resource.: performance, in general, drops when multiple representations crowd together into the same area of cortex. This is resource-like in that there is a limit to the amount of stuff we can process at
once. Further, the resource metaphor affords predictions that turn out to be true: for instance, reducing the number of objects we need to simultaneously process, in general, improves performance. However, as is true for most abstract models of cognition, things get complicated once we start looking at the implementational details. We have argued that resource models are hard to square with what we know about the brain. We have also suggested that resources as implementation does not do enough explanatory work. Why are objects harder to see when they are close together? Why do similar objects interfere with one another more than dissimilar objects? Why are objects in two hemispheres easier to process than objects in a single hemisphere? The resource metaphor does not explain these phenomena so much as it chalks up the observed differences to different levels of required resources. Again, the concern is that a resource might just be a synonym for difficulty.

Experiments 1 and 2 provide evidence that some capacity limits can arise from bottlenecks at levels lower than the hemifield (perhaps local interactions in visual cortex). These experiments also suggest that the hemifield-level bottlenecks observed in hemifield independence might in fact result from such lower level bottlenecks. The attentional-control model, as currently specified, attributes hemifield independence to hemifield-level bottlenecks and thus has trouble accounting for both Experiment 1 and Experiment 2. We have suggested ways to modify the attentional-control to account for these experiments: positing more localized attentional coordination zones. For instance, there could be regions of the brain smaller than the hemisphere where, if multiple stimuli fell in this region, the coordination of attention to one stimulus in that region would not be independent of the coordination of attention to another stimulus in that region. This would allow multiple levels of coordination bottlenecks and should predict graded levels of at different levels of the visual hierarchy. Furthermore, to be clear, while
we have argued for a locus of interference in hemifield independence at the level of visual cortex, we do not discount the possibility that attentional control bottlenecks at the level of the hemifield are important factors that limit visual processing. However, at present there exists precious little evidence that attentional control bottlenecks constrain hemifield-level processing in such a way as to explain hemifield independence. Further, the attentional-control model, like the resource model, explains hemifield independence as arising from the inability to attend to multiple stimuli in the same hemifield as effectively as one can attend to multiple stimuli in different hemifields. In other words, both models claim that a lack of attention is responsible for hemifield independence. The implication is that multiple stimuli presented unilaterally receive less attention than when the same stimuli are presented bilaterally, and that this differential amount of attention explains hemifield independence. We have seen, however, that more attention is not always the answer (Scalf & Beck, 2010), and we propose that hemifield independence may instead result from perceptual interference rather than attentional exhaustion.
6. Figures and Table

Figure 1: Example displays and conditions for Experiment 1. Top left: the target (here a dog) is alone in a hemifield and the overall display density is low. Top right: the target (here a bird) shares a hemifield with non-targets and the overall display density is low. Bottom left: the target (here a bird) is alone in a hemifield and the overall display density is high. Bottom right: the target (here a dog) shares a hemifield with non-targets and the overall display density is high.
Figure 2: Violin plots of the results from Experiment 1. Hemifield independence is here operationalized as the difference between when a target shared a hemifield with non-targets (shared) and when the target appeared alone in a hemifield (alone). There is more hemifield independence (Alone - Shared) when the displays were Dense than when displays were Sparse. White bars represent mean and 95% CI.

<table>
<thead>
<tr>
<th>Density</th>
<th>Alone in Hemifield</th>
<th>Shared Hemifield</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low Density</td>
<td>0.955 (0.036)</td>
<td>0.955 (0.056)</td>
</tr>
<tr>
<td>High Density</td>
<td>0.958 (0.027)</td>
<td>0.95 (0.028)</td>
</tr>
</tbody>
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Table 1: Accuracies and standard errors for Experiment 1.
Figure 3: Example displays and conditions from Experiment 2. Left: The target (the upright face) is alone in a hemifield. Right: The target (the upright face) shares a hemifield with non-targets.

Figure 4: Violin plots of the results from Experiment 2. Participants were better at detecting the target when it appeared alone in a hemifield than when it shared a hemifield with non-targets. White bars represent mean and 95% CI.
Figure 5: Violin plots of the results from Experiment 3. Hemifield independence is here operationalized as the difference between when a target appeared alone in a hemifield (Alone) and when a target shared a hemifield with non-targets (Shared). There is more hemifield independence (Shared - Alone) when the target was invalidly cued (Invalid) than when it was validly cued (Valid). There was hemifield independence when the target was invalidly cued (Invalid) and no evidence of hemifield independence when the target was validly cued (Valid). White bars represent mean and 95% CI.
7. References


Franconeri, S. L., Jonathan, S. V., & Scimeca, J. M. (2010). Tracking multiple objects is limited only by object spacing, not by speed, time, or capacity. Psychological Science, 21(7), 920-925.


