

# The potential roles of saturating and supersaturating contrast-response functions in conjunction detection: Reply to Peirce

Keith A. May

Division of Optometry and Visual Science,  
City University London, London, UK



Li Zhaoping

UCL Department of Computer Science,  
University College London, London, UK



## Introduction

Peirce (2007) proposed a two-stage conjunction detection model in which the outputs of first-stage neurons selective for the conjunction components were summed to give the conjunction-detector output. He argued that a saturating (monotonic) or supersaturating (nonmonotonic) nonlinearity on the outputs of the first-stage neurons made this detector more selective for conjunctions by increasing the ratio of conjunction response to component response at the output stage, i.e., the response of the conjunction detector to a conjunction divided by its response to a single component presented in isolation.

The conjunction stimulus that Peirce considered was a maximum-contrast plaid, i.e., the sum of two 0.5-contrast gratings of different orientation. The equivalent single-component stimulus was a single maximum-contrast grating. Assuming no cross-orientation inhibition, if the two first-stage neurons are each selective for a different component of the plaid, with a contrast-response function  $r(c)$ , where  $c$  is component contrast, then the sum of first-stage responses to the plaid is given by  $r_{\text{conjunction}} = 2r(0.5)$ , and the sum of first-stage responses to the grating is given by  $r_{\text{component}} = r(1)$ . Peirce defined a conjunction selectivity index (CSI), which reflects the ratio of conjunction response to component response at the output stage of his proposed conjunction detector:

$$\text{CSI} = r_{\text{conjunction}}/r_{\text{component}} - 1. \quad (1)$$

$r_{\text{conjunction}}$  and  $r_{\text{component}}$  are defined as above, and so the CSI can be calculated from the parameters of the contrast-response function of the first-stage neurons. Peirce used this index to analyze the conjunction selectivity of a population of real neurons.

If the first-stage neurons had linear contrast-response functions (as in Figure 1A), then the sum of first-stage responses to the plaid would be the same as the sum of first-stage responses to the single grating [ $2r(0.5) = r(1)$ ], giving a CSI of 0. On the other hand, if the first-stage neurons had contrast-response functions that fully saturated at a contrast of 0.5 or less (as in Figure 1C), the sum of first-stage responses to the plaid would be twice the sum of first-stage responses to the single grating [ $2r(0.5) = 2r(1)$ ], giving a CSI of 1. In the latter case, the summing circuit would be more sensitive to a maximum-contrast plaid than to a maximum-contrast grating.

In this model, saturating and supersaturating contrast-response functions give a higher CSI than linear functions because they show disproportionately high responses to low inputs. We pointed out that this benefits only plaid-type conjunctions, where the spatial superimposition of the components forces the component contrasts to be lower than the contrast of the pattern as a whole. The argument does not apply to most other types of conjunction, where the contrasts of the individual components are not limited by their membership of the conjunction. If the stimulus components have the same contrast when presented in isolation as they do when presented as part of a conjunction (e.g., individual Gabor patches vs. a contour, Field, Hayes, & Hess, 1993), then the ratio  $r_{\text{conjunction}}/r_{\text{component}}$  is always two, regardless of the shape of the first-stage output nonlinearity in Peirce's conjunction detector (May & Zhaoping, 2011). We argued that saturating and supersaturating nonlinearities cannot facilitate conjunction detection in the way that Peirce proposed.

In his thought-provoking response to our paper, Peirce (2011) has proposed a different means by which a saturating nonlinearity could improve the perfor-

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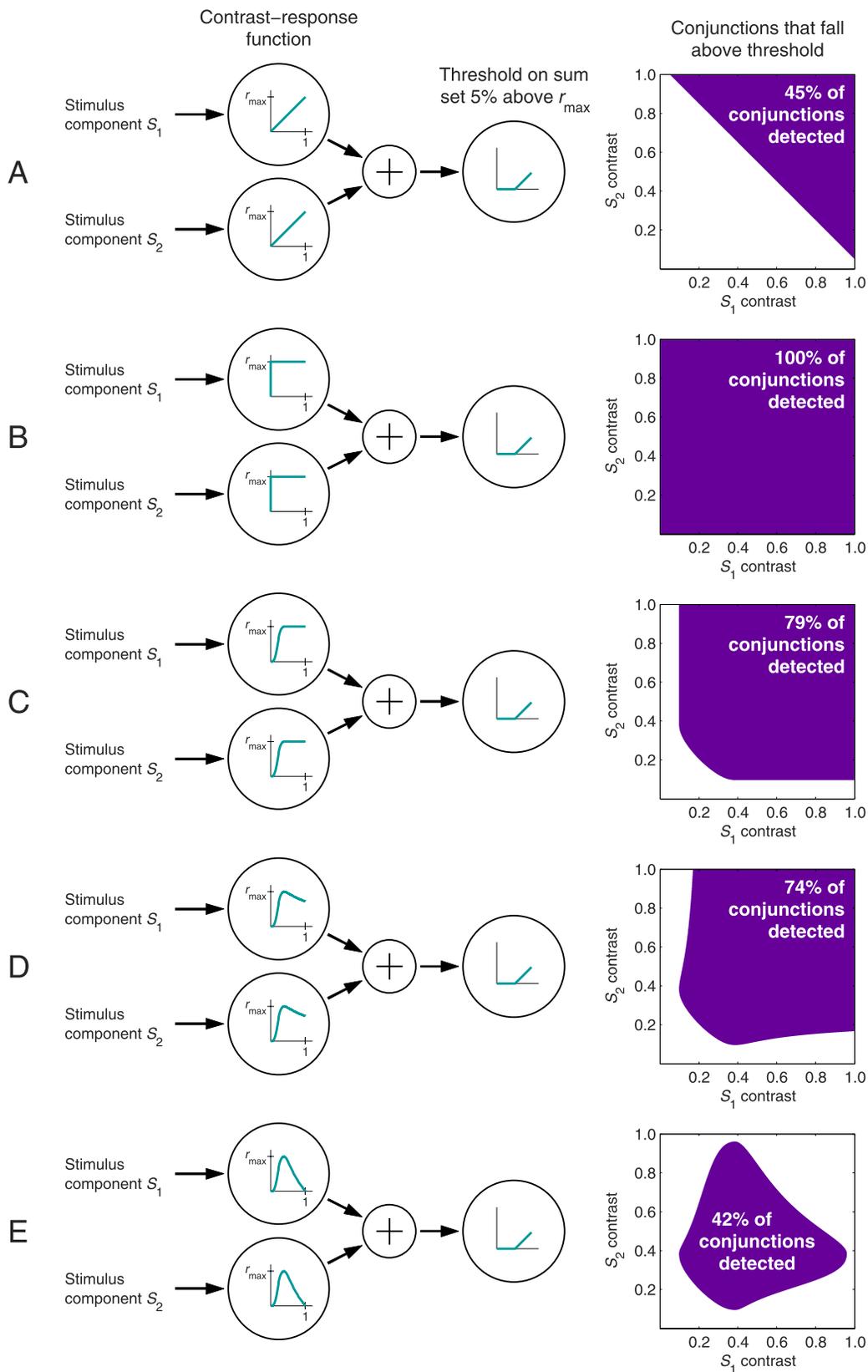


Figure 1. Peirce's conjunction detector with different first-stage contrast-response functions. Stimulus components  $S_1$  and  $S_2$  each stimulate a first-stage neuron selectively tuned to that component. The contrast-response functions of these neurons are illustrated in the leftmost column of circles. Peirce's (2007) original conjunction detector just summed the responses of the two first-stage neurons.

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mance of a summing conjunction detector: By forcing each first-stage neuron to respond close to maximum over much of the contrast range, the saturating nonlinearity allows a decision boundary or threshold to be set that reliably discriminates between conjunctions and nonconjunctions across a wide range of component contrasts. This is illustrated in Figure 1. Peirce suggests setting a threshold on the output of the conjunction detector at just above the maximum expected response to a single component: Then a single component will hardly ever yield a response, but a conjunction of components will, as long as their contrasts are sufficiently high. Misses (i.e., failure to detect a conjunction) can be minimized without appreciably increasing the false alarm rate by making sure that the response of a first-stage neuron to its preferred component is close to maximum regardless of the contrast, and this is why saturation improves performance in this model. This is a very different argument to the previous one, as it depends on the first-stage neural response being largely contrast invariant and does not depend critically on the ratio of conjunction response to component response at the output stage, which forms the basis of the CSI. We fully agree with Peirce that, in this new, extended, version of the model, a saturating nonlinearity does indeed play a key role in facilitating detection of conjunctions, even when the component contrasts are the same in both the conjunction and nonconjunction stimuli.

## What about supersaturation?

Peirce (2011) suggests that our critique of his earlier model hinges on our failure to consider the small additional detail of a nonzero physiological threshold

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Peirce's (2011) extended conjunction detector included a threshold function on the output. Like Peirce (2011), we set the threshold at 5% above the maximum expected response of a single first-stage neuron (i.e.,  $1.05 \times r_{\max}$ ) to avoid a response to a single component presented in isolation. The Cartesian axes on the right represent all possible combinations of component contrasts. The purple-shaded regions represent those pairs of component contrasts for which the sum of responses of the first-stage neurons is above threshold, thereby allowing the conjunction to be detected. Each of A to E shows a different contrast-response function for the first-stage neurons. In A, the contrast-response function is linear: 45% of the possible conjunction stimuli are detected. In B, the contrast-response function is zero for zero contrast and  $r_{\max}$  for all other contrasts. This is the optimal contrast-response function shape for this model: All possible conjunction stimuli are detected. In C, the contrast-response function saturates at a contrast of 0.386. Although suboptimal, this function allows detection of the majority of possible conjunction stimuli (79%), and is much better than a linear function. In D and E, the portion of the contrast-response function to the left of the peak is identical to that in C, but the function supersaturates to the right. As the amount of supersaturation increases, the proportion of detected conjunctions falls (74% and 42% for D and E, respectively). The contrast-response function in D is described by Peirce's (2007) modified Naka-Rushton function (May & Zhaoping, 2011, equation 11) with  $c_{50} = 0.235$ ,  $q = 3.81$ , and supersaturation parameter,  $s = 1.12$ . These parameters were fitted to the data for a supersaturating neuron shown in Peirce's Figure 2e (see May & Zhaoping, 2011, table 1, neuron e). In E, the portion of the contrast-response function to the right of the peak was constructed by taking the corresponding portion from D and linearly stretching it so that it reached all the way down to zero. The baseline firing rate was set to zero in all the contrast-response functions used here.

on the output of the conjunction detector. But, in fact, this extension to the original model is not at all trivial, as it undermines the second strand of Peirce's (2007) paper, which concerns the role of *supersaturation*. One of the major themes of that paper was to highlight and quantify this rarely discussed phenomenon, whereby the neural response initially increases with increasing contrast, but then reaches a peak and declines with further increases in contrast. Peirce (2007) argued that supersaturation had never been satisfactorily explained, and, on the basis of the CSI measure, argued that supersaturating neurons could give rise to greater conjunction selectivity than neurons that merely saturated. But, under Peirce's (2011) new proposal, supersaturation can only be detrimental to conjunction detection. In this new proposal, conjunctions are signaled whenever the sum of first-stage responses is greater than a nonzero threshold. To avoid a response to a single component, the threshold has to be set to a value slightly higher than the peak of the contrast-response function of the first-stage neurons. Any decline in response with increasing contrast will make the sum of first-stage responses to a conjunction more likely to fall below this threshold, so supersaturation will undermine conjunction detection in this model (compare Figures 1D and 1E with Figure 1C). The optimal contrast-response function for conjunction detection in Peirce's (2011) new model is one that saturates at a very low contrast and does not supersaturate (Figure 1B).

Conjunction-detection performance with supersaturating neurons could be brought up to the performance level of saturating neurons by having a number of conjunction detectors with supersaturating neurons peaking at different contrasts. But supersaturation would still be a disadvantage because it would require several pairs of neurons to achieve the conjunction

detection performance that could be achieved with one pair of saturating neurons. Supersaturation would yield no performance advantage in conjunction detection while consuming more resources.

The mild levels of supersaturation usually found in visual cortex would be unlikely to seriously impair conjunction detection performance in this model, but would certainly not improve it. On the other hand, we showed that supersaturation would improve contrast discrimination performance while reducing energy consumption (May & Zhaoping, 2011). For typical levels of supersaturation, the improvement in contrast discrimination performance would be fairly negligible, but the energy saving could still be substantial, especially at higher contrasts. We maintain that energy efficiency remains the most plausible explanation of supersaturation.

## Conclusions

Peirce (2007) presented a conjunction detector that sums the responses of neurons selective for the components of the conjunction. He argued that saturating and supersaturating contrast-response functions would facilitate conjunction detection by increasing the ratio of conjunction response to component response at the output stage. We questioned this argument and, in response, Peirce (2011) extended the earlier conjunction detector by adding a decision boundary that is set by the maximum response of a first-stage neuron. It is this feature, not mentioned in the earlier paper, that allows saturating contrast-response functions to facilitate conjunction detection in the model. However, this new feature of the model has the effect of making supersaturation disadvantageous for conjunction detection. We suggest that supersaturation serves to reduce energy consumption while, if anything, improving contrast-discrimination performance. As argued earlier (May & Zhaoping, 2011), it is likely that supersaturation in visual cortex is weak

because, although it benefits contrast coding, it would impair coding of all other feature dimensions.

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Corresponding author: Keith A. May.

Email: keith@keithmay.org.

Address: Division of Optometry and Visual Science, City University London, London, UK.

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