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Paying Attention to Neurons with Discriminating Taste

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Traditional theories of attention rely on the idea that when we search for a target in a visual display the brain boosts the activity of neurons optimally tuned for the target features. In this issue of *Neuron*, Navalpakkam and Itti take a computational approach to show that this strategy is actually very inefficient when the target is surrounded by distractors with similar features. Instead, the optimal strategy is to boost the activity of neurons that best discriminate between target and distractors, while essentially ignoring the neurons that respond best to the target.

When looking for a friend in a large crowd, a natural strategy is to focus attention on the visual features specific to this person. Hence, if the person is wearing a red coat, the nervous system should enhance the activity of neurons specifically tuned to red. Several neurophysiological experiments have confirmed that this is indeed the strategy adopted by the nervous system (McAdams and Maunsell, 1999; Treue and Maunsell, 1996), and this is also the central idea in all models of attention (Heinke and Humphreys, 2005). In this issue of *Neuron*, Navalpakkam and Itti (2007) suggest that this strategy might in fact be a special case of a more general approach. They argue that, in visual search, the nervous system should enhance the response of cells that best *distinguish* between the target and the distractors—an idea that had been mentioned in the literature before but which had never been fully explored (Wolfe et al., 2003). If the target and distractors are widely different (the case that has been typically considered in previous neurophysiological experiments), the optimal strategy remains one of

focusing on neurons that best respond to the target features. Going back to our example, if most people in the crowd are wearing blue coats, the cells encoding red will indeed be the most informative because they do not respond much to blue while responding maximally to red. The story changes, however, if the target and distractors are similar. For instance, imagine that you are looking for your friend in a stadium in which most of the fans are wearing red jerseys that are just slightly more purple than your friend's coat. In this case, the task is akin to a fine discrimination of color, and the optimal strategy is to monitor cells that best discriminate between these two similar shades of red. Interestingly, these are not the cells tuned to red, because such cells would respond almost equally well to both shades. Instead, attention should now be driven by cells that are tuned slightly away from both red and purple-red.

At first, this strategy may sound quite counterintuitive. The best way to find a target surrounded by distractors is to monitor cells that are not optimally tuned to the target! However, this is a

consequence of a well-known property of population codes. Many variables are represented in the brain with population codes, i.e., through the activity of neurons with bell-shaped tuning curves (Figure 1A). The properties of such codes have been extensively studied, experimentally as well as theoretically (Paradiso, 1988; Regan and Beverley, 1985). One of the major conclusions is that neurons play different roles depending on the nature of the tasks. Hence, more than 20 years ago, Regan and Beverley (1985) had shown that when trying to detect a grating with an orientation of 0°, the most important neurons are the ones tuned at 0°. By contrast, when trying to discriminate between two similar orientations, say –5° and 0°, the most helpful neurons are the ones preferring –15° or 15°. The reason is quite simple: the most helpful neurons are the ones with the largest change of activity between 5° and 0°, that is to say, the neurons whose tuning curves show the highest slope in this range. If the tuning curves are about 30° wide, for neurons with tuning curves peaking at –15° and 15°, the side of these

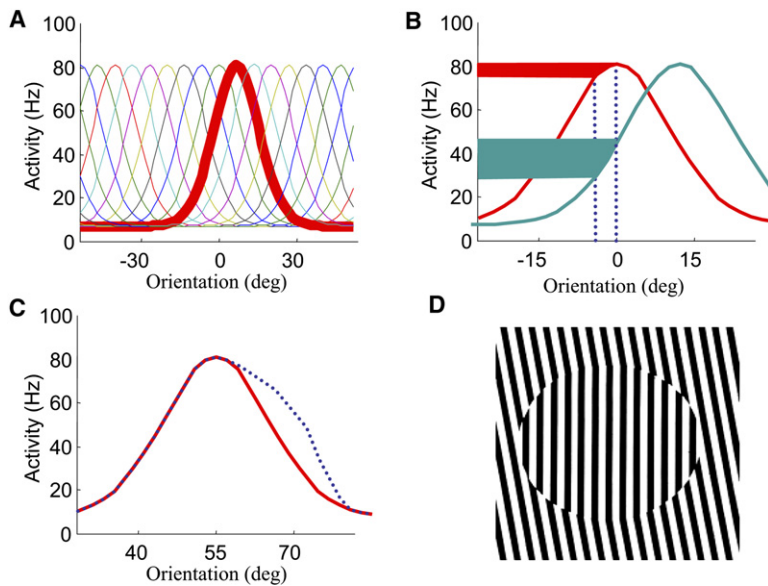


Figure 1. Population Codes and Perceptual Biases

(A) Population code for orientation. Each curve shows the mean response of a particular neuron as a function of orientation. The bold red line highlights the curves centered at 10° .
 (B) When trying to discriminate two similar orientations close to 0° (dotted lines), the neuron responding maximally to 0° (red curve) is of little help because its activity barely changes between the orientations to be discriminated (filled red polygon). By contrast, when the tuning curve are about 30° wide, the neuron responding best to 15° (blue curve) is the most helpful because its activity changes maximally between the two orientations (filled blue polygon).
 (C) Red curve: expected pattern of activity for an orientation of 55° in a population of neurons with the tuning curves shown in panel (A). Blue dotted line: pattern of activity in response to a 55° line when attention boosts preferentially neurons tuned around 70° . The resulting pattern is more consistent with an orientation of 60° than the true orientation of 55° .
 (D) The tilt illusion. When surrounded by a grating slightly tilted to the left, the vertical grating in the center appears tilted to the right.

tuning curves—where the slope is the highest—will be around the interval $[-5^\circ, 0^\circ]$ (Figure 1B). Therefore, when identifying a line oriented at 0° in the presence of distractors oriented at -5° , the best neurons to use are the ones tuned to 15° . How about the ones at -15° ? By symmetry, they should also be helpful, but there is a twist. One of the central hypotheses of models of attention is that attention is driven to locations where the target is the most salient. Saliency, in turn, is believed to be related to the amplitude of neural activity. Therefore, neurons that respond more to the target than the distractor (like the neurons tuned to 15° in our example) are the most important ones because they are the ones for which the target is more salient. In contrast, neurons at -15° respond less to the target than the distractor, and therefore, in this saliency framework, they are not particularly helpful for the search.

Now we can see why it makes little sense to use neurons tuned to red when trying to identify a red coat among purple-red jerseys. Instead, one should primarily boost the activity of neurons that are tuned away from red and purple-red, perhaps toward orange. How far away from those tuned red will depend on the width of the color tuning curves.

Navalpakkam and Itti tested their theory experimentally using a search task with oriented lines. They trained subjects to search for a line oriented at 55° among distractors oriented at 50° . If their theory is correct, top-down attention should enhance the activity of neurons tuned to orientation greater than 55° . This in turn means that, during the search, a 55° line should trigger a pattern of activity which is consistent with an orientation of more than 55° (Figure 1C). As a result, the 55° line should be perceived to be closer to say 60° than 55° . The

amplitude of the effect is hard to predict ahead of time, but the bias should be toward greater orientation. This is precisely what the authors report. In addition to the search task, they inserted a few test trials in which subjects were presented with five lines oriented at $30^\circ, 50^\circ, 55^\circ, 60^\circ,$ and 80° arranged in a circle. Participants had to report the location of what was defined in the search trials to be the target (i.e., the 55° line). They found that subjects picked the line at 60° most often, not the one at 55° . Another experiment with color shows the same effect.

This work suggests a rather counter-intuitive prediction for neurophysiological studies of attention: if an animal is trained on a search task with similar target and distractors, neurons tuned to orientations away from the target and distractors should show the greatest attentional enhancement. This would be a striking confirmation of this theory.

This approach also goes a long way toward explaining a number of effects documented in the behavioral literature on visual search. In particular, search difficulty is known to increase as the similarity between target and distractors increases as well as when distractors become increasingly more heterogeneous (Duncan and Humphreys, 1989). The theory proposed by the authors qualitatively captures these effects as illustrated in Figure 7 of their paper. Panels (C) and (D) illustrate how search difficulty increases as target distractor similarity increases, either because of greater variance in their distribution or more similar means. Panels (E) and (G) illustrate how search difficulty increases as distractors become more heterogeneous. Although qualitatively appealing, it remains unclear whether this framework appropriately captures the size (and not just the sign) of the reported effects in the literature. For example, according to the theory, searching for a well-defined target among heterogeneous distractors is barely harder than performing an oddity search among homogeneous distractors (panel [B] of Figure 7). Yet, target searches among heterogeneous

distractors are remarkably inefficient, whereas oddity searches among homogeneous distractors are roughly akin to “pop-out” searches (Santhi and Reeves, 2004).

Overall, this work elegantly captures within a single framework one of the main findings in the attention literature, namely, that competitive interactions during visual selection are the basis for attentional effects (Heinke and Humphreys, 2005). There is however one concern that would deserve to be investigated more thoroughly in future studies. The repulsion effect reported here might be the result of spatial interactions among target and distractors at nearby locations (Coltheart, 1971; Gibson and Radner, 1937). Hence, it is well known that the mere presentation of similar target and distractors in these relatively densely packed arrays

leads to a repulsion bias (e.g., a 55° line among 50° line is perceived closer to 60°, see Figure 1D for an illustration of this effect with a vertical grating). This repulsion effect is believed to facilitate visual segmentation and is observed even under tasks that do not require visual selection. This explanation and the attentional interpretation are not necessarily mutually exclusive. It is clear that visual segmentation and attention modulation interact closely (Li, 1999), and it is quite possible that the computational principle explored by Navalpakkam and Itti generalizes across these domains.

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