Explaining attention-related changes in behavior and electroencephalography data through computational modeling

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Ku Y, van Schouwenburg MR. Explaining attention-related changes in behavior and electroencephalography data through computational modeling. *J Neurophysiol* 114: 2087–2089, 2015. First published January 14, 2015; doi:10.1152/jn.01026.2014.—In a recent article, Itthipuripat and colleagues combined psychophysics, neurophysiology, and mathematical modeling to investigate the neural mechanism underlying behavioral benefits of spatial attention (Itthipuripat S, Ester EF, Deering S, Serences JT. *J Neurosci* 34: 13384–13398, 2014). They found that attention-related effects on behavior as well as neural signals could be better explained by a response gain model than by a noise reduction model or an efficient read-out model. In this Neuro Forum we discuss these results and raise several interesting questions and potential interpretations.

spatial attention; sensory gain; vision; computational models

MORE THAN A HUNDRED YEARS ago the American psychologist William James wrote "...we must conclude that the perception of figure by the eye is the result of a number of different acts of attention. These acts of attention, however, are performed with such rapidity, that the effect, with respect to us, is the same as if the perception were instantaneous" (James 1890). Since then, a plethora of empirical studies on attention has indeed shown that attention influences sensory perception and subsequent behavior (for reviews see Serences and Yantis 2006; Treue 2003). Recent advances in the field of cognitive neuroscience have led to the identification of neural circuits associated with attentional processes that presumably underlie the behavioral benefit of attention. Nevertheless, how attention affects perception at the neuronal level still remains largely unknown. A recent study by Itthipuripat et al. (2014) has combined psychophysics, neurophysiology, and mathematical modeling to address this question.

Traditionally, the relationship between the amplitude of a response (neural or behavioral) and the strength of sensory input has been estimated using the Naka-Rushton equation (*Eq. 1*) (Itthipuripat et al. 2014, Pestilli et al. 2011):

$$R(c) = G_r \frac{c^{s+q}}{c^q + G_c^q} + b \qquad (1)$$

In vision research, the strength of sensory input can be manipulated by changing the stimulus contrast, and the equation is therefore also known as a contrast-response function (CRF) where R is the response that covariates with sensory contrasts

(c), G_r is the multiplicative response gain factor corresponding to the highest response amplitude of the CRF, G_c is the divisive term that comes from the normalization pool of the targeting receptive field and determines the horizontal position of the CRF along the contrast axis, b is the baseline offset in the absence of sensory input, and s and q are exponential factors that determine how quickly the function rises and saturates. The CRF curve is shown as the black line in Fig. 1*A*.

It is often found that when a stimulus is attended, the CRF curve shifts. Previous studies have proposed several mechanisms (Hillyard et al. 1998; Serences and Yantis 2006) that can contribute to such sensory gain. Attention can cause an increase in stimulus-evoked responses through one way or a combination of three ways. First, a response gain indicates a multiplicative increase in response magnitude (an increase of G_r in the CRF as indicated by the red line in Fig. 1*A*). Second, a contrast gain means less sensory input is required to reach half of the maximum response (a leftward shift of the response curve along the sensory axis; i.e., a decrease of G_c in the CRF as indicated by the blue line in Fig. 1*A*). Third, an additive gain shows an additive effect on baseline responses (an upward shift of the response curve along the response axis; i.e., an increase of b in the CRF as indicated by the green line in Fig. 1*A*).

Recently, alternative mechanisms about attentional modulation have been proposed that do not affect the CRF function. Attention can reduce correlated noise and/or trial-by-trial variability of the neuronal responses (Mitchell et al. 2007). According to signal detection theory, sensory sensitivity depends on the signal-to-noise ratio such that a decrease in noise can explain beneficial effects of attention on behavior as well as increases in sensory response. Furthermore, Pestilli et al. (2011) implemented an efficient read-out model that uses a "winner-take-all" pooling mechanism to account for decisions based on sensory evidence and found that attention could inhibit distracting nontarget neuronal responses and pool target-related neuronal responses only. The reduction of distraction in the pool leads to a better readout of the target information. In the same article, Pestilli et al. compared all the above-mentioned models and found that the efficient read-out model described attention-related increases in blood oxygen level-dependent (BOLD) signal better than the sensory gain model and the noise reduction model. This elicits the question as to why most previous studies favored a sensory gain hypothesis (Hillyard et al. 1998; Serences and Yantis 2006). Itthipuripat et al. (2014) set out to test which model best accounts for attention-related changes in electroencephalogra-

Fig. 1. *A*: representation of how different forms of sensory gain can affect the contrast-response function (CRF) during attention conditions. *B*: example of a trial in the focused attention condition (*left*) and divided attention condition (*right*). An attention cue is followed by 2 visual presentations, each with 2 Gabor stimuli, and a response cue. Participants had to indicate if the first or second presentation contained a contrast increment in one of the Gabor patches. In the focused attention condition, participants paid attention to one cued Gabor patch, and in the divided attention condition, participants had to attend to both of the Gabor patches. *C*: a framework of experiments combining different methodologies to better understand attention processes.
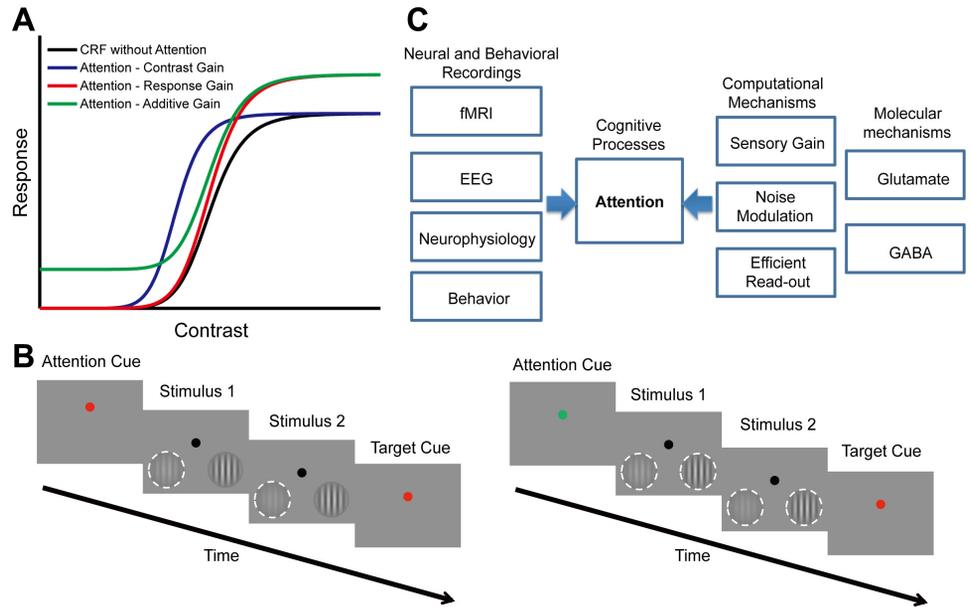
phy (EEG) data using a paradigm similar to that of Pestilli et al. (2011).

Participants performed a contrast discrimination task while EEG data were recorded. On each trial, participants viewed two consecutive stimulus presentations, each containing two Gabor patches (see Fig. 1*B*). On one of the two stimulus presentations, a small contrast increment was added to the pedestal contrast of one of two Gabor patches. Participants needed to indicate whether the first or the second stimulus presentation contained the higher contrast. To ensure that participants reached ~76% accuracy ($d' = 1$), the contrast increment was adjusted individually for each of seven different pedestal contrast levels independently. These individually defined contrast increments were used as the behavioral measure, with smaller values representing better performance.

The experiment contained two attention conditions. On focused attention trials, participants were cued at the beginning of each trial as to whether the contrast increment would appear in either the Gabor patch on the left side of the screen or the Gabor patch on the right side of the screen (Fig. 1*B*, *left*). On divided attention trials, participants were not cued and had to divide their attention (Fig. 1*B*, *right*). Attention facilitated performance, and participants could detect a smaller contrast change in focused attention trials compared with divided attention trials.

Both behavioral and EEG data were fitted to a combination of signal detection theory and Naka-Rushton functions. A number of free parameters were allowed to describe the shape of the threshold-versus-contrast function (describing the relation between pedestal contrast level and threshold contrast increment) and CRFs. Importantly, data were fitted separately for the divided and focused attention conditions, and the fitted parameters were compared between the two conditions. Attention effects on behavior were fully explained by a parameter representing a multiplicative response gain factor (G_r), in line with a sensory gain model. A parameter allowing the response curve to move along the contrast axis did not change between attention conditions. Note that parameters representing noise

and baseline response were fixed for this analysis, so they could not account for attention effects of behavior.

For EEG data, the analysis focused on two event-related potentials (ERP) of interest, the P1 component (80–130 ms) and late positive deflection (LPD; 230–330 ms). Again, attention-related increases in ERP amplitudes were selectively explained by an increase in response gain. Furthermore, no accompanying shifts of the response curve along either the contrast axis (contrast gain, changes in G_c) or response axis (additive gain, changes in b) were observed. Crucially, the authors linked the behavioral and EEG data to show that the magnitude of sensory gain observed in the ERPs could fully account for the attentional benefits observed in the behavioral data. Additional models that included an efficient read-out mechanism or noise modulation did not outperform the sensory gain model. Taking these findings together, the authors conclude that attention modulates perception through a multiplicative response gain at early stages of sensory information processing.

Their results are in line with previous findings supporting the sensory gain hypothesis (Hillyard et al. 1998; Serences and Yantis 2006), and also open up a few interesting questions for future directions. First, the article described the effects of spatial attention on behavior and neural responses to low-level visual stimuli. However, attention can also be directed to features or complex objects. Could effects of feature-based attention also be accounted for entirely by a sensory gain model? Or are additional mechanisms such as noise modulation and/or efficient read-out necessary to explain attentional benefits when attention is directed toward more complex stimuli? In addition, it has been suggested that attention directed toward targets presented at foveal retinotopic locations improves performance through mechanisms other than sensory gain (Handy and Khoe 2005). It would be interesting to repeat the experiment by Itthipuripat et al. (2014) with a paradigm that requires feature-based attention to foveal presented stimuli and compare the results to the results from the spatial attention paradigm.

Another point to consider is that the task that was used in the study requires working memory to compare the stimuli on the first and second presentations. Importantly, the working memory loads are different between the two attention conditions. It would be interesting to know how working memory load affects behavioral and neural results in this attentional context. This could be done by introducing additional working memory load into the tasks. For example, before each trial, we might ask participants to remember orientations of a certain number of Gabor patches and probe their memory immediately after each trial. By varying the load, we could investigate how working memory interacts with attention in this context. It is notable that top-down modulation has been suggested to serve as a shared neural mechanism underlying attention and working memory (Gazzaley and Nobre 2012). Working memory may impact attention performance by taxing a limited capacity system for top-down modulation. Future studies perturbing prefrontal top-down control would further help to clarify the effects of top-down modulation on attentional gain.

A third point to consider is that in three separate studies, using three different recording modalities [EEG, functional magnetic resonance imaging (fMRI), and neurophysiology], the results favored three different models, sensory gain, effective readout, and noise modulation, respectively (Itthipuripat et al. 2014; Mitchell et al. 2007; Pestilli et al. 2011). It will be important in the future to understand why this is the case. As the authors discussed, fMRI signals may be insensitive to attention-induced sensory gain changes, and noise modulation at the cellular level could also contribute to the sensory gain at the systems level. We also noticed that in the discussed article, the authors fixed the baseline response (b) and the noise level (σ) when drawing the optimal k (the parameter in the max-pooling rule). The final goodness of fit could possibly be even more optimal if they fitted those parameters (b and σ) again after reaching each individual k. In this case, it is more like a combination of different models. Nonetheless, future simultaneous multimodal recordings could equally assess all these models and potentially find one combined model that fits all the neural data.

Once we understand the neural computations that are used, the next critical step will be to understand the underlying neural mechanisms. At the cellular level, GABA has been suggested to play an important role in controlling the sensory gain (Katzner et al. 2011), and glutamate has been shown to be critical for noise modulation (Herrero et al. 2013). Understanding the neural mechanisms may also help to resolve the discrepancies among recording modalities. Overall, neural synchrony could be a candidate to unify all the computational models at both cellular and circuit levels. For example, a recent review summarized the relationship among gamma oscillations, fMRI BOLD signals, and GABA concentration in the brain (Singh 2012).

Beyond all doubt, a combination of research tools at different levels (microscopic, mesoscopic, and macroscopic), multimodal neural signals (single/multiple-unit recording, EEG, and fMRI), and mathematical modeling (as used in the study by Itthipuripat et al. 2014) will lead to a better understanding of the mechanisms of attention and other cognitive functions (see Fig. 1*C*).

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Y.K. and M.R.v.S. interpreted results of experiments; Y.K. and M.R.v.S. prepared figures; Y.K. and M.R.v.S. drafted manuscript; Y.K. and M.R.v.S. edited and revised manuscript; Y.K. and M.R.v.S. approved final version of manuscript.

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