Commentary on Mather, M., Clewett, D., Sakaki, M., & Harley, C.W. (in press). Norepinephrine ignites local hot spots of neuronal excitation: How arousal amplifies selectivity in perception and memory. Behavioral and Brain Sciences.

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The role of arousal in predictive coding

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Abstract: Within a Predictive Coding approach, the arousal/norepinephrine effects described by the GANE model seem to modulate the precision attributed to Prediction Errors, favoring the selective updating of predictive models with larger Prediction Errors. However, to explain how arousal effects are triggered it is likely that different kinds of Prediction Errors (including interoceptive/affective) need to be considered.

Classical models of information flow in the cerebral cortex consider that primary sensory regions detect the physical properties of the stimuli which are then combined into increasingly complex representations along the hierarchy of perceptual processing. As such, perceptual processing is considered to be largely bottom-up, and top-down effects are only expected to modulate the processing stream. On the other hand, the Predictive Coding framework suggests that the cortical representation of objects are largely produced by top-down feedback to sensory cortices (i.e., predictions about what is being perceived originate in higher-level regions) (Clark, 2013; Friston, 2005, 2010). In this view, sensory information is not fed forward along the cortex, but, rather, what is communicated along the cortical hierarchy is only the difference between the predicted and actual inputs: the Prediction Errors. When such a mismatch occurs, the Prediction Errors are then used at the higher levels of the hierarchy to update the predictive model as to eliminate Prediction Errors in the next round of comparisons (Clark, 2013; Huang & Rao, 2011; Rao & Ballard, 1999). Predictions and Prediction Errors are thought to be instantiated by different neural units and the balance between the two depends on

Precision cells that modulate their relative weights. Increased precision of the Prediction Errors means that the error signal will be strengthened by the precision units and lead to a stronger updating of the predictive model, whereas decreased precision suppresses the Prediction Errors and thus maintains the current model (Barrett & Simmons, 2015).

With this brief introduction in mind, I will now turn to how the GANE model may be integrated within a Predictive Coding approach – a possibility that is acknowledged by Mather, Clewett, Sakaki, and Harley in the target article.

The activity of norepinephrine (NE) neurons has been in the focus of researchers interested in the neural coding of Prediction Errors (Dayan & Yu, 2006). NE cells respond phasically to unexpected stimuli across sensory modalities and cease to respond after a few repetitions of the stimulus, a pattern of activity that is consistent with what would be expected from units coding Prediction Errors (Schultz & Dickinson, 2000). However, as detailed by the GANE model, the overall effect of NE seems to be more akin to a modulation of the precision weights of Prediction Errors. Thus, in Predictive Coding terminology, NE amplifies the stronger feedforward glutamatergic error-signals while suppressing weaker Prediction Errors, leading to a stronger updating of only the most unexpected inputs. Indeed, this is a sensible explanation: strong Prediction Errors signal highly unexpected sensory input and thus elicit orienting responses and concomitant central NE release to boost signal-to-noise ratio and favor the updating of the most relevant predictions.

However, the salience or priority of stimuli that seem to trigger NE effects is not fully dependent on sensory mismatch. It is true that phasic NE responses occur to intense unexpected sensory inputs (Peterson & Posner, 2012) but also to stimuli that are not physically extreme, namely stimuli that carry emotional or task-related significance (Schultz & Dickinson, 2000). Indeed, the affective/motivational aspect of arousal is something that has not been the focus of the more classic formulations of Predictive Coding approaches. However, recent models of Affective Predictive Coding extend the Predictive Coding framework, originally developed to account for perception of external objects, to include interoception, i.e., the cortical representation of internal states which constitute the basis of emotional experience (Barrett & Simmons, 2015; Seth, 2013). Also, Affective Predictive Coding models do not consider interoceptive inferences as independent from exteroceptive processing, but rather that affective predictions and affective Prediction Errors are a basic component of "regular" perception (Barrett & Bar, 2009). This means that the perception of an object involves not only predictions about its physical features (e.g., shape, color) but also about its affective properties (e.g., very pleasant, neutral, scary), and that the Prediction Errors that are elicited may concern sensory and affective mismatches.

One hypothesis that is consistent with this view is that engagement of NE neurons in the locus coeruleus may depend on a threshold of the net sum of Prediction Errors for a given input. This would mean that arousal effects may occur following sensory, affective, or task-related mismatch (depending on whether the stimulus is, respectively, inconsistent with perceptual, interoceptive, or goal-related predictions) or a combination of these. If this combination of Prediction Errors reaches a given threshold, then a phasic NE response is elicited in order to facilitate the selective updating of predictions in the prioritized manner that Mather and colleagues elegantly describe. Indeed it has been shown that emotionally deviant stimuli evoke larger cortical Prediction Errors than neutral deviants (Vogel, Shen, & Neuhaus, 2015), but the precise role of NE in this effect remains an issue for future investigation.

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