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Comment

Predictive coding links perception, action, and learning to emotions in music

Comment on "The quartet theory of human emotions: An integrative and neurofunctional model" by S. Koelsch et al.

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The review by Koelsch and colleagues [1] offers a timely, comprehensive, and anatomically detailed framework for understanding the neural correlates of human emotions. The authors describe emotion in a framework of four affect systems, which are linked to effector systems, and higher order cognitive functions. This is elegantly demonstrated through the example of music; a realm for exploring emotions in a domain, that can be independent of language but still highly relevant for understanding human emotions [2].

Emotion is fundamental to human life, survival and well-being [3] and music is one of the strongest and most universal sources of human emotion and pleasure [4–10]. Music also highlights a particularly interesting aspect of human emotions: the dynamical interplay between perception, action and learning, and emotion. Here, the review is less explicit in describing the mechanism by which the interaction between these systems takes place. Novel models of brain function have emerged such as the predictive coding theories [11–17] proposed to be general theories of brain function [18], explaining how brain areas exchange information. Such models offer a novel perspective on how specialized brain networks can identify and categorize causes of sensory inputs, integrate information within other networks, and adapt to new stimuli. They propose that the quartet of perception, action, learning and emotion occurs in a recursive Bayesian process by which the brain tries to minimize the error between the input and the brain's expectation. Within this framework *Perception* can be described as the process of minimizing prediction errors between higher-level "prediction units" and lower-level "error units" in the hierarchically organized brain; *Action* is the active engagement of the motor system to resample the environment in order to reduce prediction error; *Emotion* acts as weight or modulator of the prediction error itself, guiding behavior, action and learning through neurotransmitters such as dopamine [19]; while *Learning* is the long-term influence on the prediction units [17,18].

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This idea of prediction as a fundamental principle of human brain function corresponds remarkably well to theories addressing the role of prediction in governing music perception and appreciation [20–24]. Meyer [20] formulated the idea that musical anticipation and incongruity, i.e. elements that do not fit with schematic, veridical or short term memory-based predictions, may be a fundamental source of music emotion and pleasure. Hence, musical emotion and pleasure are driven by the dynamic interplay between the listener's expectations and the statistical regularities in the musical structure. Music is pleasurable when expectations are fulfilled, but probably even more so when they are slightly violated. According to this idea, unanticipated events are responded to with surprise, i.e. increased physiological arousal and optimized attention, but can be modulated by secondary cognitive appraisals of the event. So, the delights we get from unanticipated events in music are due to the contrast between our predictions and the musical structure, as well as the subsequent resolution within the music.

Hence, when listening to music with its basic elements of melody, harmony, and rhythm, the brain applies a predictive model based on prior experience, which guides our perception and emotions. Take the example of a repeated syncopated rhythm, which may make the brain expect the rhythm to be in 4/4. Here, we will experience an error at the syncopated (unexpected) note [25–28]. This may drive an impulse for action in the form of keeping the beat by tapping the foot, which again may lead to emotion, pleasure and learning.

Thus the music's predictive motion between tension and release can form the basis of musical emotion and pleasure, with the predictive coding model explaining how neural systems interact. The brain is constantly trying to minimize the discrepancy between its predictive model (or prior) and the musical input by iteratively updating the prior by weighting it with the likelihood (musical input) through Bayes' theorem. Note that Bayesian inference is assumed to take place at every level of brain processing so that higher levels of processing provide priors for lower levels, thus creating nested and hierarchical links across the entire brain. The predictive coding theory assumes a multilevel cascade of processing at different timescales, in which each level attempts to predict the activity at the level below it via back ward connections. The higher-level predictions act as priors for the lower-level processing (so-called "empirical Bayes"). Importantly, these priors are influenced by previous experience and culture [29], often called hyper-priors [30]. These backward connections. The higher-level predictions act as priors for the lower-level processing. Importantly, these priors are influenced by previous experience and culture [29,30]. They rely on cultural background, personal listening history, musical competence, context (e.g. social environment), brain state (including attentional state and mood), and innate biological factors.

So as the authors rightly points out, emotion does not exist in isolated neural systems but interact with lower- and higher level brain systems for perception, action, and learning. The predictive coding model could be a valuable addition to the 'Quartet theory' by Koelsch et al. for describing the mechanisms of how emotion, action, perception and learning interact at the neural level.

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