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Comment

Evolutionary perspectives on emotions and their link to intentions, dispositions and behavior
Comment on “The quartet theory of human emotions: An integrative and neurofunctional model” by S. Koelsch et al.

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Koelsch and coworkers present a sophisticated neuroanatomical model of emotions comprising four affect-systems and four output-systems, each bound to a specific brain area [1]. Moreover, they suggest the emergence of distinct components of subjective feelings or “emotion percepts” due to integration of the activation across these subsystems. Incorporating numerous neurobiological, psychological and philosophical findings on human emotions, the model reflects an extensive interdisciplinary approach. Considering an evolutionary perspective, however, we would like to address some issues concerning emotions and their link to intentions, dispositions and behavior that are not fully covered by the Quartet Model. Charles Darwin pointed out that individuals that are better adapted to their environment have increased chances of survival and reproduction. Therefore, natural selection leads to a rising prevalence of properties offering a survival benefit across generations [2]. To better understand the biological functions of emotions we propose to ask the question: How do emotions provide a benefit for survival and reproduction?

Considering the characterized four affect systems the following benefits can be identified: The brainstem (WAKE-system) improves survival by matching the arousal level to environmental demands. The diencephalon (SEEK-system) does so by reinforcement of the regulation of homeostatic needs. The hippocampus (CARE-system) offers a survival benefit by strengthening the relations to close relatives, especially cohabitants and offspring. The orbitofrontal cortex (NORM-system) does this by reinforcing adherence to social rules. However, there seem to be many more ways in which emotions contribute to survival:

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1) Language, anticipatory emotions and intentions

According to the Quartet Model the output of unconscious automatic emotional processes is projected to higher order language areas. Language processing is introduced as a successive step allowing (a) the communication of "emotion percepts" and (b) conscious reappraisal which in turn enables active emotion regulation. There is evidence, however, for further interaction between emotional processes and language-based cognitive processes preceding the formation of "emotion percepts". First, language-based concepts may contribute to "primary" appraisal processes during evaluation of emotional stimuli [3,4]. Moreover, conscious language-based appraisal of possible future events followed by an emotional evaluation of the anticipated outcome leads to anticipatory emotions. These anticipatory emotions are assumed to support intentional goal-oriented ("rational") behavior and thus help to increase survival [5]. Presumably they also have specific neurobiological correlates.

2) Current affects and long-term dispositions

According to Wittgenstein, "the meaning of a word is its use in the language" [6]. Examining the use of emotion-associated words reveals a distinction between current affects (e.g. "I am happy when I win the game") and long-term dispositions (e.g. "I like sports"). Some terms (e.g. "love") turn out to be rather complicated, because they can be used to denote current affects as well as long-term dispositions. Current affects imply the possibility of sudden changes (e.g. "when I get bad news my emotional state switches from happy to sad"), whereas dispositions are characterized by their persistence despite the absence of a corresponding current "emotion percept" (e.g. "this switch of my emotional state does not change the love for my children"). From the empiricist view, all dispositions and beliefs are based on prior experience including "emotion percepts" [7]. Presumably they yield further survival benefits by long-term facilitation of homeostatic and social regulation. A thorough differentiation of distinct emotion-related phenomena (e.g. current affects, long-term dispositions) is required to guide future research on their neurobiological underpinnings.

3) Diversification of emotional expressions

An evolutionary perspective on the diversification of laughter will serve as an example to elucidate the multi-faceted functions of emotional expressions. Laughter has been observed in monkeys and rats as a reflex-like response during tickling and play behavior [8]. Laughter is contagious, it can induce emotions in others. In addition to the facilitation of bonding, laughter can appease potential aggressors [9] and attract potential mating partners [10]. Therefore, the ability to laugh promotes survival and reproduction. Furthermore, in humans there is a diversification of distinct types of laughter serving even more complex social purposes (e.g. including and excluding laughter) [11].

According to the Quartet Model unconscious automatic processing within the affect-systems activates the effector systems that produce emotional expressions (among other reactions). The gain for survival and reproduction provided by deliberate modulations of emotional expressions could be considered as a further extension of the model. During the course of evolution, natural selection favors individuals that are able to vary their emotional expressions deliberately to further their aims [12]. On the flipside, a greater capability to differentiate between automatically generated ("authentic") emotional cues and deliberately controlled expressions [13] or more generally speaking the ability to predict the behavior of others [14] also represents a benefit for survival. A further extension of the Quartet Model could include the capacity to recognize others' emotional states and intentions from their emotional expressions, bound to a cerebral network including the mediofrontal cortex [15,16]. Moreover, the interaction between automatic (unconscious) and intentional (deliberate) processing of emotional expressions in order to optimize adaptation could be considered.

4) Control of emotions

In contrast to evolutionary older animals, emotions guide the behavior of humans in subtler ways. Assumingly linked to the phylogenetic growth of the prefrontal cortex, the ability of habitual, often unconscious and not necessarily language-based emotion regulation developed. This ability enables humans – to a certain degree – to behave independently of their current emotional state and represents a benefit for survival in complex environments. This becomes most obvious in psychiatric disorders where this habitual control of emotions is impaired. Examples include the spectrum of mood and anxiety disorders [17–19] as well as personality disorders with emotional instability and impulsivity [20] where decreased activity of the dorsolateral prefrontal cortex – in addition to altered activity of limbic structures and parts of the orbitofrontal cortex – represents a common correlate of emotional dysfunction.

Therefore, we argue that the potentially tonic or automatic phasic activity of the dorsolateral prefrontal cortex is a relevant component of the neurobiological system underlying normal or healthy emotion processing. This supposed automatic regulatory function should be taken into account in the future refinement of neurobiological emotion models.

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