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Reply to comment

Instruments, conductors, dancers, and intendants
Reply to comments on "The quartet theory of human emotions: An integrative and neurofunctional model"

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I am happy about each commentator's contribution [1–27], about the wealth of the kind and generally positive comments, and the many interesting and enriching remarks, observations, and extensions. In the following, I will summarize some major points of the comments, and relate them to the Quartet Theory (henceforth QT) proposed in the target article [28].

The roles of language in emotions

Several authors emphasized that language is not only important for the verbalization and regulation of emotions, but also that "words at least in spoken language are capable of eliciting strong emotional feelings" [4]. A particular question across several comments was *when* exactly emotional meaning of language is processed [4,6,12,25]. Does

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a word have to be processed "psycholinguistically" in the language-network in order to elicit emotional responses, or can words – similar to conditioned stimuli – be recognized by an affect system even *prior* to the processing in the (neo-cortical) language network? The Quartet Theory would predict that (both written and spoken) *words can gain symbolic quality (especially in the course of contextual learning) by which they can elicit affective activity in the orbitofrontal cortex (OFC), even without – or prior to – "psycholinguistic" processing in the neo-cortical language system*. In this regard, the QT would explain what Braun [4] puts nicely as "the striking fact that the emotion-eliciting function of words can be of a pre-verbal nature."

Consistent with this notion, several comments cite evidence of surprisingly speedy emotional responses to words [12,4,6]. Kuiken and Douglas [15], moreover, provide nice examples of OFC-based judgements and "emergence of a 'felt sense' of a perceptual object that precedes articulation of the 'nameable' category to which it belongs". The mechanisms of emotion–evocation by symbolic verbal stimuli are probably even more powerful in the case of words spoken with a significant voice (such as the voice of mother or father, or the affective colour of their voices), i.e. when we hear words spoken by persons with prominent roles in our personal contextual learning history. In this regard, investigations with bilingual individuals can help elucidate this issue (see also [29] and comment by Conrad [6]). While I presume that the OFC is an important structure for associations between symbols and emotions, it would be interesting to investigate to which extent the other affect systems are also capable of recognizing and learning symbolic content of words and vocalizations (see also comment by Hofmann and Kuchinke who remark that some hippocampal neurons code the coincidence of different contextually learned representations, including words [13]).

Conrad [6] even raises the question as to whether, "besides serving as a vehicle for communication of emotion, language also influences emotion percepts." When investigating this question, it would be important to differentiate the symbolic ("conditioned") quality of words and vocalizations, which might act indirectly on the emotion percept via affect-eliciting processes in the affect systems, from the neo-cortical "psycholinguistic" language processes, which might act on the emotion percept via conscious appraisal processes (as suggested in the QT).

Note that pre-verbal processing of words might also occur independently of the emotional content of words (i.e., not only with regard to emotional information). As mentioned above, Kuiken and Douglas [15] describe that categorical learning might take place "even before the basis for categorization can be stated". This might, in part, also be due to objects evoking sensorimotor codes (including the basal ganglia) before these objects can be verbally categorized. Interestingly, this raises the question as to whether the *perception* of an emotion of another individual can evoke representations of meaningful concepts *before* this emotion is mimicked, or mirrored. Kuiken and Douglas [15] also ask the question: "how do 'action tendencies' become manifest as aspects of subjective feeling? Are the processes mediated by the basal ganglia and orbitofrontal cortex separable from 'conceptual-semantic language functions'?" The QT conceptualizes "motor drives" or "motor impulses" as components that contribute to the emotion percept. Language, on the other hand, can also initiate motor impulses [30,31] (although the conceptual-semantic language system appears to be neuroanatomically different from the neural substrate of the emotion percept, as also nicely illustrated by Kuiken and Douglas).

Herbert [12] presents highly interesting evidence extending "emotional word processing to the domains of social cognition and emotion regulation" [12]. Intriguingly, she found that emotions decoded from words elicit activity in the ventromedial prefrontal cortex when these refer to an individual's own feelings [12]. This appears to be related to self-referential processing and the appraisal of stimuli in terms of their personal significance. Future work could further investigate the role that the orbitofrontal-centred affect system plays in evaluative processes when stimuli with emotional significance are related to an individual's self (and, thus, also the role of the evaluative function of the OFC in "default mode network" activity).

Finally, Engelen [8] makes the important remark that "language and cultural practices may reconfigure the neurological material and therefore build up neural correlates for the thereby arising long-term emotions." Engelen also argues that emotional expression by one individual is a means of verifying (or falsifying) the correct use of an emotion word by another individual (thus enabling a teacher to teach emotion words for basic emotions to a child). This, however, is problematic, because some discrete emotions have very similar expression (e.g. anxiety and fear, or fun and happiness). A teacher cannot look into the head of the pupil, and therefore cannot guarantee that his or her use of an emotion word is 'correct'. I would also like to note that, for "basic" as well as more "complex" emotions, the QT conceptualizes expression *and* emotion percept as parts of the emotion. Thus, the QT does not oppose "basic emotions" and "emotion percepts" (neither does it prefer one over the other).

Art-evoked emotions and aesthetic emotions

Another issue raised by several authors is art-evoked emotions and their relevance for research in emotion science [10,11,16,18,19,21,26]. Leder [16] states that "the study of human interactions with art provides an excellent window into the complex emotional reactions that can be had with the environment", and even presents an impressive and highly interesting new "integrated model of aesthetic processing and emotional experience", relating five stages of aesthetic experience (pre-classification, perceptual processing, implicit memory integration, explicit classification, and cognitive mastering) to the different systems put forward by the QT. Similarly to Leder, Nadal and Rosseló [19] remark that "distinctions that oppose art to craft, or aesthetic to practical, in reference to objects, behaviors, experiences, and emotions, make little sense in a broader historic and geographic context, and contribute to hinder empirical research". Nadal and Rosseló [19] even note that "there is nothing unique about emotions elicited by art and aesthetics" – a statement that is supported, at least with regard to neurobiological phenomena, by the QT (as further explained below).

Gingras and Marin [11] make the important point that "with respect to the regulation and communication of emotions, music is at least equal, if not superior, to language", and similarly, Meyer and Kuchinke [18] emphasize "that emotion regulation is not based exclusively on linguistic processes", but that mental imagery (often stimulated by literature, music, and the arts) can also modulate, regulate, and partly initiate activity of all four affect systems.

I would like to differentiate here between *art-evoked emotions* and *aesthetic emotions*, suggesting to use the term 'art-evoked emotions' for emotions evoked by works of art (whether they are associated with experiences of beauty or not), and the term 'aesthetic emotions' only with regard to the experience of beauty (whether evoked by art or not). Art-evoked emotions often (but not always!) differ psychologically from "real-life" emotions in the sense that they are framed in a situation of art consumption (or art production). For example, the fear experienced in a thriller movie is psychologically not the same as the fear experienced in a situation that poses a real threat to the individual because it is framed by a movie-context. Importantly, however, individuals usually seek to lose their awareness of this framing (i.e., they usually seek full immersion in the work of art) to attain the full emotional experience. Particularly during such moments of immersion it is plausible to assume that the neurobiological correlates of art-evoked emotions do not differ from those of "real-life" emotions (if these neurobiological correlates are not involved even more strongly than in "real life", because for many individuals works of art can evoke emotional responses that are more intense than those usually experienced in everyday life). Therefore, art-evoked emotions can be used for the valid investigation of "real-life" emotions.

Note that *all psychological experiments on emotions (with humans) operate within a framing* (at least if they are carried out according to the ethical guidelines of the Declaration of Helsinki): The participant is informed that s/he is in the situation of an experiment, that s/he can withdraw from this "game" at any time, that no harm will be done, etc. In this sense, all emotion experiments are more or less artificial, or artistic. Ironically, in comparison to researchers investigating art-evoked emotions, many experimental emotion researchers believe that only they investigate "real emotions", when in fact the only difference is that their stimuli have poorer artistic quality.

Also note that some art-evoked emotions do not differ from "real-life" emotions, for example emotions related to the build-up of predictions, their fulfilment or their violation, as described by Gebauer, Kringelbach and Vuust [10] and by Witek, Kringelbach and Vuust [26]. Emotional effects of such processes are also in part related to what Perlovsky [21] refers to as "satisfaction of the knowledge instinct" and "cognitive dissonances": For example, the violation of a prediction (in an environment with low to moderate entropy) is often perceived as unpleasurable [32], but may at the same time have reward quality, because it has high information content, and thus can help to improve the model underlying future predictions. An interesting question in this regard is how the play with establishing, fulfilling, and violating predictions (and the tension and release emerging from such processes [33]) makes a piece of art beautiful.

Complex emotions

Meyer and Kuchinke [18] use the term complex emotions to refer to moral emotions, partly due to the fact that moral emotions are based on comparably complex social configurations and norms. However, not all complex emotions are moral emotions: Kaernbach [14] remarks that "complex emotions might comprise components that are often considered as opposite to each other." For example, art-evoked emotions often involve the play with opposing emotions, such as "bittersweet emotions", pleasant sadness, pleasurable tension and suspense, etc. Kaernbach also presents a "real-life" example, namely "watching a thunderstorm from within a safe shelter arm in arm with one's beloved might stimulate brainstem emotions of fear and at the same time allow for tender feelings of joy about witnessing those impressive forces of nature together without any risk for one's life." This example nicely illustrates that the QT can account for complex emotions, but future work will have to specify whether affective activity generated in different affect systems blends into one 'mixed' emotion, or whether different emotions can be felt at the same time in a complex way. These considerations illustrate that the term 'complex emotions' is already quite complex in itself.

The roles of the hippocampus and the amygdala in emotions

Several authors responded to our proposal of a hippocampus-centred affect system [1,2,23,24]. Arbib states "having made the important distinction between anterior and posterior hippocampus the authors have convinced us that being in the hippocampus more broadly does not imply co-localization" [1]. In this regard, it is important to note that there is not a clear distinction of cognitive and affective functions in the hippocampus along the anterior–posterior axis, but that there are functional gradients, with a certain overlap along this axis. Strange and Yebra [23] remark that it is an open question as to whether cognitive and affective functions "are executed by segregated circuits within each structure – i.e., a 'module' for emotion residing in a sub-division of a brain structure – or whether these circuits are superimposed", and state that "whether both of these functions (spatial and unconditioned fear) rely on the same neuronal populations [in the hippocampus] is currently unknown".

Strange and Yebra [23] also make the very interesting point that "a predominantly ventral hippocampal domain [...] projects via the rostral lateral septum to hypothalamic medial zone nuclei", and that "these nuclei, which include the anterior hypothalamic and ventromedial hypothalamic nuclei, form circuits involved not only in integrating innate defensive responses to environmental threats, but also in mediating reproductive and social agonistic behaviors." Moreover, they mention that the hippocampus projects "to the paraventricular nucleus of the hypothalamus, [which] is involved in controlling release of oxytocin, a hormone critical for the development of maternal behaviour." These points beautifully extend and support the notion that the hippocampus plays a role in attachment-related emotions.

With regard to the role of the hippocampus in unconditioned fear and anxiety [23] it seems evolutionarily relevant to reduce the degrees of freedom for behaviour in dangerous situations when offspring needs to be protected. That is, in a threatening situation, it is a difficult decision whether to protect the offspring at a certain risk or to abandon the offspring. I presume that *during the course of evolution an intricate computational decision system was differentiated in the hippocampus which takes both attachment-related and threat-related information into account*.

Trost and Frühholz [24] put forward the notion of an "integrated amygdala-hippocampus complex for emotional processing," and provide interesting evidence to substantiate this notion. Indeed, the amygdala seems to function in part as a "gatekeeper" for the hippocampus, e.g. due to its role in regulating neural input into the hippocampus (as detailed in the target article). This might also explain why both amygdala and hippocampus have been implicated in fear (see also comments by Armony [2] and Strange and Yebra [23]).

In this regard I would like to emphasize that the QT proposes that the amygdala is a control and coordination structure (involved in the detection of emotional signals, and in the initiation, maintenance, regulation, and termination of activity within affect systems, effector systems, and other control/coordination structures) – this role is highly complex, and not to be underestimated. On the contrary, it puts the amygdala at a very influential position in a limbic/paralimbic hierarchy, and the role of the amygdala according to the QT is by no means to be understood as a "major downgrade" [2]. *If we think of the four of affect systems as instrument groups of an orchestra, then the amygdala is part of the conductor* (note that the sounds are produced by the instruments, not by the conductor). As Armony [2] states, entire books have already been devoted to the amygdala, and it was not intended to reiterate the contents of these books. However, the fact that not overly much text was devoted to the amygdala in the target article [28] admittedly also expresses a silent calling against the sometimes almost obsessive focus on the amygdala in affective neuroscience, in favour of a more balanced view.

With regard to the "activation" of the hippocampus in fMRI experiments, I would like to repeat here that fMRI data do not inform us about whether BOLD signal changes in a structure reflect excitatory or inhibitory processes. Therefore, although researchers often (fallaciously) tend to associate an increase in BOLD signal with excitatory processes ("activation"), it is currently not possible to tell whether a BOLD signal increase in the hippocampus in response to negative stimuli (e.g., stimuli evoking fear) is due to excitatory or inhibitory (post-syntaptic) processes, such as post-synaptic inhibition of hippocampal neurons by neurons located in the amygdala. In this light, interpretations of results of several previous fMRI studies have to be revised.

Finally, Hofmann and Kuchinke [13] suggest another antecedent for affective activity in the hippocampus, namely generation of novel knowledge. This might relate to the "satisfaction of the knowledge instinct" as one of the aesthetic emotions proposed by Perlovsky [21], and hence in more general to the human need for growth and development. Therefore, the notion that the hippocampus is involved in joy associated with epistemic emotions and thus one's own growth and development is very interesting and motivates further research on this topic.

Emotion networks – "The Quartet does not play alone"

Several authors remark that emotions do not arise from single brain structures but from integrated, complex networks, a point with which I entirely agree (and which is put forward by the QT). For example, Arbib [1] states that "the orchestra analogy reminds us that it is a mistake to link region A to function X – rather, we must seek the minimal systems". Leder [16] mentions that "there is no localized seat in the brain for our affective experience, which instead emerges from the interaction among nodes of a broadly distributed network of cortical and subcortical regions," and Bowling [3] writes that "a shift towards circuit-based approaches that emphasize the richly interconnected and distributed nature of nervous systems seems inevitable." Similarly, Fehr and Herrmann [9] state that "there are current models and scientific positions that almost completely reject the idea that modular psychological phenomena are handled by a distinct selection of regional brain systems or neural modules, but rather suggest highly complex and cross-linked neural networks individually shaped by livelong learning and experience." They also make the interesting point that "the proposed affect- and effector-subsystems are integrated parts of just *one* functional and physiological network, wherein each of the sub-systems processes basically the same phenomena at different complexity levels." Moreover, Schmidtke and Aryani [22] state that "a high degree of functional integration constitutes a necessary precondition for their emergence, making clearcut localizations of particular functions difficult," and Cochrane [7] even asks "Why can't the overall experience of an emotion simply be distributed across the brain?"

Obviously, emotions arise from activity integrated across different brain structures, and surgical isolation of the hippocampus would not create a happy soul in a Petri dish. More specifically, an emotion is defined in the QT as "the integrated result of activity in affect systems and emotional effector systems, from which an emotion percept emerges" [28], and it is emphasized in the target article that the affect systems as well as the effector systems interact with each other (as illustrated in Fig. 2 of the target article). Thus, by definition, *the QT conceptualizes emotions as arising from integrated complex networks (plural!)*. That is, the QT proposes different networks, with different affect systems functioning as sources of initial neural activity (referred to as "affect", comparable to the sound energy produced by instruments) leading to different classes of emotions. To continue the analogy of the quartet of affect systems as instrument groups, and the amygdala as part of the conductor (together with insula, cingulate cortex, and basal ganglia), one might think of the effector systems as the dancing (or panicking) audience, and of conscious cognitive appraisal as the intendant (all unified in one system with an emotion percept).

Importantly, the affect systems have different functional properties (e.g., processes that satiate and those that do not satiate), different evolutionary pathways, different antecedent pathways, and they are involved in partly different neurotransmitter systems. In this regard, Marco-Pallarés and Mas-Herrero [17] made the useful suggestion to further specify how sensory information reaches the different affect systems. Such specification should also include pathways through which pre-processed hetero-modal information (such as information from the Emotional Body Language System, as pointed out by Fehr and Herrmann [9]) gains access to the affect systems. Finally, it is worth noting that, because "the quartet does not play alone" [17], it is possible that damage of brain structures not included in the four affect systems (such as insula or cingulate cortex) can nevertheless affect emotional experience.

Evolutionary aspects

The QT considers evolutionary aspects of brain development and differentiation. Several authors picked up on this topic. Arbib [1] as well as Gingras and Marin [11] kindly acknowledged that they found the differentiation between affective processes that satiate and those that do not satiate useful. Witek, Kringelbach and Vuust [26] put forward the notion that music-associated rhythmic activities involving synchronisation, such as musical dance, "have culturally evolved as social tools, due to the demonstrated effects of interpersonal sensorimotor coupling and social bonding."

I find it plausible to assume that such social functions of music, as well as the function of music to regulate emotions (as put forward by Gingras and Marin [11], see above) were evolutionarily adaptive [33].

Wildgruber and Kreifelts [25] ask the question "How do emotions provide a benefit for survival and reproduction?" and provide several intriguing ways in which emotions contribute to survival, including "Language, anticipatory emotions and intentions", "current affects and long-term dispositions" (including long-term facilitation of homeostatic and social regulation), "diversification of emotional expressions" (including, notably, the gain for survival and reproduction provided by deliberate modulations of emotional expressions), and "control of emotions." Wildgruber and Kreifelts [25] also added, based on the QT, a WAKE (brainstem-centred) and a NORM (orbitofrontal-centred) system to Panksepp's "major emotional operating systems" [34].

With regard to the evolutionarily adaptive function of emotions, I would like to emphasize that emotions do not only guide behaviour (by selecting actions), but also attention (thus also perception), memory, and decision making (including selecting and setting goals). That is, *emotions reduce the degrees of freedom with regard to attention, memory, decisions, and behaviour*. I believe that this is a major evolutionarily adaptive function of emotions (in addition to making our lives worthwhile). For example, if a rodent did not have a system selecting information to be stored (or not stored) in long-term memory, all memory storage would be consumed shortly after birth (and no free memory would be left later on, once the way back to the nest with the offspring has to be remembered). I make this point because several authors reduced the teleological aspects of emotions to behaviour, or attention and behaviour. For example, Arbib [1] cites "Denton's notion of 'primordial emotions' as the subjective element of genetically programmed behavior patterns which support homeostasis", Wood and Niedenthal [27] state that emotions modulate attention and behaviour, Gingras [11] cites Plutchik's statement that all emotions are "means to regulate a general 'behavioral homeostasis'", and Schmidtke and Aryani [22] associate (evolutionarily simpler forms of) emotion with action selection and action planning, also referring to Rolls' conceptualization of "emotion as evolution's solution to flexibly setting goals for the organism".

With regard to emotions and language, Wood and Niedenthal [27] raise the interesting notion that "emotion words are useful for regulation, not expression", i.e., "that affect labeling has a regulatory effect on the intensity of emotion states", and present an impressive amount of evidence supporting this notion. They also make the point that "unlike dwelling on the sensational experience of the emotion percept, labeling forces it into a particular category that is cognitively economical and therefore more abstract than the percept itself." This raises the interesting idea that labelling, categorization, abstraction, and thus regulation of emotion contributed to the evolutionarily adaptive function of language. A similar importance can be assumed then for music and dance due to their role in emotion regulation, as mentioned by Gingras and Marin [11] (see also above).

Modelling

Several authors [1,5,14] mention the interesting topic of computational models of emotion processing. Arbib [1] is interested in seeking "the minimal systems that allow us to characterize key data on each function of interest", Briesemeister [5] aims to combine "the psychological with the neurophysiological domain within a single computational model", and Kaernbach [14] suggests to model "dynamical properties of emotions [...] with a dynamic systems version". Similarly, Leder [16] states that "the key to understanding the neurobiological foundations of our cognitive/emotional reactions may lie in charting the dynamics of integrative networks of interconnected brain areas." The QT can help in this regard because it suggests to consider different systems for different classes of emotions, specifying different affect and effector systems, and different antecedent pathways for these systems. Fig. 2 of the target article [28] might be a starting point for such modelling.

How many players?

Arbib [1] writes that "the structural quartet must be replaced, by at least, a small orchestra". Even large orchestras are, of course, usually divided into a quartet of instrument groups: An (activating) percussion section, a woodwind section (from funny bassons to shrill piccolo flutes), strings (which can hale souls out of men's bodies), and (awe-inspiring) brass. However, similar issues are raised by Bowling [3] and by Cochrane [7]. In particular, Cochrane [7] remarks that "many different brain structures contribute an additional sophistication to emotional function; could there not be a class of emotions associated with each of these sophistications? How distinctive does the new function, or the new class of emotions have to be to qualify? Should we be on the lookout for neural structures associated with meta-emotions or epistemic emotions as well?"

My position is that there is no definitive answer as to how 'correct' a number of subdivisions is, but only opinions about how much sense subdivisions make. In this regard, as already stated above, QT aims to point out that the different affect systems have different functional properties, some of which have not been viewed this way before (e.g., the role of the hippocampus in attachment-related emotions, the role of the OFC in moral emotions and in Kahneman's 'System 1', the different satiation properties, etc.).

Other issues

Pehrs, Samson and Gross [20] present exciting pathophysiological evidence suggesting dysfunctional interactions of the hippocampal and orbitofrontal affect systems in autism spectrum disorder (ASD). The QT would predict that such dysfunctional interactions can be found in (numerous) other disorders as well. Along the same line, Fehr and Herrmann [9] point out that "the detailed analysis of individual differences appears to be a crucial aspect that is mostly neglected, although there is evidence that there is more individuality than overlap in the processing of complex emotional content," and that "inter-individual differences in complex emotional processing are not necessarily noise that needs to be averaged out." While I entirely agree with this point, I also see the problem that questionnaires assessing personality based on the dominating five-factor model do not lead to reliable measurements of personality-related neurobiological differences in emotion processing [35].

With regard to tonic and phasic emotional phenomena, Cochrane remarks that the QT seeks "a model that encompasses an organism's wider affective life" (in contrast, e.g., to Scherer's Component Process Model). I agree, and would like to note that the neurobiological correlates for phasic and tonic emotional phenomena probably overlap to a large degree. This is the main reason why the QT seeks to include both phasic and tonic emotional phenomena in one model.

With regard to including both goal-directed emotions and emotions that are not goal-directed in the QT, Witek, Kringelbach and Vuust [26] note that "the pleasure of groove is not goal-directed in the same way as 'musical chills' are and that groove rather affords a more distributed and processual kind of affect in which predictions are stimulated more continuously and pleasure is taken in the active embodied participation in the music," a point that I find interesting and valuable.

Along with the target article, several authors concur with the criticism of dimensional models for emotion theory. For example, Kaernbach [14] notes that "emotions are not fully described by triples of numbers," and Gingras and Marin [11] state that "dimensional models also neglect the fact that, at least in the case of voice and music, some affects, such as arousal, appear to be more strongly determined by the characteristics of the stimulus than others, such as pleasantness or valence, which may be determined to a larger extent by culture, social norms, and personality traits." Notably, the 'self-assessment manikin' (SAM) scale for valence (as introduced by Bradley and Lang, see comment by Kaernbach [14]) does not even range from pleasant (i.e., positive valence) to unpleasant (i.e., negative valence), but the 'manikins' show facial expressions ranging from happy to sad.

I conclude with citing from the comment by Fehr and Herrmann [9], who remark that we need, "in addition to contemporary theoretical innovations, new and advanced analytical approaches to better catch spatio-temporal and individual characteristics of neural emotion-processing, and new experimental designs more validly inducing emotional brain responses for a comprehensive testing of the here proposed theory of human emotions and to further explore the complexity of interactions and processing principles of the proposed sub-systems." The comments on the target article host an abundance of clever and original thoughts regarding these (and many other) issues, with the potential to significantly advance the field of the neurobiology of (human) emotions in the future. I hope that the QT will be of help for such advance, and stimulate further constructive and critical discussion, as well as elucidating empirical research.

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