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The Central Role of Anterior Cortical Midline Structures in Emotional Feeling and Consciousness

Abstract

Current theories of emotion have often excluded emotional feeling from the core of emotion, thereby associating emotional feeling with high order processing. In contrast, we characterize emotional feeling as a basic process that is fundamentally involved in emotional processing. Emotional feeling is further described by the phenomenal features of unity and qualitativeness. Based on recent imaging data, we assume that neural activity in the anterior cortical midline structures is crucial for constituting emotional feeling. The phenomenal feature of unity could be reflected in the connectivity pattern of the aCMS. What phenomenally is described as qualitativeness may correspond to what is psychologically termed valence.

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Feeling and Emotions

Emotions can be defined as an "umbrella concept that includes affective, cognitive, behavioral, expressive, and a host of physiological changes" (see Panksepp, 2005; Lambie and Marcel, 2002, who presuppose a similar understanding of emotion). The affective component refers to the subjective experience of emotion, such as fear, anger/rage, sex/lust, panic, or joy. I experience something when I am in the state of fear or am angry, and I feel a certain way when I panic or when I experience joy. This subjective experience of emotion is referred to as emotional feeling or the affective component in the following.

Recent neuroscientific theories seem to exclude emotional feeling from the core of emotions, thereby associating emotional feeling with metarepresentation and high order processing of emotions. By this means awareness or consciousness appears as a necessary condition for emotional feeling. For example, Rolls (1999, 2000) assumes that higher-order linguistic thought processing is essential for the occurrence of consciousness and consequently for the emergence of feelings. LeDoux (1996, 2002) considers working memory to be crucial for consciousness, which in turn allows for feelings to occur. Analogously, Damasio (1999) characterizes consciousness by meta- or second-order representation of contents, such as emotion, giving rise to feeling. He considers the distinct types of emotions as contents that can be represented on a higher level, that is, meta-represented, thereby inducing feeling. Though these approaches differ in various aspects, they all have in common that they account for emotional feeling by higher-order processing. Emotions, as lower-order (and unconscious) processes, are supposed to be represented on a higher level (on second- or even third order) that makes us conscious of them, and gives us the ability to report and thus to know them as such.

This type of consciousness has been described as reflective, higher-order, or secondary consciousness (LeDoux, 1996, 2002; Rolls, 1999, 2000; Damasio, 1999; Panksepp, 1998, 2005; Edelman, 2003; Metzinger, 2003; Chalmers, 1996; Lycan, 1995, 2001; Rosenthal, 1986, 1997; Block, 1996; Crick and Koch, 2003; Gray, 2004; Northoff, 2003). Reflective consciousness refers to higher cognitive capacities like introspection and reflection of one's emotional state (Rolls, 1999; LeDoux, 1996, 2002; Baars, 2003) that are closely tied to our ability to focus attention, sustain contents in working memory, and to voluntarily control our behavior (see Damasio, 1999; LeDoux, 1996; Crick and Koch, 2003). In the case of emotion, reflective consciousness accounts for "realizing what emotion one feels," and "to be conscious of an emotion" is "to know (and report) my feelings" (LeDoux, 1996, 2002; Rolls, 1999; Lambie and Marcel, 2002; also speak of emotion thoughts as propositional awareness of emotion on second order level).

Reflective consciousness has to be distinguished from what has been called phenomenal consciousness. Phenomenal consciousness does not describe cognitive and behavioral aspects associated with subjective experience. Instead, it focuses on the subjective experiential aspect itself that is described as the "phenomenal aspect" (Chalmers, 1996; Block, 1996). A number of alternative terms and phrases pick out approximately the same core property of phenomenal consciousness. These include “qualia,” “phenomenology,” “subjective experience,” and “what it is like,” which, despite subtle differences, we here consider to describe the same phenomenon for pragmatic purposes.

To account for the crucial role of subjective experience in emotion, we would like to characterize emotional feeling by phenomenal consciousness rather than by reflective consciousness. We consider feeling a subjective experience of emotions, including what is called qualia and “what it is like,” and presupposing phenomenal consciousness. The general aim of our paper is to develop a neuroscientific hypothesis about the neural correlates of emotional feelings. We hypothesize that the medial cortical regions in the anterior parts of the brain, the so-called anterior cortical midline structures (aCMS), may be crucial in mediating the phenomenal character of emotional feeling. More specifically, emotional feeling has been characterized by different phenomenal features including unity-homogeneity and qualitativeness. Therefore, the specific aims of our paper are the following: (i) To associate the unity-homogeneity of emotional feeling with certain anatomical, connectional, and functional patterns of neuronal organization in aCMS; (ii) to associate the qualitativeness of emotional feeling with a specific psychological dimension, that is, affective valence, that in turn is supposed to be accounted for by neural activity in anterior cortical midline structures.

The aCMS include the medial orbital prefrontal cortex (MOFC), the ventromedial prefrontal cortex (VMPFC), the sub/pre- and supragenual anterior cingulate cortex (PACC, SACC), and the dorsomedial prefrontal cortex (DMPFC) (see Figure 1). Based on empirical evidence, we suggest that their anatomo-connectional and functional characteristics make the aCMS a suitable neural candidate to underlie the two phenomenal features, unity-homogeneity and qualitativeness, of emotional feeling.

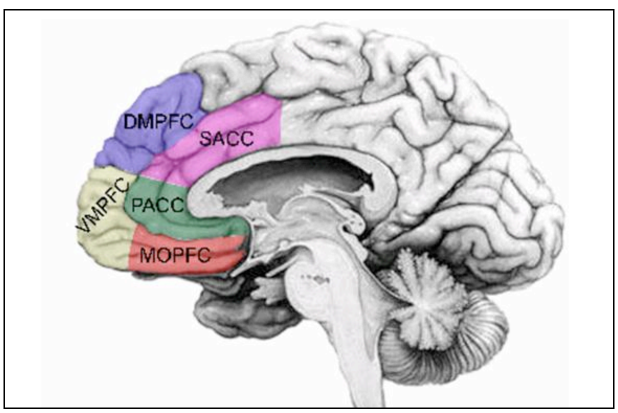

Figure 1: The anterior cortical midline structures (aCMS):
ACMS include the medial orbital prefrontal cortex (MOFC), the ventromedial prefrontal cortex (VMPFC), the sub/pre- and supragenual anterior cingulate cortex (PACC, SACC), and the dorsomedial prefrontal cortex (DMPFC).

The aCMS must be distinguished from more lateral cortical regions. The lateral prefrontal cortex (LPFC) is involved in processing of working memory, linguistic functions, and other higher cognitive functions (Duncan and Owen, 2000) that are supposed to be necessary for meta-representing (and expressing) emotions on a higher level, such as second- or even third-order. Since it apparently accounts for higher-order processing, the LPFC is often associated with reflective consciousness (LeDoux, 1996, 2002; Rolls, 1999, 2000; Edelman, 2003; Crick and Koch, 2003; Gray, 2004; Northoff, 2003). Our focus here is on emotional feeling as the affective aspect of emotion, rather than on the cognitive and reflective aspects of emotion. We, therefore, do not extensively discuss emotion processing and knowledge of emotion or emotional attitudes in relation to the LPFC (see for example Grafman, Vance, Weingartner, Salazar, & Amin, 1986; LeDoux, 1996, 2002; Rolls, 1999, 2000; and Wood, Romero, Knutson, & Grafman, 2005).

In the following, we first develop a phenomenal account of emotional feeling, which must be distinguished from reflective concepts as predominant in current discussion. Then, we discuss several methodological issues of how phenomenal concepts, such as unity and qualitativeness of emotional feeling may be tested empirically, thereby aiming to delineate the borders of empirical testability. Finally, by relating the empirical results to the phenomenal features, we aim to develop a hypothesis on the neural correlates of emotional feeling.

Since emotions and their phenomenal features are rather diverse and complex, it should be mentioned explicitly that we are leaving out a number of issues. First, from the neuroscientific perspective, our hypothesis focuses on the central role of the aCMS, while neglecting other areas of the brain, such as the subcortical regions. This does not mean that these regions do not have any importance in emotional feelings, but only that, due to space constraints, we remain unable to discuss their role in generating the phenomenal features of feeling (see for example Panksepp, 2005). Second, other theories of emotion, like perceptual or cognitive approaches, are not discussed here, since our focus lies only on the phenomenal character of emotional feeling. Third, since our focus is on the phenomenal character of emotional feeling, we do not discuss the distinct types of emotion in length. Fourth, we limit ourselves empirically to predominantly imaging studies, while neglecting other empirical approaches like human lesion studies, animal experiments, neuropsychological work, and brain stimulation. Fifth, it should be considered that many of the neuroimaging studies cited here were not primarily designed to address the phenomenal features of emotional feeling, but rather to isolate some specific affective or cognitive function in relation to emotion. Accordingly, there is some interpretation involved in placing and referencing empirical studies in the present context. Sixth, we focus predominately on emotional feeling, which is considered to be a part of subjective experience and phenomenal consciousness. Thus our hypothesis is limited to emotional feeling. It remains open as to what extent this hypothesis can be generalized to other kinds of feeling.

Properties of Emotional Feeling

In the first place we want to briefly discuss the characteristics of emotional feeling. Relying on philosophical and neuroscientific discussion, emotional feeling can be characterized (among other features) by unity and qualitativeness (see Searle, 2000; Edelman, 2003; Chalmers, 1996; Block, 1996; Bennett and Hacker, 2003; Metzinger, 1995; Northoff, 2003). Note that due to our focus on their possible empirical underpinnings, we remain unable to fully account for all details in the definition of these features.

What is qualitativeness? Every conscious state has a certain qualitative feel to it. If you experience tasting a beer or if you experience anxiety, in each case --it is something that it is like --to have that conscious experience. Nagel (1974) made this point when he claimed that if bats are conscious, then there is something that "it is like" to be a bat. Accordingly, there is something that it is like to experience anxiety and something that it is like to be in the state of anxiety (Metzinger, 1995, pp. 22-24; Northoff, 2003). Conscious states including conscious feelings are subsequently characterized by phenomenal-qualitative properties, which have also been designated as qualia.

The crucial point about the qualitativeness of feeling is that there is no trivial way to directly access it through associated cognitive capacities allowing for reflection and introspection. Following Nagel, we have to assume that even if we know everything about the behavioral and cognitive processing of a bat, we still do not understand what it is like to be a bat. Even the complete knowledge of all associated behavioral and cognitive aspects of emotions will, therefore, not allow us to infer subjective emotional experience and thus feeling.

In this paper, we aim to develop a hypothesis about the neural correlates of qualitativeness in emotional feeling. One should, however, consider that we have no direct access to the qualitativeness of feeling. Instead, we have only indirect access through introspection and verbal reports. Introspection and verbal reports, however, involve higher cognitive abilities such as attention, working memory, and linguistic functions being associated with reflective consciousness, rather than with phenomenal consciousness. This leads to another problem: It cannot be excluded that those very same cognitive abilities may modulate subjective experience, including qualitativeness, by allowing indirect access to them. What we obtain in introspection and verbal reports may thus reflect cognitively-modulated qualitativeness, rather than qualitativeness per se. Another problem is conceptual in nature. The meaning of qualitativeness can vary, for example, by including or excluding associated cognitive function as attention and a mental conception of it as such. The current philosophical or neuroscientific discussion rarely presupposes qualitativeness in its original and rather strict definition as suggested by Lewis, where it is considered as fully available for attention, motor behavior, and mental concepts (see below for details as well as Metzinger, 2003). Accordingly, the meaning of the concept of qualitativeness presupposed in empirical investigation should be clarified.

Taken together, the neuroscientific investigation of qualitativeness raises several empirical and conceptual methodological problems. Whether these methodological issues can be overcome by refining conceptual clarification and more appropriate experimental designs, or whether they remain principle constraints, cannot be decided here, and will be left for future discussion. What, however, is necessary within the current context, is to consider these methodological problems and their implications for interpreting current empirical data, and to design future studies.

What is unity? The subjective experience of emotion comes as part of one unified conscious field (Searle, 2000). If I am sitting at my desk anxiously taking an exam, whatever I happen to see in that moment will not be seen independently from my current state of mind. If I look out the window and see the sky above, and the tree shrouded brook below, then my experience of that scene will include my anxiety, my racing heart, and the bad taste in my mouth. I do not experience these features separately. Instead, I experience all of these as part of a single conscious field (see Searle, 2000; Cooney and Gazzaniga, 2003). Subsequently, conscious experience mirrors wholeness that cannot be separated and reduced to distinct structures, parts, or elements. This wholeness and inseparability have also been called non-structural homogeneity (Metzinger, 1995, 2003; Northoff, 2003). Moreover, I experience certain gestalts with specific events in the environment being predominant, while others, such as those of my own body, remain in the background. Or conversely, one's own body could be the figure in subjective experience that remains linked to, and integrated within, the environment as the background. Accordingly, unity of conscious experience can be characterized by both non-structural homogeneity and by gestalts with figure and background (Gadenne, 1996, pp. 26-28).

This contrasts with reflective consciousness, from which I am able to dissect distinct parts and structures resulting in diversity with structural heterogeneity. For example, reflection on my own feelings, with the consecutive knowledge of my emotions, allows me to separate and dissect body and world, so that, ultimately, I am able to make a clear-cut distinction between others and myself. I am able to trace the origin of my feeling back either to my own body, to other people, or to events in the environment. The non-structural homogeneity and figure-background gestalts of phenomenal consciousness (comprising emotional feeling) are thus replaced by structural heterogeneity and figure-background separation in reflective consciousness; the unity is replaced by diversity (Gadenne, 1996; Metzinger, 1995; Northoff, 2003).

Qualitativeness of Feeling and Neural Activity in Anterior Cortical Midline Structures

Conceptual Issues in the Empirical Investigation of Subjective Experience

Systematic examination of subjective experience must preserve its subjective richness and structural complexity on the one hand, and must objectify and quantify it on the other. Although this seems to come close to a contradiction, one way out is to objectify and quantify the main phenomenal features of subjective experience. Objectification and quantification of phenomenal features can provide valid and reliable data resulting in a "science of experience" (Varela, 1996; Jack and Roepstorff, 2002; Shear & Varela, 1999; Lutz, Lachaux, Martinerie, & Varela, 2002). For example, one approach is to let the subjects' evaluate their own subjective experience by using visual analogue scales, idiographic instruments, or scripts with semi-structured interviews (see Jack and Roepstorff, 2002). These data about subjective experience can then be related to data about neuronal measures of the brain. The recently proposed concepts of "neurophenomenology" (Varela, 1996; Shear and Varela, 1999) and First-Person Neuroscience (Northoff, 2003; see also Panksepp 1998, pp. 29-30, 205, 330; Panksepp, 2005) provide methods for systematically linking subjective and neuronal data: "… it would be futile to stay with first-person descriptions in isolation. We need to harmonize and constrain them by building the appropriate links with third-person studies. […] To make this possible we seek methodologies that can provide an open link to objective, empirically based description" (Shear and Varela, 1999, p. 2).

There is, however, a serious conceptual problem in establishing a "science of experience." Any evaluation of the own subjective experience requires introspection that by itself is associated with additional cognitive and reflective processes. These cognitive and reflective processes may influence and modulate the phenomenal-experiential aspects of feeling. Lambie and Marcel (2002, pp. 225, 235, 237-8) speak of modulation of "first-order emotion experience by second-order awareness." This could make complete isolation of phenomenal and experiential aspects from reflective and cognitive components impossible. We, therefore, have to question whether the objectified and quantified subjective reports really reflect "pure" subjective experience without any cognitive and reflective ingredients, or rather cognitively-modulated phenomenal features.

What does this imply for neuroscientific investigation of subjective experience? One should be careful in interpreting the observed neuronal activity because its exact origin remains unclear. Neuronal activity observed in the studies cited below could either really account for feeling as subjective experience of emotion (including its phenomenal features) or instead, could be traced back to cognitive and reflective processes associated with introspecting and reporting the feeling. Finally, the observed neuronal activity could also result from interaction between phenomenal and reflective processes both becoming merged, which makes their isolated identification almost impossible. Taken together, since any "science of experience" necessarily has to rely on introspection and reflection, we may have difficulties, if not remaining principally unable, to determine the exact origin of the observed neuronal activity during subjective experience. Why do we apparently lack direct and independent access to subjective experience? We suggest that this could be due to what we call the pre-linguistic nature of phenomenal consciousness. We have no independent language for describing conscious experiences and their phenomenal-qualitative properties (see Chalmers, 1996, pp. 22-3; Edelman, 2003; Edelman and Tononi, 2000). For instance, when one speaks about feeling happy, the reference to the term *happiness* is implicitly fixed via some causal role in judgment and behavior: the state where one judges all to be good, jumps for joy, does nice things, and so on (see also Chalmers, 1996). This suggests that the language for describing phenomenal-qualitative experiences refers to the one for exteroceptive properties and causal roles; therefore, it relies on and is a derivative of our language for non-conscious properties, that is, non-phenomenal language. Goldie (2000, pp. 60-1) notices that we use the same words for situations with and without feelings and emotions. The difference in contents between situations with and without feelings is thus not appropriately reflected in a difference in words: "… I can now add that there is no requirement to give a substantial characterization of what is the difference in content between thinking of something with feeling, and thinking of it without feeling. It might even be that no words are sufficient to capture this difference" (Goldie, 2000, p. 61). For example, patients with clinical depression can try to convey their subjective experiences in words, but they often fail because they cannot appropriately describe their contents of experience in linguistic terms.

Consider the example of a wine taster who is trying to evaluate two different wines. He is easily able to express in linguistic terms his experiences distinguishing and discriminating the distinct tastes. In contrast, he remains unable to positively identify and recognize the two different wines independent of each other: The wine taster can articulate that wine number one is sweeter than wine number two; nevertheless, he remains unable to directly describe the flavor of both wines in positive terms independent of each other. One could, however, object that the wine taster can characterize a wine as sweet independent of other wines. This describes a general property of the wine or the type of wine, but it does not specify that particular wine in further detail; that is, it neglects the token (referring to its concrete instances). Is the experienced wine taster not able to characterize the degree of sweetness of one particular wine independent of other wines? We argue that he may be able to do so only because he already presupposes an implicit scale of subjective experience of sweetness based on his previous exposures to different wines. He is thus able to specify the sweetness of a particular wine only by implicitly comparing it with other wines. Accordingly, phenomenal consciousness seems to have access to language only for discriminating and distinguishing between different subjective experiences. In contrast, there seems to be no access to language for independent and positive identification and recognition of each phenomenal feature by itself (see also Raffmann, 1995). This may be called the “pre-linguistic” nature of phenomenal consciousness characterizing subjective experience including its phenomenal features. This must be distinguished from the linguistic character of reflective consciousness that allows for independent and positive linguistic description of reflected features.

Methodological Problems in the Empirical Investigation of Qualitativeness in Imaging Studies

What do the above-discussed conceptual problems imply for the empirical investigation of qualitativeness in feeling? First, due to possible interference between phenomenal and reflective components, complete isolation of feeling from associated cognitive function could remain impossible in experimental paradigms. All neuronal measures during feeling must be interpreted with respect to the exact origin of neuronal activity because it could be associated with the phenomenal-experiential aspect as well as with the reflective-cognitive one. Rather than attempting to isolate feeling, one should probably shift the focus to study the neuronal processes underlying phenomenal-reflective interference (see for example Prohovnik, Skudlarski, Fulbright, Gore, & Wexler, 2004). Second, one could rely on indirect measures such as behavioral or somatic markers indicating feeling (e.g. see Bechara’s and Damasio’s investigation of skin conductance response as somatic markers of feeling (Bechara & Damasio, 2002)). Most interestingly, the modulation of such somatic markers during phenomenal-reflective interference could be investigated. Third, due to the apparent pre-linguistic nature of phenomenal consciousness, we may not possess linguistic or phenomenal concepts for all our distinct shades and nuances (i.e., what the philosophers call “tokens”) of feeling. Instead, we may only be able to distinguish between different “types” (as distinguished from “tokens”) of feeling in our experimental paradigms. Consider the example of anxiety. We remain unable to linguistically articulate all the different forms, shades, and nuances of anxiety we are able to feel because we cannot recognize and identify them in positive linguistic terms independent of each other. We are, however, able to distinguish and discriminate anxiety from other types of feelings such as fear, panic, sadness, and so forth. This implies that conceptually, the "science of experience" must be considered a "science of discrimination and distinction," rather than a "science of identification and recognition." Therefore, we cannot exclude the possibility that our experimental paradigms to investigate feeling could be constrained by some vagueness (see Papineau, 2002, p. 178, who uses this term "vague" for phenomenal concepts) that makes it principally impossible to exactly and positively identify and recognize the phenomenal referent of our neuronal measures.

How can we reliably link data about the subjective experience of feeling to neuronal measures? For example, as observed in functional imaging, individualized subject ratings of subjective experience can serve as parametric or modulating regressors, fitted to the changes in neural activity. This enables one to determine whether the signal changes (i.e., BOLD signal in the case of fMRI) in any brain region are correlated with the changes in subjective experience. This approach has recently been pursued by Phan et al. (2003, 2004), who investigated the neuronal correlates of subjective-experiential dimensions of emotions, such as valence and intensity (see below for description). Functional imaging data could also be analyzed oriented to the phenomenal characteristics obtained in first-person reports, and then be grouped and contrasted along the lines of these "phenomenological clusters." "Thus, for example, a large-scale integration mechanism in the brain such as neural synchrony in the gamma band should be validated also on the basis of its ability to provide insight into first-person accounts of mental contents such as duration. The empirical questions must be guided by first-person evidence" (Varela 1996, p. 343).

What does this imply for the particular case of imaging studies on emotional feeling and qualitativeness? Imaging studies distinguish between an activation and control condition. The difference between both reveals the factor of interest. In our case, the activation condition targeting qualitativeness may be generated along the lines of the subjective data, indicating and isolating at best qualitativeness of emotional feeling. An appropriate control condition should then include everything but qualitativeness; there should be subjective experience but without qualitativeness. This would correspond to emotions with feelings but without qualitativeness.

This raises another problem. Is subjective experience without qualitativeness possible at all? If qualitativeness is considered as an intrinsic feature of subjective experience, as presupposed in a strict definition of qualia (in the original sense of Lewis'), its elimination should result in the absence of any subjective experience, that is, feeling. This, however, would make an appropriate control condition for qualitativeness principally impossible. Instead, the control condition could then consist only in the non-experience of emotion, emotion without feeling, probably mirroring what is subsumed under unconscious emotion (see above). In this case, the difference between both the activation and the control condition would not only include qualitativeness, but would also include subjectivity and unity as other phenomenal features of feeling. Thus, the imaging study would not specifically target qualitativeness, but rather subjective experience in general, including all its phenomenal features. Another option is to control subjective experience of emotional items by subjective experience of neutral stimuli; this control condition is chosen by almost all imaging studies on emotion. Though this approach accounts for emotion, it neither controls for subjective experience in general, nor for qualitativeness in particular. This is because the experience of neutral stimuli supposedly also involves subjective experience, including its three phenomenal features.

Though our discussion is far from being exhaustive, neglecting other empirical and conceptual problems, it already shows that serious methodological problems arise in human imaging studies if one wants to target subjective experience in general, and even more specifically, qualitativeness in particular. Nevertheless, keeping all these conceptual and methodological problems in mind, we want to put forward a preliminary hypothesis about the neural correlates of the qualitativeness of feeling. We focus on imaging studies that relate distinct psychological measures of emotional experience, such as valence and intensity, to neural activity in different regions. We propose that the specific emotional dimension of valence, mirrors, on a psychological level, what phenomenally is described by qualitativeness. There is empirical evidence for both psychological distinction and underlying neural segregation of emotional valence and intensity. Based on these findings, our hypothesis focuses on linking neural and psychological segregation to the phenomenal level, and thus to the distinction between qualitativeness and quantitativeness. We are aware that, due to the methodological shortcomings discussed above, we cannot exclude that empirical proof of such neuro-phenomenal linkage could remain principally impossible. This issue, however, must be left for further conceptual discussion within a neurophilosophical framework. We, therefore, cannot exclude that our hypothesis about qualitativeness could remain principally preliminary. It is waiting for further empirical and conceptual support.

Qualitativeness and Anterior Cortical Midline Structures

Recent imaging studies have incorporated individual ratings of emotional valence as regressor in the analysis of functional activation data, which was obtained either during passive viewing or valence evaluation of emotional pictures (Grimm et al., 2006; Heinzel et al., 2005). Regions specifically activated in relation to subjective ratings of emotional valence included the VMPFC and the DMPFC. Finally, in an earlier study, Lane et al. (1998) investigated regional cerebral blood flow (rCBF) changes during film- and recall-induced emotion; these were related to scores on the Levels of Emotional Awareness scale (LEAS), a measure of individual differences in the experience of emotion. Covariate analysis revealed activation in the PACC: The more activation was observed in PACC, the higher scores of emotional awareness were obtained. Grimm et al. (2006) included subjective ratings of emotional valence as regressors for both contrasts: emotional picture perception (reflecting the affective component of emotion), and emotional judgment (indicating the cognitive component of emotion). Interestingly, neural activity in VMPFC correlated with subjective ratings of emotional valence only during emotional picture perception, but not during emotional judgment.

The studies reported so far relied on visual emotional stimulation, that is, visually-induced feeling. Using non-visual tasks, other studies that induced feeling in different sensory modalities revealed more or less similar regions, with predominant involvement of the MOFC and the VMPFC. In a gustatory whole-food experiment, Kringelbach, O'Doherty, Rolls, & Andrews (2003) determined the subjective pleasantness ratings when a liquid food was eaten to satiety. These ratings, mirroring the feeling of satiety, correlated with the activation of a region in the left mediolateral orbitofrontal cortex. Small et al. (2003) demonstrated regional association of subjective affective valence with the MOFC during presentation of unpleasant and pleasant taste in fMRI. In contrast, neural activity in subcortical regions, including the amygdala, pons and cerebellum, correlated with intensity irrespective of valence. An analogous result was obtained in the case of olfaction. Anderson et al. (2003) observed activity in orbitofrontal cortical regions to be related to valence, independent of intensity.

In contrast, Anders et al. 2004, observed no correlation of neural activity in the aCMS with emotional valence. During fMRI, they recorded startle reflex modulation and skin conductance responses in healthy volunteers while they viewed a set of emotional pictures. After scanning, they took verbal ratings of the emotional valence and arousal of each picture. The discrepancy of their results, compared to those of the other studies, appears difficult to account for, since they used the same stimuli applying a similar paradigm. It may be speculated that this is related to the application of the startle reflex recording that may interact with the neural activity in aCMS. Due to the lack of empirical data, however, this remains unclear.

Some indirect support for the association of affective valence with neural activity in aCMS is coming from patients with lesions in these regions. Among other parameters, Rolls' group (Hornak et al., 2003) investigated feeling in patients with lesions in (medial) orbitofrontal cortex (OFC), anterior cingulate/medial prefrontal cortex (ACC/MPFC), or dorsolateral prefrontal cortex (DLPFC) with a subjective emotional change questionnaire. Patients with lesions involving the medial OFC or ACC/MPFC showed strong changes in subjective experience of affective valence (see also Rolls, 2004; Berlin et al., 2004; Damasio, 1999). The intensity and frequency of their emotions increased, and they became hypersensitive, especially to sad events, resulting in a far more emotional state. In contrast, patients with DLPFC lesions showed no changes in subjective emotional experience. Finally, patients with subcortical lesions, such as those found in the amygdala in Urbach Wiethe disease, show changes in affective processing (e.g. Siebert et al., 2003). Unfortunately, valence and intensity ratings were not obtained in either group of patients. Taken together with the imaging findings in healthy subjects, one could hypothesize that neural activity in anterior aCMS contributes to valence irrespective of intensity.

Both imaging and lesion studies suggest that the MOFC and medial prefrontal cortical regions including the ACC, VMPFC, and DMPFC could be key regions in mediating subjective experience of affective valence. Almost all studies investigating subjective experience of affective valence in different sensory modalities (visual, olfactory, gustatory) reported involvement of at least one of these regions. What is valence? Valence describes the affective value of a stimulus independent of its sensory modality. For example, an emotion can be experienced on a continuum between positive and negative. The affective value corresponds to the subjective experience of the meaning, and the importance of the respective emotional content for that particular subject.

Psychologically, the affective value is supposed to include two components, an affective one and an evaluative one (Russell, 1980; Barrett and Russell, 1999; Northoff et al., 2004b). The affective component of valence reflects the quality of the stimulus, whereas the evaluative component concerns its distinction and discrimination as positive or negative. We suggest that what psychologically is referred to as the quality of the stimulus, could correspond to what phenomenally is described as qualitativeness mirroring the "What it is like to feel that emotion" (see Figure 2). In contrast, the evaluative component of valence could correspond to associate cognitive processing, providing the basis for subsequent discrimination and distinction of the stimulus as positive or negative.

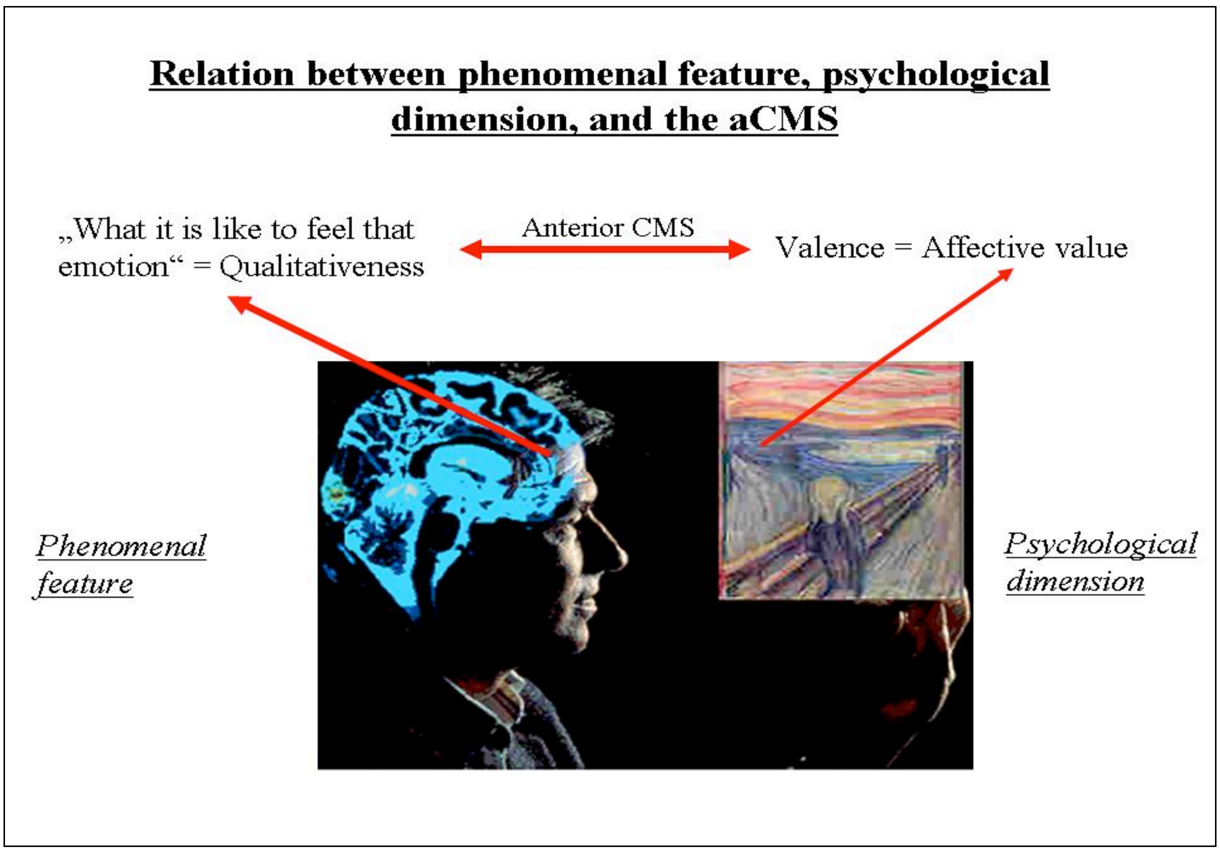

Figure 2: Relation between phenomenal features, psychological dimensions and the aCMS.

Interestingly, recent studies demonstrated neural segregation between both components (Northoff et al., 2004b; Grimm et al., 2006). The affective component correlated with neural activity in aCMS during mere emotional picture viewing, whereas the evaluative component was related to activation in lateral prefrontal cortex (LPFC) during judgment of emotional pictures (see also Dolcos, LaBar, & Cabeza, 2004). These results lend strong support to the distinction between the affective and evaluative component of affective value in neural respect. Furthermore, these results support our assumption that there is a crucial involvement of aCMS in the affective component of valence and, possibly, in what phenomenally is described as qualitativeness. This must be distinguished from the evaluative component of valence indicating associated cognitive processing; this is further supported by association with the LPFC that has been closely linked with reflective processes in general (Duncan and Owen, 2000) and in emotions in particular (Northoff et al., 2004b, LeDoux, 2002).

Taken together, empirical results lend support to the association of valence with neural activity in the aCMS. However, empirical results alone cannot solve the rather conceptual issue of whether the psychological concept of valence corresponds to (or is even identical with) the phenomenal concept of qualitativeness. This can ultimately be decided only on conceptual grounds revealing the exact nature of neurophenomenal relationship. Though this issue cannot be decided here, it becomes, nevertheless, clear that empirical correlates of the phenomenal features of emotional feelings can be discussed. This may empirically complement current philosophical theories of emotions that emphasize the crucial relevance of feelings and their possible phenomenal, unreflective character (Goldie, 2000, pp. 68-69) that may be reflected in their qualitativeness, that is, “what it is like.”

Unity of Feeling and Supramodal Processing in Cortical Midline Structures

Unity of Emotional Feeling and aCMS

Subjective experience and emotional feeling have been described by a unified conscious field, which can be characterized by non-structural homogeneity and figure-background gestalts. Non-structural homogeneity is characterized by inseparability between stimuli of different sensory origins (i.e., auditory, visual, etc.): Sensory stimuli are linked and processed together in a supramodal way. If neural processing in aCMS is supposed to underlie phenomenal consciousness, it should be independent of the sensory modality of the stimuli; that is, stimuli are processed independently of their different sensory origins.

In order to show supramodal processing in aCMS, different sensory stimuli should be compared with respect to neural processing. Unfortunately, currently there is no study available directly comparing neural processing in different sensory modalities in aCMS (see, however, the reviews by Wicker et al. ,2003; Northoff and Bermpohl, 2004a; Northoff et al., 2006; Gillihan and Farah, 2005). As reported below, however, there are several imaging studies applying different domains/modalities of self-related stimuli (auditory, visual, emotional, facial, verbal etc.) that obtained aCMS activation. This may at least provide some indirect support of supramodal processing in aCMS.

In addition to imaging studies, our assumption of supramodal processing could also be supported by the anatomical connectivity pattern. The aCMS should receive connections from all different sensory modalities, which is indeed the case, as reported below. Ideally, imaging studies applying self- and non-self related tasks should investigate functional connectivity pattern on the basis of known anatomical connectivity. One would probably expect increases in functional connectivity from sensory afferences to the aCMS during neural processing. This, however, remains to be shown. Finally, non-structural homogeneity of emotional experience may be accounted for, and quantified by, phenomenal measures like semi-structured interviews with scripts and reports. These then could be related to imaging data. One would expect a specific correlation between neural activity in aCMS and the degree of non-structural homogeneity in phenomenal measures. Unfortunately, such empirical support of our hypothesis is currently not available.

Description of the subjective experience of emotional feeling by gestalts with figure and background presupposes linkage between body and environmental events, that is, between intero- and exteroceptive stimuli. Once intero- and exteroceptive stimuli are linked to each other, the content of subjective experience depends on which type of stimuli is predominant: If interoceptive stimuli are dominant, the own body is the figure in subjective experience with the environment remaining in the background. If, in contrast, exteroceptive stimuli outweigh interoceptive stimuli, the respective environmental event becomes the figure in subjective experience and feeling, whereas the own body remains in the background. Since we assume that neural activity in aCMS is central in constituting figure-backgrounds gestalts in emotional feeling, the aCMS should allow for the linkage between intero- and exteroceptive stimuli as well as for their mutual adjustment via for example bottom-up and top-down modulation.

One would also expect direct interference between intero- and exteroceptive sensory processing in the aCMS, especially in the anterior aCMS. For example, bottom-up processed interoceptive sensory stimuli could be top-down modulated by exteroceptive sensory processing. Though, as reported below, data about bottom-up and top-down modulation of aCMS are available, the direct interference between intero- and exteroceptive sensory processing in ACMS and connected sensory regions remains to be investigated. We suggest that the direct interference between intero- and exteroceptive sensory processing could correspond to the close linkage between body, environment, and self in subjective experience of emotional feeling. Interoceptive sensory processing is associated with delineating the own body, exteroceptive processing codes for environmental events, and intero-exteroceptive interference in aCMS may result in experience of a self. What remains to be done, however, is first to develop phenomenal measures to quantify subjective experience (see also 3.1. for more detailed discussion), and second to relate these phenomenal data to neural activity observed in imaging studies during intero- and exteroceptive neural processing.

Non-structural Homogeneity and Supramodal Processing in Cortical Midline Structures

The MOFC and VMPFC, acting as the entrance door to the aCMS, receive connections from all regions associated with primary and/or secondary exteroceptive sensory modalities (olfactory, gustatory, somatosensory, auditory, and visual) (see Rolls, 1999, 2000; Kringelbach and Rolls, 2004; Barbas, 2000; Damasio, 2003b). The aCMS are also densely connected to regions (insula, brain stem regions like hypothalamus, PAG, colliculi, etc.) processing interoceptive sensory signals; these include the proprioceptive and vestibular senses, the visceral sense, and the sense of the interoceptive milieu which can be taken together with that of pain and temperature (Barbas et al., 2004; Damasio, 2003b; Rolls, 1999, 2000; Kringelbach and Rolls, 2004; Carmichael and Price, 1996; Price, 1999).

The aCMS, especially the MOFC, VMPFC and ACC, are also connected to regions associated with distinct functional domains including motor (premotor and motor cortex, basal ganglia), cognitive (lateral prefrontal cortex), and emotional (amygdala, brain stem) domains (Barbas, 2000; Oengur and Price, 2000; Carmichael and Price, 1996; Rolls, 1999, 2000; Kringelbach and Rolls, 2004). Due to such extensive intero- and exteroceptive connections involving different functional domains (see also Figure 3), the MOFC and VMPFC (and, in conjunction, the amygdala) can be characterized as a polymodal convergence zone (Rolls 1999, 2000; LeDoux, 2002; Schore, 2003).

This connectivity pattern predisposes the aCMS for neural processing irrespective of the sensory modality of the respective stimulus, that is, supramodal processing. The assumption of supramodal processing in aCMS is supported by results from imaging studies. Emotions in either exteroceptive modality (visual, auditory, gustatory, olfactory) induce neural activity in various regions of the aCMS (see above as well as Phan et al., 2002; Northoff and Bermpohl, 2004a). Moreover, processing of interoceptive stimuli also induces activation in aCMS regions like MOFC, VMPFC, and ACC (Critchely et al., 2004; Nagai et al., 2004; Craig, 2002, 2003, 2004; Wicker et al., 2003). Finally, stimuli from different origins, that is, of different sensory modalities or of different functional domains (motor, emotional, cognitive, and sensory), induced analogous activation in aCMS (Northoff and Bermpohl, 2004a; Northoff et al., 2006). Taken together, connectivity pattern and imaging data led us to suggest that neural processing in aCMS is supramodal and domain-independent: What apparently matters for inducing neural activity in the aCMS is not so much the modality or domain (that is, the origin of the stimulus, be it either intero- or exteroceptive or cognitive, motor, sensory, or emotional), but whether it is neural or not.

The supramodal and domain-independent character of neural processing in aCMS could account for our inability to distinguish distinct sensory modalities and functional domains in emotional feeling. This may provide the neural basis for what phenomenally is described as non-structural homogeneity characterizing emotional feeling. One could argue, however, that it is nevertheless possible to distinguish between distinct modalities or domains of consciousness: for example, if one were to speak of auditory, visual, olfactory, emotional, motor (and so forth) consciousness. The respective domain, however, is not detached from the others in subjective experience and emotional feeling in these cases. Depending on the predominant input, one modality (or domain) may outweigh the respective others, resulting in figure-background gestalts. The apparently different domains of consciousness would subsequently be distinct figure-background gestalts rather than being truly different and exclusive domains of consciousness.

Though presupposing a different level, it may be speculated that such figure-background gestalts could also characterize the relation between phenomenal and reflective consciousness. For example, reflective consciousness subsumes or takes up phenomenal consciousness, so that it shifts into the background. Conversely, phenomenal consciousness may become the figure, with reflective consciousness shifting into the background; this is, for example, the case in states of strong anxiety or panic, where one remains almost unable to reflect and introspect. Following our line of thought, the figure-background gestalts between phenomenal and reflective consciousness may ultimately be traced back to the relation between neural processing and higher-order processing. Their relation may be continuous and flexible with possible co-occurrence of both kinds of processing, the one being predominant, and the respective other being less dominant.

Finally, figure-background gestalts between phenomenal and reflective consciousness should not seduce us to assume that phenomenal consciousness can occur only in the presence of reflective consciousness. In this case, contrary to our assumption, higher-order processing is presupposed as the basis of neural processing; the latter is, then, at best, considered a subset of the former. We call this model the reflective concept of phenomenal consciousness; we argue that it is inappropriate for both empirical and conceptual reasons. First, the reflective concept cannot account for empirical cases of strong anxiety illustrated above, where reflection and introspection remain almost impossible. According to the reflective concept, there should be no feeling or emotion in the absence of reflection and introspection. The opposite, however, is the case in states of anxiety: The reflective concept remains unable to account for the origin of anxious feelings. Second, conceptually, the reflective concept relies on problematic ground. By presupposing that reflective consciousness (with higher-order processing) is necessary for neural processing and phenomenal consciousness to occur, a problematic assumption is made: Why should the existence of a higher-order or cognitive representation of an emotional state (with knowledge about feeling) induce "something it is like to be" in that state, and thus, subjective experience that is feeling? If this were true, conscious experience of emotion, that is, feeling mirroring phenomenal consciousness, could no longer be distinguished from reflective consciousness (as consciousness of conscious experience of emotion). One way out would be to assume that higher-order thought theories of phenomenal consciousness describe the mechanisms underlying reflective consciousness, rather than the ones accounting for phenomenal consciousness and feeling as the subjective experience of emotion (see also Izard, 2000; Ben-Ze'ev, 2000). Then, however, a separate and complementary account of feeling and phenomenal consciousness is needed: This is the aim of our paper.

Distinct Types of Feelings and Figure-background Gestalts with Reciprocal Modulation between Intero- and Exteroceptive Processing

The MOFC and other aCMS (especially VMPFC and ACC) receive and send connections to the anterior (and posterior) insula, which in turn is closely connected to subcortical regions (hypothalamus, PAG, colliculi, and other regions of the brain stem) associated with interoceptive senses (Damasio, 2003b; Craig, 2002, 2003). Studies investigating interoceptive awareness (for example, the regulation of heart beat, biofeedback arousal and relaxation), that is, phenomenal consciousness of the own body, show activation sites in right anterior insula, MOFC, VMPFC and ACC (Critchely et al., 2004; Nagai, Critchley, Featherstone, Trimble, & Dolan, 2004; Craig, 2002, 2003, 2004; Wicker et al., 2003), though not all studies demonstrated activity in all these regions (see also Phillips et al., 2004, who link activation in the insula to the conscious experience of disgust). Neural activity in anterior CMS may reflect bottom-up modulation by interoceptive processing in subcortical regions, which corresponds to their close connectivity with the aCMS (see above, as well as Nagai et al., 2004). Analogous neural activity in anterior aCMS may also be induced by exteroceptive stimuli via bottom-up modulation that may be traced back to the close connections of the aCMS to sensory cortical regions (see above and Figure 3). In addition to bottom-up modulation of the aCMS by regions involved in intero- and exteroceptive processing, the aCMS may also modulate, (that is, top-down modulate) the very same regions. For example, the aCMS may top-down modulate interoceptive processing in subcortical regions via the anterior insula (Critchely et al., 2004; Nagai et al., 2004; Craig, 2002, 2003). Or, as supposed by Davidson (2000, 2004), the medial prefrontal cortex may top-down modulate or inhibit neural activity in the amygdala, which receives strong intero- and exteroceptive inputs. Since anterior aCMS regions like the MOFC and the VMPFC are regarded as polymodal convergence zones, intero- and exterocpetive processing may interfere via top-down and bottom-modulation. This could result in mutual adjustment and reciprocal modulation between intero- and exteroceptive processing.

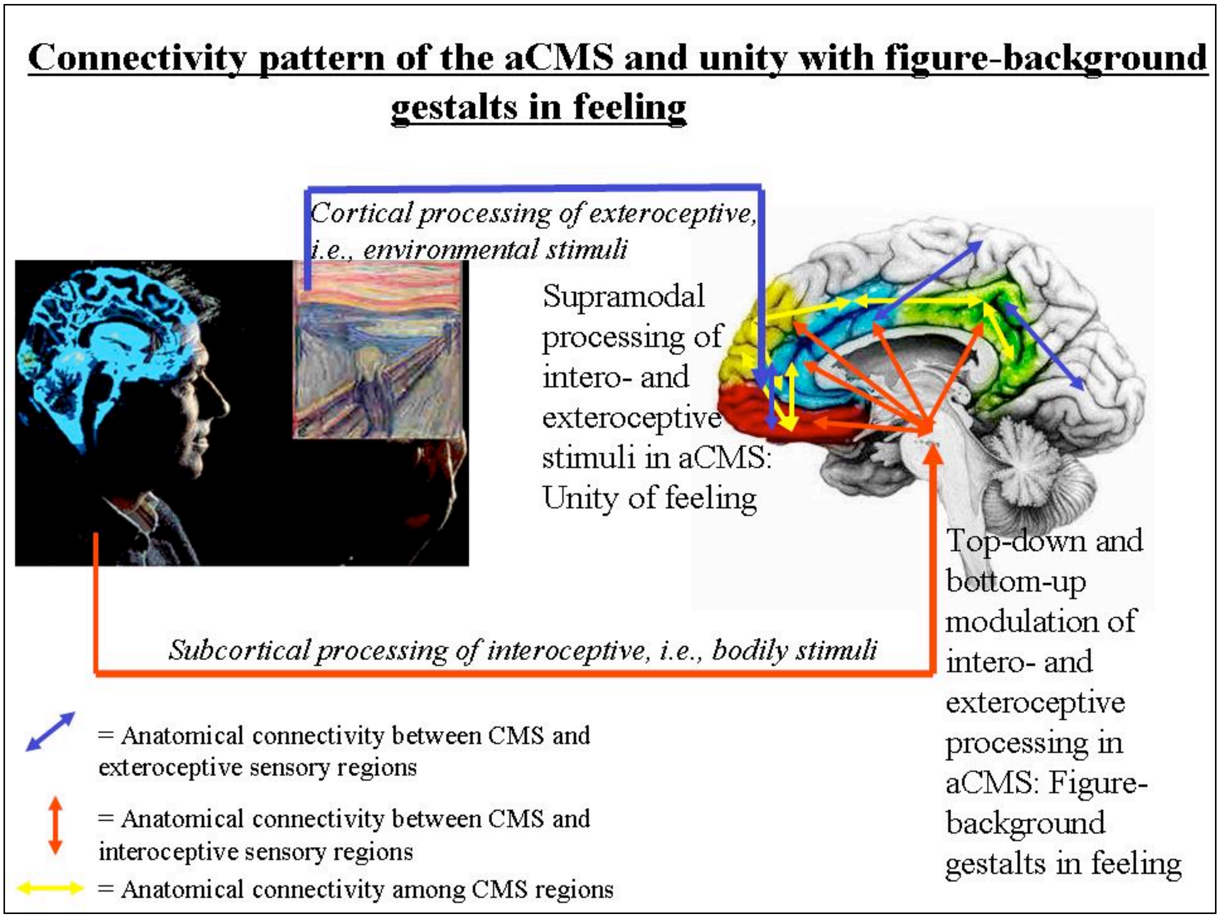

Figure 3: Connectivity pattern of the aCMS and unity with figure-background gestalts in feeling.

We suggest that reciprocal modulation serves two purposes: generation of different types of emotion and figures-background gestalts between intero- and exteroceptive stimuli. Neuroanatomically, this may be achieved by top-down and bottom-up modulation of intero- and exteroceptive sensory processing across subcortical and cortical regions. The aCMS may directly interact with subcortical midline regions like the hypothalamus, PAG, the stria terminalis, the preoptic areas, and the dorsomedial thalamus. Following Panksepp (1998, 2005), different subcortical regions may be involved in generating different types of feelings like fear, anger/rage, sex/lust, panic, and joy (see Winkielman and Berridge (2004) who also point out the importance of subcortical regions in generating distinct types of emotion). We, therefore, assume that the interaction between neural activity in aCMS and emotion generation in subcortical midline regions may give rise to the distinct types of feelings in humans; the type of feeling may then depend on which subcortical midline region the aCMS predominantly interacts with.

The interference between intero- and exteroceptive processing in aCMS may ultimately account for the gestalt character of subjective experience with figure and background. If interoceptive inputs predominate neural processing in aCMS, the own body is subjectively experienced as figure, with the environment remaining in the background mirroring less dominant exteroceptive stimuli. If, in contrast, exteroceptive inputs predominate neural processing in aCMS, the respective environmental event is subjectively experienced as figure, with the own body shifting into the background corresponding to the less dominant interoceptive stimuli (see Figure 3). Due to the interference between intero- and exteroceptive processing in the aCMS, one can neither subjectively experience and phenomenally feel the own body in an isolated way independent of the respective environmental context nor can environmental events be subjectively experienced and phenomenally felt in isolation from the own body.

Conclusion

We defined emotional feeling as subjective experience of emotion, characterized by unity and qualitativeness. We hypothesize that neural processing in the anterior medial regions of the anterior brain's cortex, so-called anterior cortical midline structures (aCMS), may be crucial in mediating these phenomenal features of feeling.

Based partly on indirect empirical evidence, we suggest that neural processing in cortical midline structures, the aCMS, could underlie these phenomenal features of feeling. We assume that what phenomenally is described as qualitativeness could correspond psychologically to valence (the affective value of a stimulus for the self of a particular person). The anatomical connectivity pattern of the aCMS that receive afferences from all intero- and exteroceptive sensory modalities may provide the basis for supramodal processing in aCMS. This could allow integrating sensory stimuli from different modalities, resulting in wholeness and homogeneity, and ultimately, in unity. Furthermore, empirical data suggest direct linkage and interference between intero- and exteroceptive processing in aCMS, possibly resulting in figure-background gestalts in phenomenal consciousness that may be related to what has been described as the intentionality of feelings.

Taken together, the aCMS are assumed to be crucially involved in generating the phenomenal features of feeling. This complements current theories about the neural correlates of emotion in affective neuroscience. These focus predominantly on higher-order processing in lateral prefrontal cortex associated with the cognitive and reflective aspects of emotion. Since we focus rather on the aCMS associated with the experiential or affective component of emotions, our hypothesis complements current neuroscientific theories of emotion. In addition, they also complement current philosophical theories of emotion by providing a neuroscientific hypothesis about the neural correlates of the phenomenal features of feeling.

Finally, our hypothesis about feeling and aCMS contributes to long-standing issues of debate in neuroscientific and philosophical emotion theory. Our hypothesis sheds further light on the question of whether language is constitutive for emotion and feeling. We suggest that feelings can be characterized by their pre-linguistic nature, implying that we remain unable to identify and recognize them in linguistic terms independent of each other. This contrasts with the cognitive and reflective aspects of emotion, which must be considered linguistic in nature.

Moreover, our hypothesis defines the role of the body in emotion and feeling in a complex way. Interoceptive stimuli from the own body are an essential input into neural processing in aCMS. However, since exteroceptive stimuli from the environment are also processed in aCMS, neural activity in aCMS cannot be equated with interoceptive bodily processing. Though the own body may be essential in neural activity in aCMS, it may not be indispensable. ACMS neural activity can also be sustained by exteroceptive stimuli from events in the environment. Since we assume that neural processing in aCMS is essential for the occurrence of the phenomenal features of emotional feeling, emotional feeling may ultimately be traced back to the linkage between intero- and exteroceptive processing. Accordingly, most emotional feelings may crucially involve the own interoceptive body, but we may have also feelings whose predominant origin may rather be exteroceptive from events in the environment. This may also shed new light on another feature of emotional feeling, intentionality: That is, their directedness towards objects in the world. As such our hypothesis may be considered a first step towards bridging the gap between philosophical theories and neuroscientific data about feelings and emotion.

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