Review

The quartet theory of human emotions: An integrative and neurofunctional model

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Abstract

Despite an explosion of research in the affective sciences during the last few decades, interdisciplinary theories of human emotions are lacking. Here we present a neurobiological theory of emotions that includes emotions which are uniquely human (such as complex moral emotions), considers the role of language for emotions, advances the understanding of neural correlates of attachment-related emotions, and integrates emotion theories from different disciplines. We propose that four classes of emotions originate from four neuroanatomically distinct cerebral systems. These emotional core systems constitute a quartet of *affect systems*: the brainstem-, diencephalon-, hippocampus-, and orbitofrontal-centred affect systems. The affect systems were increasingly differentiated during the course of evolution, and each of these systems generates a specific class of affects (e.g., ascending activation, pain/pleasure, attachment-related affects, and moral affects). The affect systems interact with each other, and activity of the affect systems has effects on – and interacts with – biological systems denoted here as emotional *effector systems*. These effector systems include motor systems (which produce actions, action tendencies, and motoric expression of emotion), peripheral physiological arousal, as well as attentional and memory systems. Activity of affect systems and effector systems is synthesized into an *emotion percept* (pre-verbal subjective feeling), which can be transformed (or *reconfigured*) into a symbolic code such as language. Moreover, conscious cognitive appraisal (involving rational thought, logic, and usually language) can regulate, modulate, and partly initiate, activity of affect systems and effector systems. Our emotion theory integrates psychological, neurobiological, sociological, anthropological, and psycholinguistic perspectives on emotions in an interdisciplinary manner, aiming to advance the understanding of human emotions and their neural correlates.

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1. Introduction

Over the last few decades, numerous neurobiological emotion models have been proposed [1–9]. Our motivation for establishing yet another neurobiological emotion model was to explicitly consider the following four aspects, each of which we regard as fundamentally important for the understanding of human emotions:

(1) Inclusion of emotions that are uniquely human. Most previous neurobiological emotion models are primarily based on animal data, such as Walter B. Cannon's *Thalamic Theory* of emotion [10], Paul D. MacLean's Theory of the *Triune Brain* [11,2], Jaak Panksepp's *General Psychobiological Theory of Emotions* [4], or the model on neural pathways underlying emotion generation described by Joseph E. LeDoux [6]. While each of these models provides invaluable information on neural circuits of emotion, they hardly include emotions that appear to be uniquely human, such as complex social ("moral") emotions. The model proposed here aims to contribute to neurobiological understanding of complex social emotions, in addition to other classes of emotions as well as the interplay between these different types of emotions.

(2) Interaction between emotion and language. Language has two main functions for human emotions: (a) Regarding subjective feelings, it is an important means of expressing as well as communicating emotions (and, therefore, also to elicit emotions in other individuals). (b) With regard to conscious appraisal, language is an important means of regulating emotions. Previous neurobiological emotion models have remained silent with regard to the role of language (and psycholinguistic models generally disregard the role of emotions). We aim at bridging this gap by considering interactions between emotion and language, and how these interactions might be implemented on a neural level.

(3) Emphasis on attachment-related emotions. With the exception of Panksepp's *General Psychobiological Theory of Emotions* [4], previous neurobiological emotion models have been rather myopic with regard to attachment-related emotions (such as love in humans). Here we put forward the hypothesis that the generation of attachment-related emotions involves the hippocampus as one central structure for emotion generation.

(4) Interdisciplinarity. Our model integrates perspectives from different disciplines: In addition to capturing the neurobiological and psychological aspects of emotion, the present model also seeks to capture facets of emotion traditionally attributed to social, cultural, and psycholinguistic factors. We thus aim at developing a neurobiological emotion theory that integrates perspectives on emotion from various disciplines (psychology, neurobiology, sociology, anthropology, and psycholinguistics) within a general framework.

1.1. A new theoretical framework

We propose a new theory that differentiates four emotional core systems, referred to here as *affect systems*: A brainstem-centred, a diencephalon-centred, a hippocampus-centred, and an orbitofrontal-centred affect system (Fig. 1). These affect systems were increasingly differentiated during the course of evolution, and each of these systems is capable of generating a specific class, or quality, of affects (note that we do not use the term "affect" here to refer to the conscious subjective aspect of an emotion, nor to the public expression of feeling). These affect systems interact with each other, and activity in these affect systems has effects on, and interacts with, biological systems that are referred to here as emotional *effector systems* (see also Fig. 2). These effector systems include motor systems producing actions or action tendencies, motor systems producing expression of emotion, physiological arousal systems (which partly include motor aspects, such as changes in heart activity, breathing, vasoconstriction, etc.), as well as attentional and memory systems (note that attentional systems also include motor aspects). In his *Component Process Model of Emotion* (CPM), Klaus Scherer [12] refers to three of these effector systems (motor systems producing actions or action tendencies, motor systems producing expression of emotions, and physiological arousal systems) as "organismic subsystems of emotion" (the other two subsystems being cognitive appraisal and subjective feeling). As will be elaborated in more detail in this article, activity of the affect systems and of the effector systems is synthesized into an *emotion percept* (unverbalized subjective feeling). Such emotion percepts can, in turn, be transformed (or *reconfigured*) into language (Fig. 2). We will also describe how the language system interacts with the conscious appraisal system in a way in which conscious appraisal can involve language (or other symbolic codes) in terms of rational thought and logic. In the following sections, we will describe the model, specifying typical antecedent pathways and processes of the four affect systems, and dealing with the interactions between these affect systems, interactions
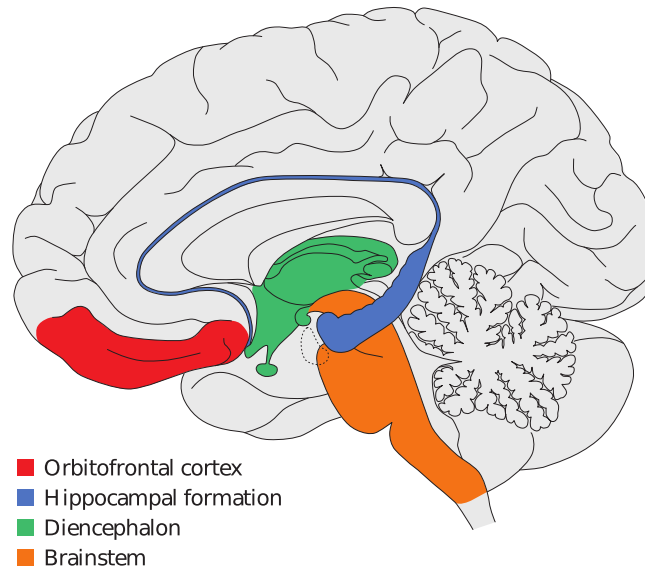
Fig. 1. The four affect systems: brainstem-centred (orange), diencephalon-centred (green), hippocampus-centred (blue), and orbitofrontal-centred (red) system. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
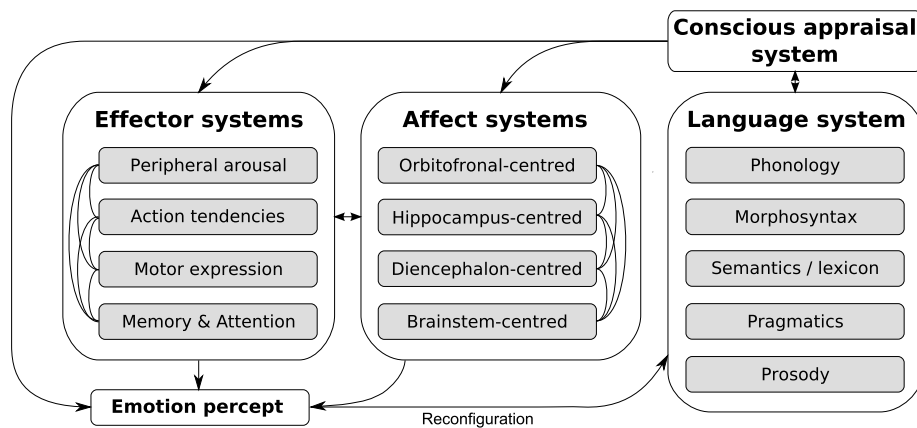

Fig. 2. Systematic illustration of the proposed emotion model. Connections between the affect systems, as well as between the effector systems, are bidirectional. Note that limbic/paralimbic emotional control systems (not shown) coordinate activity of affect systems and effector systems (see text for details). Information of affect systems and effector systems is synthesized into an emotion percept (i.e., unverbalized subjective feeling). The emotion percept can be reconfigured into a symbolic code such as language.

between the affect systems and the emotional effector systems, as well as interactions between these effector systems and the language system.

2. A quartet of affect systems

2.1. Brainstem-centred affect system

Phylogenetically, the brainstem (see Fig. 1) is the oldest brain structure and is present in all vertebrates. One immediate function of the brainstem for emotional processes is ascending activation mediated mainly by the *reticular formation* (RF). The RF consists of numerous nuclei and represents an area occupying the central portion of the brainstem. It extends throughout all subdivisions of the brainstem, from the caudal medulla oblongata to the rostral mesencephalon. The RF activates (and deactivates) higher brain structures via an ascending system, and partly

overlaps with brainstem nuclei of the *vegetative* (or *autonomic*) nervous system that activates and deactivates organs outside the nervous system.

2.1.1. Courage and ascending activation

The RF mediates ascending activation and deactivation via cholinergic and monoaminergic (i.e., serotoninergic and catecholaminergic) projections into all subdivisions of the brain. Via these pathways, the RF modulates attention, alertness and vigilance, and exerts control (together with the hypothalamus) over the wake and sleep cycle [13,4, 14]. Electrical stimulation of the cat's RF during sleep, for example, leads to instant awakening of the animal [13]. Ascending activation is related to feelings such as 'energized', 'courageous', 'alerted', and 'fit', whereas deactivation is related to feelings such as 'tired', 'weary', 'powerless', 'drowsy', or 'sick'. Therefore, Walter A. Siebel poetically referred to the reticular formation as the "Mutzentrum" ("centre of courage") [15].

2.1.2. Descending activation/deactivation

Together with the hypothalamus, the brainstem is also involved in descending activation/deactivation via the vegetative nervous system (also referred to as the autonomic nervous system). Neurons in the raphe nuclei directly project to the intermediolateral cell column of the spinal cord containing the sympathetic preganglionic neurons [16] and the nucleus reticularis rostroventrolateralis (an area of the rostral ventrolateral medulla oblongata [17]) is crucial in maintaining the tonic discharge of spinal preganglionic sympathetic neurons [18]. Brainstem nuclei overlapping with the RF also contain preganglionic parasympathetic neurons (of cranial nerves VII, IX, and X), and RF neurons innervate autonomic brainstem nuclei not belonging to the RF, namely those of the cranial division of the parasympathetic system. These nuclei give rise to preganglionic fibres terminating in various autonomic ganglia.

Via the autonomic nerve fibres, the brainstem modulates activity of all extra-nervous organ systems, and thus modulates *peripheral-physiological arousal*. For example, the sympathetic sweat response can be elicited by electrical stimulation of different brainstem nuclei [19–21], and stimulation of neurons of the nucleus tractus solitarius (NTS, which has direct bidirectional connections with the RF) [22,23] decreases blood pressure and heart rate. Note that the NTS also projects to the hypophysotrophic zone of the paraventricular nucleus of the hypothalamus (PVN) [24], and that serotonergic neurons of the (median) raphe nuclei activate serotonin 2A receptors on PVN neurons [25]. Thus, both autonomic brainstem nuclei and endocrine hypothalamic nuclei (e.g. those regulating blood pressure and sexual functions) organize peripheral arousal (i.e., descending activation/deactivation). Peripheral arousal (due to sympathetic/parasympathetic and endocrine activity) contributes to the sensational aspects of emotion, for example related to feelings such as 'agitated', 'tensioned', or 'relaxed'. Sympathetic activity is associated with increased arousal, or dynamization (e.g., during feelings of excitement, joy, worry, etc.), and parasympathetic activity is associated with decreased arousal, or immobilization (e.g., during feelings of relaxation, tranquillity, sadness, fright etc.).

It is interesting to note that already at the level of the brainstem, music can give rise to autonomic (and muscular) responses. In addition to the auditory nerve, the vestibular nerve contains a substantial number of acoustically responsive fibres, and both the vestibular nuclei and cochlear nuclei project to the reticular formation [24]. In addition, the vestibular nucleus projects to the parabrachial nucleus, a convergence site for vestibular, visceral and autonomic processing. Such projections initiate and support movements and contribute to the arousing effects of music [26]. It is important to note that such arousing (sympathetic) effects can co-occur with relaxation and stress reduction during music listening (e.g., even heavy metal enthusiasts use music to relax and to reduce stress, probably related to corresponding endocrine effects [27]). That is, effects traditionally viewed as directly opposed (arousal and relaxation) are not mutually exclusive. Therefore, dimensional models such as Wilhelm Wundt's tri-dimensional model [28,29], or James A. Russell's *Circumplex Model of Affect* [30] can sometimes be problematic for the measurement and understanding of emotion.

2.1.3. Affective brainstem functions beyond arousal

The brainstem-centred affect system should not simply be equated with the vegetative nervous system. As described above, a major function of the RF is ascending activation/deactivation, and non-reticular and non-autonomic brainstem nuclei are involved, for example, in the following affective functions: (1) *Expression of emotions*, such as vocal expression mediated by the periaqueductal gray (PAG) [31]. (2) Control of nociceptive transmission and thus *modulation of pain* [24]. (3) The PAG also plays an important role in *mating behaviour*, and (4) in coordinating behavioural and autonomic activity aimed at ensuring the survival of the individual in threatening situations. Thus, threatening sit-

uations give rise to emotions (and behaviours) such as fear and anxiety (freeze), panic (flight), and aggression (fight) [24] (note, however, that other affect systems also contribute to fear, anxiety, and aggression). (5) Other brainstem structures such as the mesencephalic and the pontine tegmentum also play a role in *attack behaviour* (i.e. aggression, which is subjectively also perceived as anger) [32], and structures such as the caudal pontine reticular formation play a role in the control of *startle behaviour* [33] (which is subjectively also perceived as fright). (6) The brainstem hosts peptidergic neurons that influence behaviours such as intake of food and water, and behaviours aimed at the maintenance or regain of *homeostasis* [24]. (7) The brainstem controls defecation, micturition, ejaculation as well as other sexual functions.

Thus, the brainstem hosts the phylogenetically oldest system that generates, modulates, and integrates somatomotor, visceromotor, and partly neuroendocrine activity (e.g. through sympathetic innervation of the adrenal medulla) [34] that is aimed at the survival of the individual and the species. Affective functions of the brainstem have also been advocated previously by others, e.g., by Nieuwenhuys et al. [24] as part of the "Greater Limbic System", by Panksepp [4] in his *General Psychobiological Theory of Emotions*, by Damasio and Carvalho [35], or by MacLean in his concept of the *triune brain* as part of the "reptilian brain" [2].

2.1.4. Antecedents of affective activity

It is worth noting that the ascending arousal during wakefulness mediated by the reticular formation (RF) is not simply determined by external stimuli, but first and foremost by the sleep-wake cycle (which is organized in part by the brainstem). That is, the RF continuously generates ascending arousal during wakefulness in accordance with the sleep-wake cycle, and this arousal can be modulated by external or internal stimuli (e.g., threatening stimuli can increase ascending arousal, or sickness can decrease such arousal) [36].

External or internal stimuli that incite the brainstem-centred affect system include: (1) Novel stimuli. The RF is sensitive to novelty and thus capable of performing "novelty checks" in the course of relevance detection (as formulated in the "Sequential Check Theory of Emotion Differentiation" by Scherer) [37]. For example, noradrenergic neurons in the locus coeruleus of the RF can detect novel sensory information and generate attentional orienting, i.e. interest, to this novel information [38] (note that other brainstem structures and brainstem transmitter systems are also able to detect novelty, and to modulate attention [39,40]). Novelty detection by brainstem structures possibly contributes to feelings of surprise. However, note that the other affect systems are also sensitive to novelty (and, thus, also contribute to feelings of interest or surprise). Also note that "novelty" implies memory functions, and that such functions are presumably accomplished due to connections between the brainstem and the cerebellum (which can form and store memory traces) [41]. (2) Signals of danger. Several brainstem structures (such as the PAG, as well as inferior [42,43] and superior [44,45] colliculi, can detect auditory and visual signals of danger, and initiate escape and defence behaviour in response to such signals (these signals of danger can be modified during ontogeny, and it would be interesting to investigate whether such signals might even include symbolic cultural signals). (3) Circulating chemical information. The brainstem has circumventricular chemosensitive zones that regulate homeostatic function, e.g. water-electrolytic balance, and cardiovascular regulation. In this regard, it is worth noting that the brainstem is sensitive to numerous hormones (such as insulin and angiotensin) [46], and other mediators (such as cytokines) [47]. For example, the brainstem is sensitive to circulating pro-inflammatory cytokines (produced by immune cells in response to peripheral infection), and initiates sickness behaviour (in concert with the hypothalamus), as well as feelings of sickness in response to increased activity of the peripheral immune system [36]. Such sickness behaviour and feelings of sickness include, e.g., fatigue, reduction of appetite and interest, immobility, impaired attention, as well as impaired learning and memory [36]. (4) Sexual information. The brainstem also hosts aggregations of gonadal steroid-receptive neurons in the PAG, the parabrachial nucleus, and the solitary nucleus [24]. Moreover, the brainstem modulates spinal sexual reflexes [48], e.g. in response to stimulation of sexual organs.

Beyond such sensory information, the antecedents for affective brainstem activity include input from the other affect systems, i.e., from the diencephalon, the hippocampus, and the orbitofrontal cortex (OFC), in addition to input from the amygdala, the anterior cingulate cortex, and the insular cortex [24,49]. Moreover, it is important to emphasize that, in addition to generating ascending and vegetative descending activation/deactivation, the brainstem also generates somatomotor, and partly even neuroendocrine activity in response to external and internal stimuli with emotional valence: As mentioned above, the brainstem hosts nuclei involved in defensive, escape and fight behaviour, as well as in behaviour serving the survival of the individual and the species (such as food and water procurement or sexual

behaviour). Therefore, the brainstem does not simply represent an arousal system that is only controlled and regulated by other affect systems.

2.2. Diencephalon-centred affect system

The diencephalon (see Fig. 1) is situated on top of the brainstem, and phylogenetically later differentiated than the brainstem (e.g., in the course of the development of ovulation, thermoregulation, lactation, etc.). The main components of the diencephalon are the (dorsal and ventral) thalamus, hypothalamus, epithalamus, habenular complex, pineal gland, and subthalamic nucleus (the latter is also often considered as part of the basal ganglia) [24]. As will be elaborated below, the diencephalon plays an important role in *pain/pleasure*, for *urges*, and for *homeostatic emotions* [50,4]. Homeostatic emotions are motivations originating from "bodily need states", a term used by Panksepp (as opposed to drive) to "indicate the presence of regulatory imbalances. For instance, need states such as energy depletion lead to dramatic increases in motor arousal only when animals are in the presence of incentive stimuli – namely, those stimuli that predict the availability and characteristics of relevant primary rewards such as food" [4].

2.2.1. Thalamus and pain

The thalamus is a key structure for the generation of perceptual aspects of pain (for reviews see Refs. [51,52], for involvement of the insular cortex and somatosensory cortices in the processing of pain see, e.g., Refs. [53–55]). For example, microstimulation of the posterior part of the ventromedial nucleus of the thalamus (VMpo) in awake humans elicits discrete pain sensations (microstimulation of this area can also elicit thermal and visceral sensations) [56–58,51]. Interestingly, this region is proportionately very large in the human compared to the macaque monkey and to sub-primates [59], perhaps arguing for different pain sensitivities between these species. Analgesic effects elicited by electrical stimulation of the thalamus have been reviewed elsewhere [60].

2.2.2. Thalamus and emotional valence

Note that, in addition to generating perceptual aspects of pain, the thalamus can also imbue sensory information with affective valence: Information from all sensory channels, except the olfactory channel, is relayed through the thalamus, where the information is filtered, and in part imbued with affective valence, e.g. when a stimulus is threatening, painful, incentive, or pleasant [24] (the role of the orbitofrontal cortex in the imbuement of stimuli with affective valence is described further below). Such imbuement, notably, can occur *before* the sensory information is perceived consciously. This role of the thalamus was first emphasized by Cannon, who noted that "the peculiar quality of the emotion is added to simple sensation when the thalamic processes are aroused" [10].

2.2.3. Hypothalamus and pleasure

The hypothalamus controls and regulates endocrine functions, and initiates as well as modulates vegetative reactions via projections to preganglionic autonomic neurons in the brainstem and the spinal cord. In addition to these arousal-related functions, the hypothalamus generates basic behavioural patterns critical for immediate survival, such as defensive behaviour and attack behaviour [61,62,24]. Importantly, the hypothalamus is involved in homeostatic activity, including the generation of the aforementioned "bodily need states" [4,63] and the motivation to engage in activities that satisfy such need states. For example, the hypothalamus plays a role in the regulation of water-electrolytic balance, blood pressure, thermoregulation (in mammals), as well as the arousal of thirst and hunger. In addition to these functions that are critical for immediate survival, the hypothalamus is also involved in functions related to the survival of the species, such as maternal and sexual behaviour. Panksepp [4] denoted the system underlying the satisfaction of drives and urges related to the survival of the individual and the species the *SEEKING system*. Note that the hypothalamus also plays a role in several other functions not elaborated here, such as food intake, circadian rhythm, wakefulness and sleep, and stress response (for a review see Ref. [24]).

The satisfaction of bodily need states is a powerful source of pleasure, and the hypothalamus does not only generate urges, but also initiates neural activity that gives rise to feelings of pleasure when such urges are satisfied. The most effective sites in self-stimulation paradigms with rats are located in the lateral hypothalamus [64] which partly projects via the medial forebrain bundle to the ventral tegmental area in the midbrain, in which dopaminergic neurons innervate the nucleus accumbens (NAc), as well as other cell groups located in the ventral striatum and ventral pallidum [65] (systematic data on human subjects are not yet available). Note that this so-called *reward circuit* can also be activated

by the other structures (such as the amygdala, the hippocampus, and the orbitofrontal cortex) via projections to the lateral hypothalamus (the hippocampus also directly projects to the NAc) [24]. Thus, this pathway can be activated by virtually any rewarding stimulus, and activation of this pathway results in feelings of pleasure, reward, or fun (even if there is no immediate urge or homeostatic need). For example, monetary rewards, sexual activity, intake of drugs, or the omission of an anticipated negative consequence are perceived as pleasurable, and correlate with activity within this reward pathway [66,67]. Interestingly, music listening can also activate this reward circuit [68,26], and so can presumably also other forms of art.

2.2.4. Differences between brainstem- and diencephalon-centred affects

Concerning our reasons for distinguishing between brainstem- and diencephalon-centred affects, we would like to note that, although MacLean's triune model subsumes the diencephalon and the brainstem (among other structures) under the term *reptilian brain* [11], others have provided compelling evidence that the two systems should be differentiated: Cannon [10] and Bard [69], for example, argued that ablation of the thalamus in animals is accompanied by marked changes in emotional behaviour, and Cannon [10] emphasized in his *thalamic theory of emotion* that, in humans, "processes in the thalamus are a source of affective experience" such as weeping or laughing (see also [70]). The latter statement is supported by more recent findings showing that stimulation of the subthalamic nucleus (a cell mass situated in the caudal part of the diencephalon) [24] can evoke laughter [71] or crying [72–75]. Both the generation of perceptual aspects of pain, as well as the pleasure resulting from hypothalamus-centred neural activity (partly transmitted via the medial forebrain bundle and the ventral tegmental area to the nucleus accumbens), are such distinctive affective processes that, in our view, it warrants considering the diencephalon as a separate affect system (for an overview regarding the differentiation of emotion and motivation see, e.g., Ref. [3]). This consideration parallels the distinction of the endocrine centres in the diencephalon and the autonomic centres of the vegetative system in the brainstem (although both centres are always active in concert).

2.2.5. Antecedents of affective activity

The thalamus generates perceptual aspects of pain following the activation of nociceptors (often, but not always, in response to noxious stimuli). The hypothalamus generates behavioural, autonomic, and endocrine activity, as well as affects of pleasure or fun (mainly via the so-called reward-pathway, see above) through mainly two factors: (1) Homeostatic needs, the fulfilment of homeostatic needs, incentive stimuli (that is, stimuli that have the potential to fulfil such needs), threatening stimuli, and novel stimuli. (2) Input from the other affect systems, i.e. from the brainstem, the hippocampus, and the orbitofrontal cortex (additional afferents originate from the amygdala, anterior cingulate cortex and insular cortex) [76].

2.3. Hippocampus-centred affect system

In contrast to the brainstem and the diencephalon, the hippocampus consists of cortex. The hippocampus is phylogenetically later differentiated than the diencephalon, and far more developed in mammals than in fish, amphibians, and reptiles [77]. In contrast to the six-layered neocortex, the hippocampal cortex is transitional mesocortex consisting of three to five layers [24]. The hippocampal formation is situated around the diencephalon and consists in primates of the well-developed retrocommissural hippocampus (which is the main portion of the hippocampal formation), a supracommissural part, and a precommissural part rostral to the septum verum (see Fig. 1).

In textbooks, the function of the hippocampal formation is usually only considered with regard to learning and memory, spatial orientation, novelty, familiarity, and expectancies (for reviews see e.g. [78]). However, such textbooks, as well as the prevailing neurobiological theories of emotion, ignore that the hippocampus also plays an important role in emotional processes. This notion was first put forward by James W. Papez, based on the observation that hippocampal lesions (caused by injection of the rabies virus into the hippocampi of cats) lead to marked changes in emotional behaviour [1]. Based on such observations, Papez concluded that "the hippocampus participates in some important way in the central production of the emotive process" [1]. Later on, MacLean (who was acquainted with Papez) supported this hypothesis [2], based on the observation that typical aural symptoms of epileptic seizures triggered by epileptic foci located in the rostral hippocampal formation (as well as in other limbic structures) include a variety of strong emotions (see also [79]). Subsequently, however, the notion that the hippocampus plays an important

role in emotion was hardly considered by neurobiological theories of emotion, except a theory from Siebel, according to which the hippocampus is the neural correlate of "genuine emotions" [80].

The hippocampus has dense reciprocal connections with structures involved in the regulation of behaviours essential for survival (such as ingestive, reproductive, and defensive behaviours), and with structures involved in the regulation of autonomic, hormonal, and immune system activity. Such structures include the amygdala, the hypothalamus, thalamic nuclei, the septal-diagonal band complex, the cingulate gyrus, the insula, and autonomic brainstem nuclei. Efferent connections project to the NAc, other parts of the striatum, as well as to numerous other limbic, paralimbic, and non-limbic structures [24]. The functional significance of these connections places the hippocampus in a pivotal position for emotional processing, and it has previously been noted that the key to understanding the function of the hippocampus lies in the fact that it has major projections not only to cortical association areas, but also to subcortical limbic structures [24].

Several groups emphasized that (a) emotional processes interact with the memory function of the hippocampus [81–83], (b) autobiographical memory, i.e., memory with strong emotional components [84] preferentially involves the left anterior hippocampus [85–89], (c) the hippocampus plays a role in familiarity (a memory-related phenomenon with emotional quality) [83], (d) the hippocampus is involved in the establishment of preferences for places [4], and (e) the hippocampus plays a prominent role in the sense of smell [90], i.e. a sensory function that usually has direct emotional effects. During the last years, a view has emerged that the anterior hippocampus is preferentially involved in emotional functions (such as music-evoked emotions and autobiographical memory) [26], and that the posterior hippocampus is preferentially involved in cognitive functions (such as spatial memory and navigation) [91–94]. Thus, this view emphasizes that cognitive and emotional functions are co-localized in the hippocampus.

2.3.1. Is the hippocampus a neural correlate of attachment-related affects?

Here, we endorse the hypothesis that the hippocampal formation generates attachment-related affects [26] which are perceived by humans as *tender positive feelings* [95,26,96]. The latter term is derived from Charles Darwin's *The Expression of Emotions in Man and Animals* [97], in which Darwin wrote that "tender feelings [...] seem to be compounded of affection, joy, and especially of sympathy" (p. 247). These feelings are "of a pleasurable nature", and it is interesting to note that Darwin writes in this chapter also about the "wonderful power of music" (p. 250), an idea which is elaborated in more detail in *The Descent of Man* [98].

Attachment-related behaviour includes kissing, caressing, hugging, softly touching, softly vocalizing, and in animals behaviours such as licking, grooming, nest-building, and pup retrieval. A neurobiological system underlying attachment-related emotions and behaviours has been referred to as *CARE system* by Panksepp [4]. In humans, attachment-related emotions are also related to inclusion in close-knit social groups and communities. Extant research indicates that social contact and group-inclusion are fundamental human motivations (see e.g. Baumeister's "need to belong") [99] whose fulfilment or disruption are major antecedents of affective activity [100]. Notably, at least in humans, attachment-related affects give rise to love, an emotion that is usually not considered in neurobiological theories of emotion (one of the few exceptions being Panksepp's *General Psychobiological Theory of Emotions* [4]).

Several lines of evidence point to the involvement of the hippocampus in attachment-related affects: *First*, lesions of the hippocampus lead to impairment of maternal behaviour in rats [101], as indexed by less frequent and less efficient nursing, poorer nest building, increased maternal cannibalism, poorer retrieving, and fewer pups surviving weaning (for similar effects caused by septal lesions in mice see Ref. [102]). *Second*, the hippocampus is damaged by chronic emotional stressors, particularly by violence, helplessness and despair [103]. The hippocampus is unique in its vulnerability to emotional stressors, and presumably the only brain structure in which severe emotional stress can lead to the death of neurons, as well as to reduced neurogenesis in the dentate gyrus of the hippocampal formation, resulting in a decrease of hippocampal volume [103]. Dysfunction and reduced volume of the hippocampus were observed in individuals suffering from post-traumatic stress disorder such as Vietnam veterans who had witnessed extreme violence or had committed extremely violent acts against other individuals [104,105]. Similar findings were reported for individuals that had been sexually abused as a child [106]. *Third*, with regard to tender positive feelings, dysfunction and reduced volume of the hippocampus were also observed in depressive patients [107,108]. *Fourth*, individuals with flattened affect and reduced tender positive emotionality show reduced (anterior) hippocampal activity in response to emotion-evoking stimuli [95], and reduced (anterior) hippocampal gray matter volume [109]. *Fifth*,

an overwhelming number of studies on music-evoked emotions have reported activity changes within the anterior hippocampal formation [26], associated, e.g., with feelings of tenderness [96], peacefulness [96], or joy [110].

Regarding hippocampal lesions in humans, the most obvious impairment of a patient with hippocampal damage is a memory deficit [111]. However, the fact that (unilateral) lesions of parts of the hippocampus do sometimes not lead to obvious emotional impairment does not rule out that the hippocampus plays a role in the generation of affect: On the one hand, emotionally relevant parts of the hippocampal formation might have been spared in a patient. On the other hand, emotional functions might have reorganized quickly. Moreover, it is possible that emotional impairment might have gone unnoticed, or that a unilateral lesion might not have led to marked emotional changes: Heinrich Klüver and Paul Bucy [112] reported that bilateral, but not unilateral, removal of the temporal lobes of macaques, including the amygdala and the hippocampal formation, caused severe changes in cognition and emotional behaviour (notably, such behaviour was not observed when only the amygdala was removed). In this regard, it is also worth noting that no one would argue that the basal ganglia are critically involved in motor processes; yet, if damage to the internal capsule is avoided, even large bilateral lesions of the striatum or globus pallidus do not necessarily result in motor deficits [113].

2.3.2. Neurobiological differences between "fun" and "joy"

Klüver [112] described the changed condition after bilateral temporal lobe removal as "Seelenblindheit" ("soul blindness"), giving rise to the interesting notion that the hippocampus is the neural correlate of the human soul. According to our experience from experiments using music as stimuli to evoke emotions, anterior hippocampal activity is often related to feelings described by the participants as being touched, or being moved. This stands in contrast to diencephalon-generated pleasure, which is rather associated with reward-related feelings such as "fun". For example, the diencephalon-centred pleasure experienced when satisfying a homeostatic need, such as drinking a glass of water when thirsty, will hardly be described as "touching", nor "moving". On the other hand, we are moved when the hungry boy shares his last piece of bread with his little sister. This example is supposed to illustrate that there are two different classes of positive emotions that originate from two different affect systems: Diencephalon-centred affects evoking feelings of fun and reward, and hippocampus-centred affects evoking positive tender feelings such as being moved, joy, or love (an idea first put forward by Siebel [114]). Note that, although it is important to differentiate the feelings related to the activation of the 'reward circuit' from attachment-related (tender positive) emotions that involve activity of the hippocampus, both are naturally not mutually exclusive: having joy is fun, and the hippocampus hosts a large number of direct projections into the ventral striatum [24]. On the other hand, however, the experience of "having fun" does not necessarily implicate joy, or happiness.

2.3.3. Hippocampus and diencephalon have different satiation properties

Another important differentiation between diencephalon-centred affects and hippocampus-centred affects is that the diencephalon-centred affects satiate: Once an organism has satisfied bodily needs and achieved homeostasis, the organism is satiated, and stimuli that previously functioned as incentives can even become aversive (e.g., because too much of a chemical compound can be harmful for an organism). This stands in contrast to the hippocampus-centred tender positive affects, which do not satiate. Note that a brain system for attachment-related affect that does not satiate is evolutionary adaptive, because feeling attached to a child, loving a child and feeling the joy of being together with the child are emotions that serve the continuous protection, and nurturing of the offspring. Similarly, the need to belong to a social group and the feeling of social inclusion (both of which do not appear to satiate) serve the formation and maintenance of social bonds, thus strengthening social cohesion.

In this regard, it is interesting to note that Brodal [115] reported that "man, a representative of the microsmatic mammals, possesses a very large hippocampus. Indeed, if comparisons are made between the size of the olfactory bulb and the hippocampus in various mammalian species, the extreme position is occupied by man, who has relatively (and absolutely) the largest hippocampus" [115]. He also wrote that "it is worth emphasizing that the development not only of the fornix, but also of the mamillary body, the mamillo-thalamic tract, the anterior (more particularly the antero-ventral) nucleus of the thalamus and the cingular gyrus runs roughly parallel with the degree of development of the hippocampus. All these structures reach their peak of development in man" [115]. These observations might be related to stronger and more differentiated attachment-related emotions, as well as to stronger and more extensive social networks in humans.

2.3.4. Hippocampus and negative emotions

In addition to generating positive attachment-related affects, the hippocampus might also play a role in affects with negative valence: For example, in the face of danger, hippocampal activity (and inflow of neural information into the hippocampal formation) appears to be inhibited, e.g. by virtue of projections originating in the (basolateral) amygdala [116,24,117–119] in order to (a) focus resources on behaviour relevant to deal with the threatening situation, e.g. flight or fight behaviour, and (b) prevent hippocampal damage due to severe emotional stressors (see above). Perhaps such inhibition contributes to feelings of fear and unpleasantness [120,26,91,93,94]. When related to social loss, such inhibition might contribute to feelings of sadness and depression [121,122].

2.3.5. Affective and cognitive functions are co-localized in the hippocampus

As mentioned above, hippocampal activity is necessary for a range of learning and long-term memory processes, that is, for processes that are classically considered as *cognitive* processes. In this regard, cognitive and affective processes appear to be co-localized in the hippocampal formation. Such co-localization serves at least two functions: On the one hand, affective activity might help to select information for (long-term) memory storage, both when awake and during sleep. Note that during sleep, thus during phases of memory consolidation mediated by the hippocampus [123], humans often experience emotions while dreaming. Perhaps this reflects, at least in part, a connection between emotion, selection of information for long-term storage, and memory consolidation. On the other hand, retrieval of emotional (long-term) memories, including autobiographical memory, helps to guide social cognition and behaviour. The hippocampus-centred affective memory network probably includes the temporal poles (Brodmann's area 38), as well as parahippocampal and possibly entorhinal cortex [24,92].

2.3.6. Antecedents of affective activity

In view of the experimental data on hippocampal function, particularly data obtained with electrophysiological recordings [124,125], it seems reasonable to assume that the hippocampus-centred affect system is usually active, probably unless hippocampal activity is inhibited, for example due to threatening stimuli, or emotional stressors. Such inhibition can originate from the other affect systems (due to projections from the brainstem, the thalamus, the hypothalamus, and the orbitofrontal cortex via the entorhinal cortex to the hippocampus), as well as from a range of further limbic/paralimbic as well as from neocortical structures, such as the amygdala, ventral insula, anterior and posterior cingulate cortex, and dorsolateral prefrontal cortex [24].

2.4. Orbitofrontal-centred affect system

The orbitofrontal cortex (OFC, see Fig. 1) is phylogenetically later differentiated than the hippocampus. It corresponds to the Brodmann areas (BAs) 47 and 11 (and partly 10), each of which can be parcellated into several distinct areas [126,127]. The cytoarchitecture of the numerous OFC regions appears to be similar in humans and non-human primates, but there are some important changes in the relative size of many of the OFC regions [126]. These areas show a posterior-anterior gradient from five-layered agranular periallocortex, over dysgranular, to fully differentiated granular isocortex in BA 10 [128].

A review of the entire array of OFC functions is beyond the scope of this article (for reviews see Refs. [129,24, 130,126]). Here we focus on the following affective aspects: automatic cognitive appraisal, generation of "somatic markers", reward and punishment, as well as moral emotions.

2.4.1. Automatic cognitive appraisal and "the unaware mind"

The OFC performs a fast and automatic (non-conscious) cognitive appraisal of both external and internal information. Though beyond awareness, this appraisal is referred to here as "cognitive" due to the fact that it is based on a number of high-level processes that are classically considered as cognitive, such as integration of sensory information with information stored in long-term memory, decision-making, and changing preferences (note that non-conscious appraisal in the sense of an evaluation of the significance of external or internal stimuli for immediate survival of the individual or survival of the species can be performed by all four affect systems). Such fast and automatic appraisal represents so-called "primary appraisal" (a term coined by Richard S. Lazarus et al. [131]). Here, it is important to understand that appraisal can be conscious (deliberate) as well as non-conscious [132–135], and that the OFC is involved in non-conscious (but not in conscious) appraisal (for recent reviews on consciousness see [136–140]).

OFC-based appraisal includes the *Stimulus Evaluation Checks* (SECs) proposed by Scherer [37]: (a) Relevance detection with regard to learned associations between stimuli and reinforcers (see also section on reward and punishment below), or with regard to social norms (see also the section on moral emotions below). This includes the selection and filtering of sensory information identified as relevant, as well as the automatic shift of attention [141,80]. (b) Implication assessment in terms of the estimation of outcome probability, the estimation of goal/need conduciveness, and the detection of discrepancies from expectations [129,142,143]. Moreover, the SECs performed by the OFC include (c) Coping potential determination, and (d) Normative significance evaluation.

These SECs are performed in a fast, parallel, and automatic fashion even outside of conscious awareness. In the case of moral emotions, these SECs are performed with reference to internalized knowledge of social norms. The attribute "fast" means here that, during perception, the automatic evaluation and appraisal of sensory information appears to begin with the processing of information that reaches the OFC via unspecific thalamic projections (except olfactory information, and with certain exceptions also taste information). That is, automatic evaluation and appraisal of sensory information is performed by the OFC even before, or while, neocortical sensory neurons receive information from the thalamus and, thus, before sensory percepts are fully established in primary sensory cortices (for the visual domain see, e.g., Ref. [144]). The evaluation and appraisal performed by the OFC is then possibly carried out in an iterative fashion using more and more fine-grained information from sensory cortices [8].

According to the outcome of such evaluation and appraisal of information, the OFC also performs an immediate, automatic, and non-conscious imbuement of information with emotional valence [145]. Such imbuement appears to serve decision making as well as the motivation (or inhibition) of behaviour, and is presumably performed by virtue of the information described in the next section as "Somatic Markers". It has been suggested that the automatic and non-conscious cognitive processes performed by the OFC are fast, intuitive, seemingly facile, and not rational, in contrast to processes of conscious cognitive thinking which are slower, deliberate, seemingly laborious, but rational [146]. In this regard, we propose here that many of the cognitive biases described in the *prospect theory* [147,148] are due to processes performed by the OFC, and that the OFC is the primary neurophysiological correlate of the "System 1" proposed by Daniel Kahneman (a system characterized by fast, effortless, emotional thought, and incapability of logical thought). Others have used the term "the unconscious mind" [149], we prefer the term "the unaware min" (because it is a mind of which conscious individuals are usually unaware).

2.4.2. The OFC generates "somatic markers"

The OFC automatically ("non-consciously") generates somatic markers (for a review of the *Somatic Marker Hypothesis* see Ref. [7]), that is, biological signatures that are relevant for the selection of alternatives during decision making. Such markers can be produced via several routes: *Firstly*, via direct projections to the neocortex, the OFC can generate impulses with affective quality that aim at influencing decision making and behaviour (even in the absence of conscious awareness [150,151]). *Secondly*, the OFC initiates, and modulates endocrine as well as vegetative activity via direct connections with the hypothalamus and the brainstem. The peripheral physiological changes then contribute to subjective feeling (for details see the section on emotion percepts below). *Thirdly*, the OFC can initiate, and inhibit, actions via projections into the basal ganglia.

2.4.3. The OFC is sensitive to reward and punishment

Implication assessment also includes decoding and representing primary as well as secondary reinforcers, learning and reversing associations of external stimuli to these reinforcers, and controlling as well as correcting reward-related and punishment-related behaviour [152]. In this regard, the OFC also plays a crucial role in the fast, automatic, and flexible processing of rewards and punishers, which makes the OFC an important structure for almost all aspects of human behaviour, particularly for goal-directed behaviour. Patients with OFC lesions have profound difficulties making appropriate decisions [153,154], learning that reinforcers have changed, and learning that reward configurations have changed [129]. However, note that the notion that emotions are nothing else than states elicited by rewards and punishers, as put forward, e.g., by Edmund T. Rolls [5] should be expanded, because at least the hippocampus-centred (and partly also the brainstem-centred) affects are not only determined by reward and punishment: One example is that attachment-related affect is not only generated in response to reward or punishment.

2.4.4. The OFC generates moral affects

The OFC also generates affects based on representations of relatively complex social norms, roles, and conventions. Such affects are hereafter referred to as *moral affects*. Patients with OFC lesions show abnormal social behaviour, including a striking disregard for, and transgression of, social norms and moral principles, a lack of 'bad conscience' after the transgression of social norms, and a compromised ability to express emotions according to social norms [155–159]. Patient and functional neuroimaging studies showed involvement of the OFC in guilt [160], shame and embarrassment [160–162,156,160], regret [163], attribution of stereotypical gender characteristics [164], and indignation (for reviews see Refs. [165–167]). Due to its cognitive capabilities, the OFC is perhaps also critically involved in the generation of emotions such as gratitude, vengeance, jealousy, fascination, worship, nostalgia, and admiration. Note that the OFC is involved in the control of emotional behaviour, and that this type of control is, in humans, shaped by social and cultural norms.

2.4.5. The OFC and primary internalization during early childhood

It appears that, in humans, the OFC develops mostly within the first seven years after birth (i.e., prior to puberty): Given the general trend of the phylogenetically older zones of the brain (such as median thalamus and hypothalamus) to maturate earlier (as indicated by myelination) than the phylogenetically younger neocortex [168], it is reasonable to assume that the orbitofrontal periallocortex develops and maturates earlier than the neocortical mantle (the latter maturing well into at least the second decade of life). Therefore, it is tempting to speculate that "primary internalization" [169] during early childhood has long-lasting effects on the generation of moral affects within the OFC in later life. That is, during the social calibration of a child into the configuration of norms and roles within a family, norms and roles are stored in the OFC and influence behaviour (according to the learned norms) also later in life. Therefore, such contents (internalized in the OFC) have a major influence on the apparent personality of an individual throughout life. Because the OFC is not a language area (and because the OFC does not consist of neocortex), such internalized contents cannot be directly verbalized (i.e., they are not propositionally available), and are thus non-conscious (see also [149,170]).

2.4.6. Antecedents of affective activity

The OFC evaluates external as well as internal stimuli (including information from the other affect systems) with regard to their potential to harm, punish, or reward the individual. In response to such stimuli, the OFC initiates vegetative, neuroendocrine, behavioural, and cognitive programs according to social requirements and social norms. During wakefulness, the OFC performs stimulus evaluation checks, and attributes emotional valence to sensory stimuli (perhaps also to conscious thoughts). The OFC also generates expectancies, and is sensitive to breaches of expectancy (which give rise to feelings of surprise) [142]. For example, unexpected chords in harmonic progressions elicit OFC activity [143]. Moreover, the OFC appears to provide impulses to act in any given situation, according to internalized directives (such as norms and roles), often without conscious awareness or conscious decision, although such unconscious impulses have volitional quality [150,151]. Conscious decisions can overrule such impulses and lead to alternative actions, although such actions are then often perceived as less pleasant and as requiring more effort compared to actions following OFC-generated impulses to act (or following OFC-generated impulses *not* to act). In this regard, it is interesting to note that since antiquity, philosophers such as Aristotle and Epicurus advocated that virtuous actions, in the sense of carrying out an action A (which is judged as the best course of action) instead of an action B which is more comfortable but not the best course of action (see the problem of akrasia), are a necessary condition for happiness.

2.5. Beyond appraisal theories

Currently, appraisal theories are the dominant theories in the affective sciences. Appraisal-theories focus on the situations, objects, or events that elicit (and differentiate) a certain emotion (a central, sometimes defining, tenet of appraisal theory) [171–173]. For example, Scherer states that "emotion is defined as an episode of interrelated, synchronized changes in the states of all or most of the five organismic subsystems in response to the evaluation of an external or internal stimulus event as relevant to major concerns of the organism" [174] (p. 706), and Frijda states that "Emotions arise in response to events that are important to the individual's goals, motives, or concerns" [172] (p. 351).

In the previous sections, we have already described antecedents of affective activity in the four affect systems. However, it should be noted that the affect systems are not simply mechanistic stimulus-response operators, and that the affect systems do not exclusively respond phasically to external stimuli: (1) As already mentioned above, the ascending arousal during wakefulness mediated by the brainstem is determined by the sleep-wake cycle (which is organized in part by the brainstem), and not simply a phasic response to an external stimulus. That is, the RF continuously generates ascending arousal during wakefulness in accordance with the sleep-wake cycle (unless disturbances such as sickness or emotional stressors interfere with this activity) [36]. Importantly, this ascending arousal has emotional effects in terms of subjective feeling (e.g., 'feeling energized', or 'feeling fit'). This is one example for the *primacy of affect*, that is, for the phenomenon that, under certain circumstances, affective processes can be observed prior to, and independent from, "higher" cognitive appraisal processes [28,175,3]. (2) Hypothalamic activity is in part related to gradually changing needs (such as generation of hunger and thirst), and thus not only generated in response to phasic (external or internal) stimuli. Moreover, in addition to the brainstem, the hypothalamus promotes sleep and maintains wakefulness [176]. (3) As mentioned above, we assume that the hippocampus-centred affect system is usually active, unless hippocampal activity is inhibited, for example due to threatening stimuli or emotional stressors (and we suggested that such inhibition of hippocampal activity can be associated with fear and anxiety). Thus, we propose that affect systems can not only generate phasic affective changes, but also generate tonic affectivity (e.g., positive emotion generated in the hippocampus). (4) The orbitofrontal centred affect system can produce long-lasting moods, or *background affectivity* (such as demotivation, lethargy, melancholy, rumination, spritlessness etc.) according to internalized roles, norms and self-concepts [80,177].

These examples are supposed to illustrate that activity of the affect systems cannot only be observed in response to goal-relevant stimuli. This is important because such activity is also a major determinant of long-term phenomena such as moods or attachment-related emotions. To understand the neurobiology of human affect, and disorders of mood and affect, this issue has to be dealt with in addition to research on short-term emotional phenomena. Up until now, only little has been known about the neurobiology of long-term emotional phenomena, and about differences of the neural correlates underlying short-term and long-term emotions.

3. Emotional effector systems and emotion percepts

So far, we have proposed four different affect systems that generate four different classes of affect: brainstem-centred, diencephalon-centred, hippocampus-centred, and orbitofrontal-centred affects. These affect systems interact with each other via direct reciprocal fibre connections (with certain exceptions for the hippocampal formation, which partly receives projections from the other affect systems via the entorhinal cortex as well as parahippocampal cortex, and which projects only indirectly to the brainstem). For example, hippocampus-centred affective activity has effects on the brainstem-centred affect system in terms of ascending activation, vegetative arousal, and motor expression (including vocalization), on the hypothalamus (i.e., part of the diencephalon-centred affect system) in terms of endocrine activity and activation of the reward and pleasure pathway, and on the orbitofrontal-centred affect system in terms of the control of emotional behaviour according to social norms.

The affects generated in these affect systems only occur in combination with other biological systems that we refer to as emotional *effector systems*. These include motor systems, peripheral physiological arousal systems, attention systems, and memory systems. The motor systems produce on the one hand actions or *action tendencies* in terms of skeletal muscle activity related to behaviour (e.g. movement towards incentive stimuli, or moving away from a threatening stimulus). On the other hand, the motor systems produce *expression of emotion* (for example facial expression and vocalization). Peripheral physiological arousal supports action as well as perception due to changes in vegetative (i.e., sympathetic/parasympathetic) and hormonal (endocrine) activity (thus modulating activity of all organ systems). Note that peripheral physiological arousal usually also includes motor activity, such as heart activity, breathing, vasoconstriction or vasodilation etc. (see also the conception of emotions as "action programmes" proposed by Damasio and Carvalho [35]). However, not all peripheral physiological arousal mechanisms are associated with motor activity (e.g., serum mediators impact on cognitive processes, immune function, wound healing, diuresis, and energy metabolism). Similar to arousal, attention usually (but not necessarily) includes motor activity, such as head turning and gaze direction. Finally, affective activity has effects on memory systems with regard to the selection of information for (long-term) memory storage. Scherer [12] refers to action tendency, motor expression, and physiological arousal (in addition to cognitive appraisal and subjective feeling) as *organismic subsystems of emotion*. The

effector systems interact with each other, as well as with the affect systems. As will be outlined in the following section, sensory aspects of these effector systems contribute to pre-verbal subjective feelings, which we refer to as *emotion percepts*.

3.1. Four factors contribute to emotion percepts

What constitutes an *emotion percept*? Here we propose that four different feeling-components contribute to the emergence of subjective feeling. (1) An *affective component* due to projections from the affect systems to the somatosensory cortices, e.g. from the thalamus to secondary somatosensory areas. This component was first formulated in the so-called *Cannon–Bard theory of emotion* [10,69]. (2) A *sensory-interoceptive component* synthesized in the insular cortex [51,178,9]. A.D. Craig [9] proposed that the anterior insula (as well as adjacent areas in the frontal operculum that also host von Economo cells) synthesizes a "unified final meta-representation of the 'global emotional moment'" based on the integration of the physiological, including homeostatic and autonomic, condition of the body ([9], p. 67). The sensory-interoceptive component also includes proprioceptive feedback from skeletal muscular fibres (e.g., due to facial expression of emotion), as well as from striped muscular fibres (e.g., due to vegetative and endocrine activity). (3) A *motor component*. The tendency to act (whether or not an action is actually executed) significantly contributes to subjective feeling (e.g., feeling the impetus to hug, kiss, and stroke a person to which we are emotionally attached, or moving away from a threatening stimulus). That is, sensorimotor-related codes presumably represent important signals contributing to subjective feeling. Such action tendency can originate (a) from the basal-ganglia (which receive projections from all four affect systems), and (b) from impulses generated in the orbitofrontal cortex that progress superior-posteriorly along the fronto-median wall up to the motor cortices [24]. That is, both basal ganglia and orbitofrontal cortex are involved in generating sensorimotor action codes and thus in generating a drive to act. This component corresponds to the *action tendency* component of Scherer's *Component Process Model of Emotion* [174]. For example, activity in the ventral striatopallidum can initiate, and modulate, activity in cortico–basal ganglia–thalamo–cortical loops, thus modulating (covert) premotor activity as well as (overt) psychomotor behaviour [179]. The sensory-interoceptive component and the motor component parallel the so-called *James–Lange theory of emotion* [180,181]. (4) A *cognitive component*, that is, conscious cognitive appraisal (this component parallels the *two-factor theory of emotion* by Schachter and Singer [182]).

Notably, the insula is not only involved in representing sensory-interoceptive information, but is also active in a similar manner during the perception of information expressing the feeling states of other individuals. For example, the (anterior) insular is active both when subjects experience pain and when they observe pain in other individuals [183,178,184]. Similarly, a study by Jabbi et al. [185] reported bilateral anterior insular activation both when subjects tasted and saw other people taste unpleasant or pleasant drinks. Therefore, the (anterior) insula appears to play a role in empathy and mirroring emotions (along with the anterior midcingulate cortex) [183,178,184]. Interestingly, two studies reported differences in (anterior) insular cortex activation between individuals with alexithymia and control subjects, with the degree of alexithymia correlating with BOLD signal change in the insular cortex [186,187]. These findings indicate the importance of the insula for sharing and understanding the emotional states of others.

3.2. Where in the brain are emotion percepts represented?

We propose that the information from the feeling-components is synthesized into an *emotion percept*. The conscious experience of an emotion percept is usually referred to as *subjective feeling*, but we avoid the latter term here because it is often associated with verbalization (and we want to differentiate between emotion percept and verbalization of the emotion percept, for reasons explained in the following section). The brain region underlying the synthesis of emotion percepts is not known. Some would argue that the posterior insula represents this information, often referring to experimental data indicating activations that could equally well be ascribed to the secondary somatosensory cortex (SII) located in the deep parietal operculum, which is located adjacent to the posterior insular cortex [188]. In addition to insular cortex, SII is surrounded by primary somatosensory cortex (SI) and inferior parietal cortex [188]. That is, SII is located directly adjacent to intero-, extero-, and proprioceptive cortex. Here we suggest that SII is a likely candidate for the synthesis of emotion percepts. Only few studies have investigated this area, showing that SII is sensitive for pain, touch, pressure, vibration, temperature, or vestibular information, and that this region responds to various and often complex stimuli, including input from other sensory modalities, but not simply pure somatosensory

stimuli [189–193]. Notably, parts of SII (OP2 and OP3) are sensitive for slow and soft touch (also referred to as *limbic touch*) [194]. The primary somatosensory (lemniscal) network which represents exteroceptive (touch) and proprioceptive information is different from the network representing interoceptive information (for which the insular cortex, or "*primary interoceptive cortex*" [51] plays a central role). For example, "'pain and temperature sensations remain after cortical lesions of the postcentral gyrus, spinal hemisection produces contralateral loss of pain and temperature sensations, and ipsilateral loss of fine-touch perception (the Brown–Sequard syndrome)'" [9]. However, both of these somatosensory systems contribute to subjective feeling. Therefore, we put forward the hypothesis that information of both systems converges in SII, in which full-fledged emotion percepts are synthesized. It is also interesting to note that OP2 (which is one of the SII subregions) appears to exist only in humans (i.e., no area corresponding to OP2 has so far been found in the SII of non-human primates).

An important aspect of emotion percepts is that they are pre-verbal (neither the somatosensory cortex, nor insular cortex hosts conceptual-semantic language functions). That is, in order to communicate *about* subjective feelings, an individual has to transform (or *reconfigure*) emotion percepts into language (although such reconfiguration is not obligatory for subjective feeling); this issue will be dealt with in more detail in the following section.

4. Interactions with the language system

Language has two main functions for human emotions: (a) With regard to subjective feelings, language is an important means of expressing as well as communicating emotions (and, therefore, also to elicit emotions in other individuals). (b) With regard to conscious appraisal (see also following section), language is an important means of regulating emotions. Despite this important relationship between language and emotion, previous neurobiological emotion models have remained mute regarding the role of language (and psycholinguistic models generally disregard the role of emotions).

4.1. Emotion percepts can be reconfigured into language

Concerning the verbalization of subjective feeling, it is commonly assumed that subjective feeling can simply be translated into or directly expressed with words. This seemingly convincing supposition, however, is subject to serious criticism from analytical philosophy. In the paragraphs about rule following and the argument against the idea of a "private language", Ludwig Wittgenstein demonstrated that "feeling states" (Wittgenstein's "Empfindungen") cannot be directly observed and verbally denoted by the subject experiencing these states [195]. Wittgenstein's argument shows that the language about feelings functions in a different mode than the grammar of words and things: Wittgenstein argues that it is not possible (1) to correctly identify an inner state, (2) to guarantee the correctness of a language use which cannot be controlled by other speakers. This means (3) that it is impossible for the speaker to know whether his or her use of emotion words corresponds to the rules of the linguistic community, and (4) whether his or her use of feeling words refers to the same feeling states in different situations. That is, an individual cannot guarantee that the use of words referring to his or her own feeling state (i.e., to an emotion percept) corresponds to the same feeling state in different situations, and an individual cannot guarantee that the use of words referring to his or her feeling state corresponds to the same feeling state of another individual even if the other individual uses the same words. According to Wittgenstein, correct use of the feeling vocabulary is only possible in specific language games. Instead of assuming a direct "translation" of subjective feelings into language we propose that emotion percepts are *reconfigured* by linguistic expressions (though such reconfiguration is not obligatory for subjective feeling). This means that there is no direct bridge or translation between feelings and words, although biological processes are the basis for the construction of these specific language games (see also the *Panksepp–Jakobson hypothesis* [196]). The neural correlates of such reconfigurations are not yet known.

4.2. Affective prosody and music

Affective prosody (also "emotional prosody") [197–202], and probably even more so music [203–205,26], can evoke sensations (e.g., due to emotional contagion) [204,26] which, *before* they are reconfigured into words, bear greater inter-individual correspondence than the words that an individual uses to describe these sensations [206]. In this sense, music (as well as affective prosody) has the advantage of evoking a feeling sensation (i.e., an emotion

percept) *without* this sensation being biased by the use of words. In other words, one should keep in mind that although music seems semantically less specific than language, music can be more specific when it conveys information about sensations that are problematic to express with words because music can operate *prior* to the reconfiguration of emotion percepts into words. With regard to affective prosody, the acoustical-prosodic features of spoken language (as well as of non-verbal vocalizations) can elicit affective processes, and it appears that such processes are already triggered at the level of the inferior colliculus, the thalamus, and the amygdala [207,6,208].

4.3. The role of language for conscious cognitive appraisal

In addition to its role in communicating subjective feeling, language codes are also involved in *conscious cognitive appraisal* (recall that we use the term *automatic cognitive appraisal* to refer to appraisal processes on the level of the OFC). Conscious cognitive appraisal (also referred to as "secondary appraisal" and "reappraisal" in the *Cognitive-relational Theory of Emotion and Coping* by Lazarus et al. [131]) encompasses rational thought, logic, and usually language. These processes involve numerous neocortical areas, including BA 7 in the superior parietal lobe (due to its role in attention and awareness), the dorsolateral prefrontal cortex (due to its involvement in working memory), the anterior fronto-median cortex (due to its involvement in social cognition and evaluative judgement), as well as the *neocortical-centred language system* [209–214].

The neocortical-centred language system mainly involves Wernicke's area (part of BA 22, 21, and 37), Broca's area (as well as adjacent premotor, motor, and supplementary motor cortices; BAs 44/45/46, 6, and 4), in addition to subcortical structures such as the basal ganglia, the ventrolateral thalamus, and the cerebellum. Functionally, both reconfiguration of emotion percepts into words, and verbal forms of conscious appraisal involve (vocal or subvocal) language production, that is, a conceptual system, a grammatical and a phonological coding system, as well as an articulatory system [215,216,214,217–219,213] (see also Fig. 2).

Interestingly, emotion words (e.g., "happy", "sad") or words with emotional valence (e.g., "dentist's drill") [220–222], metaphors [223], idioms [224], proverbs [225], irony [224], literary texts [226], and perhaps even grammatical constructions (e.g. structures of poems and other literary texts, unexpected structures in literary texts) [227], can be antecedents for emotions, e.g. due to automatic appraisal (this applies to both spoken and written language; for a review see Ref. [196]). Therefore, it is likely that both language production and language perception are usually intertwined with emotions due to the emotional imprints of language [228,196].

It is important to note that, because all affect systems (as well as the emotional effector systems) are under the modulatory influence of the neocortex [24], language-driven appraisal processes can be antecedents for changes of affective activity in all four affect systems. Therefore, the neocortical-centred language-system is one medium to modulate, regulate, and partly initiate, activity of the affect systems as well as of the emotional effector systems. Thus, language is important for intentional emotion regulation, for cognitive behavioural psychotherapies, and for social practices involving mindfulness, such as prayers and meditation.

The neocortical-centred language system is phylogenetically younger than the *limbic vocalization system*, which is involved in the production of non-verbal vocal expressions of emotion, such as laughter, groans, crying, etc. Such non-verbal vocalizations are part of the motor expression system of emotion. The central structures of this limbic vocalization system are the periaqueductal grey (involved in initiating and producing emotional utterances), and the anterior cingulate cortex (involved in the imbuement of vocalizations with emotional tone as well as the volitional control of emotional vocalizations). Electrical stimulation of these structures evokes vocalizations of different valence [31].

5. Limbic/paralimbic coordination systems

Other limbic/paralimbic structures, in particular the basal ganglia, the amygdala, the insular cortex, and the cingulate cortex are also critically involved in affective processes, but do not appear to generate, or serve, a particular class, or quality of affect. These structures receive direct projections from all four affect systems [24], and appear to be primarily involved in the coordination of the activity of affect systems and effector systems (including selection, patterning, integration, monitoring, and regulation of activity).

5.1. Basal ganglia

The basal ganglia (BG) are involved in automatic motor responses to emotional stimuli [229], and in the automatic recognition of emotional stimuli [229]. For example, the basal ganglia participate in recognizing facial expression of emotions [230] and emotional tone from speech [231]. Moreover, the BG play a role in spontaneous, extrapyramidal motoric expression of emotion [229]. It has also been suggested that the BG represent a central selection and switching mechanism [232], specialized in resolving conflicts over access to limited motor and cognitive resources [232]. That is, the BG have been implicated in the selection of actions and allocation of attentional resources, in particular in the face of conflicting demands from different cerebral systems. Following up on this idea, Marcus Stephenson-Jones [233] suggested that the BG represent a core selection architecture processing cognitive, emotional, motivational, and motor information in parallel in order to control a broader range of behaviours (for a review on the role of the ventral striatum and the ventral pallidum in affective processes see Ref. [66]).

A recent functional neuroimaging study [234] also suggests that the striatum functions as a computational hub in which sensorimotor, attentional, and emotional processes converge during the perception of positive music. Another study showed increased dopamine availability in the ventral striatum (probably the nucleus accumbens) during music-evoked frissons (so-called "chills", involving piloerection [235] and shivers) [68]. The nucleus accumbens is sensitive to rewards, and motivates, initiates and invigorates behaviours to obtain and consume rewards [26]. That study [68] also showed increased dopamine availability in the *dorsal* striatum during the anticipation of a frisson.

5.2. Amygdala

The amygdala is situated in the inferior-medial portion of the temporal lobe (in humans anterior to the hippocampal formation, see dotted line in Fig. 1), and comprises several distinct nuclei groups [236,26]. In addition to projections from the four affect systems, the amygdala receives direct projections from the olfactory system (from both the olfactory bulb and the olfactory part of the cerebral cortex), and receives pre-processed information via the thalamus from all other sensory modalities (including visceral information). Electrical stimulation of various sites within the amygdala can elicit marked changes in autonomic and endocrine activity, orienting responses, flight, attack and defensive behaviour, feelings of fear, feelings of pleasantness, as well as facial expression of emotion [24]. The (superficial) amygdala appears to be sensitive to socio-affective information [24,237–241], and to modulate approach-withdrawal behaviour in response to such information [26]. The (laterobasal) amygdala appears to code the positive or negative reward value of external stimuli, and to regulate neural inputs into the hippocampal formation (see also above).

Therefore, the amygdala plays a crucial role in the integration of the emotional and motivational information of complex sensory inputs, and in initiating appropriate integrated neuroendocrine, autonomic and behavioural responses [242]. The amygdala thus plays a role in the detection of emotions, the registration of conditioned stimuli, the initiation of affective, autonomic, and hormonal activity, as well as the termination of positive emotions in the face of danger. In addition, the amygdala has, due to its massive projections to the striatum, access to the initiation and patterning of somatomotor behaviour [24]. Notably, several studies showed that activity changes within the amygdala are not only related to fear, but also to positive emotions [243–245,239,234]. Thus, the amygdala is clearly not simply a "fear centre" (nor the only brain structure involved in fear, see also the section on the brainstem- and diencephalon-centred affect system).

In our view, the integrative function of the amygdala, i.e., its capability to initiate, modulate, maintain, and terminate activity in the affect systems, is more characteristic for this brain structure than a particular class, or quality of emotion. For example, the amygdala is involved in emotions as diverse as fear, disgust, anger, sexual arousal, joy, and humour [245], and it seems likely that the amygdala activates or inhibits neural activity in affect-generating structures (i.e., in the hippocampus, the diencephalon, the brainstem and the orbitofrontal cortex), rather than generating all of these affects itself. For example, the amygdala plays a role in fear due to its connections to the PAG [246], in sexual arousal due to its connections to brainstem and hypothalamus [247], and in joy due to its connections to the hippocampus (as reviewed above).

The amygdala has also been conceived of as a "system for relevance detection" [248]. However, relevance detection is a function that structures such as the brainstem and the OFC perform as well. Therefore, unless evidence arises implicating the amygdala in a particular class of emotions, we consider the amygdala as an emotional control structure, rather than as a separate affect system.

5.3. Insula

Details on anatomy and function of the insular cortex have been reviewed elsewhere [249,250,51,9,251]. Here, we briefly mention three points relevant for the role of this "limbic integration cortex" [249] for emotion. *Firstly*, the insula is a visceral sensory, somatosensory, visceral motor, and motor association area that plays a major role in the regulation and adjustment of the intensity of vegetative activity to an appropriate level according to somatosensory, visceral sensory, and vegetative information. Particularly the anterior insular cortex has subcortical, limbic/paralimbic, as well as brainstem connections, and plays a specific role in the integration of visceral and somatosensory information with vegetative activity. Thus, the insula is also in a position to prevent vegetative activity from going overboard, as well as from being blunted, or from instantly ebbing away [120].

Secondly, the posterior insular cortex is conceived of as "primary interoceptive cortex" [51] which provides a representation of the physiological condition of the body [51]. As discussed above, the posterior insular cortex thus is a neural substrate for one major component contributing to the establishment of emotion percepts. Recall that the *posterior insula* is not to be equated with *posterior insular cortex* (or retro-insular cortex) because the posterior insula is often occupied by cortex of the parietal operculum [188].

Thirdly, insular cortex is implicated in self-recognition, and differentiating between self and object. Thus, the insula is a paralimbic structure that fulfils an important function for the establishment of the relationship between inner feelings and outer objects [9].

5.3.1. Insula and disgust

The insula has been implicated in toxicity- and disease-related forms of disgust [252–254]. With regard to disgusting tastes, it is important to consider that the (anterior–superior) insula (and adjacent frontal operculum) represents the primary gustatory cortex [24]. However, other modalities can also evoke disgust, and other structures such as the basal ganglia have been implicated in disgust as well (although to a lesser extent than the insula) [253]. Reflexive vomiting and retching is organized under the control of the nucleus tractus solitarius [252], although it appears that there is no single "vomiting centre" which could be activated by electrical stimulation. The latter suggests that emesis is organized by multiple brain structures [252]. With regard to learned disgust, formation of a conditioned taste aversion (in rats) requires not only an intact anterior insula, but also an intact amygdala [252]. Moreover, a meta-analysis of functional neuroimaging studies on perception of faces reported that processing of disgusted faces (compared to neutral faces) activated not only the insula, but also the thalamus [254], and moral disgust activates the OFC (not the insula) [255]. Physiologically, it seems likely that disgusting sensory information (such as gustatory information represented in the insula, or olfactory information represented in the orbitofrontal cortex) automatically activates brainstem centres involved in retching and emesis, and it is likely that visceral back-projections (particularly from the stomach) are represented as interoceptive information in the insula. For these reasons, we do not conceive of the insula as an affect centre for disgust.

5.4. Cingulate cortex

In addition to the insula, changes in vegetative activity are also modulated by the anterior and mid-cingulate cortex (ACC) [256,257]. Already Papez and MacLean observed that "tumors of the corpus callosum impinging on the cingulate gyrus are often associated with changes of the personality, loss of affect, and various degrees of somnolence and stupor" [258] (p. 341). However, the anterior and mid-cingulate cortex is involved in numerous functions, including pain perception and pain control, motivational processes, as well as in processes not directly related to emotion such as error monitoring, motor programming, performance monitoring, and immediate adjustments of actions to achieve a goal [259,260]. With regard to these different functions, it was recently proposed [120] that the cingulate cortex hosts a biological substrate of the *synchronization of biological subsystems*, a term coined by Scherer [261] who defines an emotion as a synchronization of the emotion components formulated in his *Component Process Model* (physiological arousal, motor expression, motivational processes, subjective feeling, and monitoring processes). Synchronization is likely to occur in the course of every emotion, and the anterior- and mid-cingulate cortex is in a unique position to establish, monitor and regulate such synchronization due to its involvement in cognition, autonomic modulation, motor activity, motivation, and monitoring.

The posterior cingulate cortex and the anterior fronto-median cortex constitute a midline core of the "default network" (or "default mode network") that is active during mind-wandering, when individuals make self-relevant, affective decisions (including remembering and prospection), and think about current concerns or social interactions [262]. Particularly the posterior cingulate cortex has been implicated in memory-based thoughts, and regulating the balance between internally versus externally directed attention [263].

6. Returning to William James' question "What is an emotion?"

In this article we propose that four different classes of affect originate from neural activity in four different affect systems. This quartet of affect systems consists of a brainstem-centred, a diencephalon-centred, a hippocampus-centred, and an orbitofrontal-centred affect system. Examples for affect classes characteristic for these affect systems are ascending activation (brainstem-centred), pain/pleasure (diencephalon-centred), attachment-related affects (hippocampus-centred), and moral affects (orbitofrontal-centred). These affect systems interact with each other, and activity of the affect systems interacts with activity of emotional effector systems (action tendencies, motor expression, modulation of physiological arousal, attention, and memory). The effector systems, in turn, interact with each other and with the affect systems. Activity of affect systems and effector systems is integrated, monitored, and regulated by limbic/paralimbic control systems. The distinction between affect systems and effector systems is important, because it differentiates between the source of emotional activity in the affect systems, and its physiological effects in the effector systems. This distinction is complicated by the fact that affect systems and effector systems overlap in part. For example, both brainstem and hypothalamus host nuclei involved in the expression of emotion.

We consider an emotion as the integrated result of activity in affect systems and emotional effector systems, from which an emotion percept emerges. The emotion percept can be reconfigured into language, and the emotion percept might elicit conscious cognitive appraisal. That is, in our terminology, 'affect' only refers to the activity in the affect systems, and 'emotion' is the broader term because it includes (a) activity of affect systems as well as effector systems, (b) an emotion percept, and possibly (c) the use of language as well as conscious appraisal.

These considerations set up a framework from which testable hypotheses can be derived, and that aims at understanding the intricate neurobiology underlying human emotion by virtue of differentiating between the four affect systems (from which emotions originate). The affect systems operate in different ways with regard to (a) antecedents of affective activity, (b) learning and memory, (c) the degree to which emotions satiate, (d) cognitive complexity, (e) the effects that they exert on emotional effector systems, (f) their subjective feeling quality, and (g) the degree by which they can be modulated by conscious appraisal. For example, the "*explanation of emotion*" by Rolls [130] or the eleven "*Laws of Emotion*" by Frijda [172], can all well be applied to orbitofrontal-centred affect, but not equally well to emotions originating from other affect-systems. Another example is that the moral emotions arising from orbitofrontal-centred affective activity (such as guilt, shame, and regret) have a different subjective feeling quality than the hippocampus-centred attachment-related emotions (such as love). The latter emotions, to name a final example, do not satiate, in contrast to the diencephalon-centred feelings of reward and pleasure perceived when fulfilling a homeostatic need. These differences call for a specific, and more accurate differentiation than has previously been common.

7. Conclusions

In this article we present a new theory of emotions, the *Quartet Theory of Human Emotions*. The term Quartet Theory refers to four core emotional systems, the *affect systems*. These affect systems operate in fundamentally different ways with regard to (a) antecedents of affective activity, (b) learning and memory, (c) the degree to which emotions satiate, (d) cognitive complexity, (e) the effects that they exert on emotional effector systems, (f) their subjective feeling quality, and (g) the degree by which they can be modulated by conscious appraisal. There is no doubt that the four affect systems also have a number of features in common. For example, (a) they serve in the selection and modulation of biological processes such as behaviours, perceptual processes, attention, and memory processes [264,265,6,266], (b) they are capable of operating in the absence of conscious attention and awareness [238,237], and (c) their activity usually results in an emotion percept (i.e., in subjective feeling). However, the significant differences between the four affect systems call for a specific, and more accurate differentiation of different classes of emotions as well as of their neural correlates than has previously been common. This is also a reason why our article deals with a model of

emotions (plural), and not with a model of emotion (singular) in general: Depending on the affect system from which an emotion originates, the quality of an emotion can be fundamentally different from an emotion originating from another affect system (with regard to learning and memory, satiation, subjective feeling quality, etc.). Furthermore, our Quartet Theory accommodates the following aspects:

1. *The need for a neurobiological model of human emotions.* Most previous emotion models are based on animal data and do not include emotions that are uniquely human. The Quartet Theory includes such uniquely human emotions: We put forward the hypothesis that the orbitofrontal cortex is the neural correlate of the generation of moral affects of humans, and that the hippocampus is the neural correlate of the generation of attachment-related affects. These emotions are more differentiated, and related to more extensive social networks, in humans compared to animals.

2. *Emotions and language.* The Quartet Theory is the first to include language, which has two main functions for human emotions: the communication (including the evocation) and the regulation of emotions. We argue that there is no direct "translation", that is, no one-to-one neural code that would directly translate feeling states into words. Instead, we propose that feeling states (i.e., *emotion percepts*) are *reconfigured* by linguistic expressions (though such reconfiguration is not obligatory for subjective feeling). However, we also emphasize that affective prosody, and probably even more so music, can evoke sensations (e.g., due to emotional contagion) which, *before* they are reconfigured into words, bear greater inter-individual correspondence than the words that an individual uses to describe these sensations. In addition to the role of language for communicating subjective feeling, language codes are also involved in *conscious cognitive appraisal* (in terms of rational thought and logic), which makes the language-system an important means of regulating emotions, and thus an important working factor of cognitive behavioural psychotherapies, as well as of emotion-regulating practices such as mindfulness, prayers and meditation.

   The neocortical processes underlying rational and logical thinking require conscious attention and awareness (in contrast to the processes performed by the affect centres). These processes are deliberate, and they are slower, and seemingly more laborious, than the automatic and non-conscious cognitive processes performed by the orbitofrontal cortex, which are fast, intuitive, seemingly facile, but not rational [146]. Whether the cognitive biases of fast human thinking [148] are due to processes performed by the orbitofrontal cortex remains to be specified, but these considerations illustrate that more detailed neurobiological classification and categorization of the neural correlates of human emotion is also necessary to pave the way to a better understanding of human cognition.

3. *The importance of differentiating between affect systems and effector systems.* We differentiate between the affect systems and emotional *effector systems*. These effector systems include motor systems (producing actions, action tendencies, or expression of emotion), physiological arousal systems, attention systems and memory systems. If emotions serve the selection and modulation of biological processes such as behaviours, perceptual processes, attention, memory, etc., then our distinction between affect systems and effector systems is important because it differentiates between *input systems* (i.e., perceptual systems that provide information about external and internal stimuli), *affect systems* (producing biological signals with the function of selecting or modulating behaviour, memory, etc.), and *effector systems* such as output (motor) systems, arousal, attentional and memory systems.

4. *Beyond appraisal theories and short-term emotional phenomena.* Appraisal-theories focus on the situations, objects, or events that elicit (and differentiate) a certain emotion. We argue that the affect systems are not simply mechanistic stimulus-response operators, and that the affect systems do not exclusively respond phasically to external stimuli. One important example is the attachment-related emotion of love, another example is a long-term background affectivity such as rumination or depression. That is, one reason why it is important to consider that an affect system is not only active in response to a goal-relevant stimulus is that such activity is a major determinant of long-term emotional phenomena (such as moods), and of emotional phenomena occurring consistently in response to particular individuals over long time spans (such as love). It is important to deal with this issue, in addition to research on short-term emotional phenomena, to understand the neurobiology of human affect, and disorders of mood and affect. Up until now, only little has been known about the neurobiology of long-term emotional phenomena, and about differences of the neural correlates underlying short-term and long-term emotions. Our Quartet Theory also reflects that the strict dichotomy of "emotion" and "cognition" is more and more vanishing [267] – memory and learning (classically considered as cognitive functions) appear to be co-localized with emotional processes in the hippocampus, and the orbitofrontal cortex is capable of performing (non-conscious)

cognitive appraisal. Moreover, conscious cognitive (neocortical) appraisal involves symbolic systems such as language, and regulates as well as modulates emotions. Rational thought and logic often also have the function of selecting behaviour (in this regard cognition and emotions fulfil the same function).

5. *Several factors contribute to subjective feeling.* We propose that activity of the affect systems and of the effector systems is synthesized into an *emotion percept*. We use the term emotion percept to explicitly refer to *unverbalized subjective feeling* (such emotion percepts can, in turn, be *reconfigured* into language). We propose that four different feeling-components contribute to the emergence of subjective feeling: (1) An *affective component* due to projections from the affect systems to insular and somatosensory cortices. (2) A *sensory-interoceptive component* synthesized in the insular cortex based on the integration of the physiological, including homeostatic and vegetative, condition of the body. (3) A *motor component*, that is, the tendency (or drive) to act, originating from the basal-ganglia as well as from the orbitofrontal cortex. (4) A *cognitive component* involving conscious cognitive appraisal. Future research is needed to specify the interactions between these feeling-components, and how the synthesis of these components into an emotion percept, as well as the reconfiguration of the emotion percept into language, is neurally implemented.

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