

Opinion

From Architecture to Evolution: Multisensory Evidence of Decentralized Emotion

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Emotional appraisal in humans is often considered a centrally mediated process by which sensory signals, void of emotional meaning, are assessed by integrative brain structures steps removed from raw sensation. We review emerging evidence that the emotional value of the environment is coded by nonvisual sensory systems as early as the sensory receptors and that these signals inform the emotional state of an organism independent of sensory cortical processes. We further present evidence for cross-species conservation of sensory projections to central emotion-processing brain regions. Based on this, we argue not only that emotional appraisal is a decentralized process, but that all human emotional experience may reflect the sensory experience of our ancestors.

The Experience of Emotion

To describe a feeling of happiness, one may invoke sensations of a cup of hot cocoa and warm blanket on a cold snowy day, or the scent of fresh flowers during an afternoon walk, arm in arm with a loved one. For fear, we may invoke the racing heart, sweaty palms, and tunnel vision experienced when standing on the edge of an imposing precipice or the shiver down your spine after hearing an unexpected piercing shriek in the night. Yet these bits of imagery and physiological phenomena, however vivid they may be, are only gestures toward the actual emotional state experienced internally; they are descriptions of situations and physiological responses, often specific to shared cultural experiences, that evoke, or are evoked by, a given **emotion** (see [Glossary](#)). By contrast, the subjective experiences of happiness and fear come from within. They cannot be measured directly and objectively or described accurately in the language of **exteroceptive sensation**.

Abundant evidence indicates that emotional states are often **supramodal** motivators; they are states coloring all sensation and experience that drive the behaviors of an organism, curated by a lifetime of interactions with the world around us, and catered to the specific context in which we find ourselves situated [1–3]. Research in human affective neuroscience has suggested that objects evoking such visceral emotional responses are not inherently emotional at the point of sensation; it is the **affective value** we attribute to them that affords them salience and sensory prioritization [4]. The experience of sensory information is itself shaped by internal **motivational states** [3–6], task-relevant goals [5–8], and history of experience [7,9,10]. Such motivationally modulated sensory experience then acts to guide cognition and behavior in a way that allows us to maximize our acquisition of biological resources (i.e., nutrients, shelter, reproductive opportunities) while simultaneously minimizing our exposure to threat [2,11].

Evidence supporting centralized processing of emotional salience is garnered from decades of human neuroscientific studies investigating emotional modulation of the visual system. Yet it remains unclear whether an understanding of emotion–sensation interactions from one sensory modality is generalizable to a global framework of emotion processing. The persistent focus on cortical pathways of the human visual system and their interaction with affect-related frontotemporal structures has

Highlights

Emotions function to motivate adaptive patterns of behavior and cognition, increasing the chance of an organism's survival and reproduction by allowing it to compare objects, events, and cognitions in a modality-general manner.

Current theories of human emotion appraisal as a centrally mediated process neglect evidence from nonvisual modalities, indicating that sensory afferents can reflect the adaptive value of external objects.

In humans, valence-coded sensation informs modality-general representations of emotion and well-being independent of modality-specific processing.

Whereas emotion processing in humans is predominantly informed by processed cortical signals, emotional processing in many non-human species is characterized by responsiveness to raw sensation.

We propose that centralized human emotion-processing structures are the evolutionary descendants of regions once dedicated to interpreting valenced-sensation, with valenced sensory inputs an artifact of this developmental history.

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resulted in an understanding of emotional processing that espouses **modality-general central-mediation** of affect appraisal, yet this approach neglects additional routes of emotional assessment. In this paper, we argue that central modulation of perception by emotion is neither the whole story of human emotion assessment, nor is it an accurate reflection of the evolutionary development of human emotional states.

There is increasing evidence that, beyond the central modulation of sensory experience, most sensory systems are tuned to conduct value-based appraisal of the environment before signals reach the cortex. Through 'labeled lines', **valenced** signals can communicate an object's adaptive value to an organism from the point of environmental interaction [12–16]. Such signals communicate harm versus pleasure [17,18], threat versus safety, and contamination or distaste versus nutritional benefit [12,15,19,20]. These signals are projected to the cortex along routes distinct from those that communicate discriminatory nonaffective sensation. They may even bypass primary sensory cortices (defined by dominant inputs from sensory-specific thalamic nuclei) entirely [21,22]. Valenced sensory signals modulate activity in structures associated with emotional evaluation and regulation, including the insula, orbitofrontal cortex (OFC), and anterior cingulate cortex (ACC) [22–24]. In our view, valenced sensation likely did not develop as a mechanism of emotional appraisal ancillary to centralized assessment. Rather, we propose that modality-general cognitive states experienced as emotions, and the structures in which they are instantiated, are born out of processing of valence-labeled exteroceptive signals.

We will present evidence demonstrating that theories of centralized appraisal of emotionality omit critical features of affective-sensation present in nonvisual modalities, including their instantiation in the periphery and their contributions to modality-general emotional states. Furthermore, we will outline evidence obtained from non-human animals to argue that many of the neural structures involved in the 'central-mediation' of emotional appraisal are likely the evolutionary descendants of sensory structures once dedicated to making sense of, and guiding responses to, sensory information. Viewed through this lens, projections of peripheral sensory information to central emotion-processing regions not only allow rapid prioritization of what is affectively salient; they also reflect the ancestral role of these structures in processing sensory information. By examining these pathways, we can infer the formerly sensation-dominated functionality of emotion-related structures. Such inferences will provide insight into the behaviors and cognitive states they currently drive. Happiness might not only be described as similar to a cup of hot cocoa and a warm blanket on a cold snowy day; it may, neurologically and experientially, be one and the same.

Assessing Emotional Information

Emotions are often conceptualized as cognitive and physiological states elicited by **instrumental reinforcers** in our environment [2,25]. That is, emotions are produced by appraising thought contents or sensations and identifying characteristics indicating reward or punishment [26]. Emotional states act as motivational states, guiding goal-directed actions and updating perceptual mechanisms to maximize beneficial interactions with the environment. The diversity of possible motivational states, and how they may relate to internal emotional landscapes and overt behavioral responses, have been described in detail elsewhere [27,28]. In the current perspective piece, we will focus on the role of emotional states as mechanisms that motivate adaptive behaviors in complex environments to contextualize the role of human emotional processing and the structure in which it is subsumed, within its putative path of evolutionary development.

Integral to the role of emotion in motivation across species is the appraisal of adaptive value, or valence; that is, the ability of an organism to discriminate and identify what is good from what is

Glossary

Affective value: the characteristic of an object, sensation, or cognitive state informing an organism of its impact on well-being; whether it is experienced as 'good' or 'bad'.

Amniote: vertebrates, including reptiles, mammals, and birds, protected by an amniotic membrane during embryonic development.

Amodal: information or experience that is not constrained to sensation but is independent of sensory experience.

Central-mediation: neural processing of modality-general information that occurs in the central nervous system and typically involves the integration of processed cortico-cortico inputs rather than unprocessed sensory signals.

Corticate: describing a nervous system containing a distinct outer layer of cortex. The precise architecture of this layer varies between species.

Emotion: cognitive or physiological states that occur in anticipation of, or as a response to, affective information, which reflect the value and/or the intensity of eliciting stimuli. Emotions can act as motivational states aimed at the attainment or avoidance of instrumental reinforcers.

Exteroceptive sensation: sensory information generated by interactions with an environment external to the sensing organism and indicative of observer-independent features of this external world.

Instrumental reinforcers: objects or outcomes in the environment that modulate patterns of behavior through either reward or punishment of specific actions.

Interoceptive sensation: sensory information indicating the internal homeostatic and physical well-being of an organism.

Modality-general: information unfettered to a specific sensory modality, either by being represented as omnipresent across all sensation (supramodal), or independent of sensation altogether (amodal).

Motivational state: goal-driven internal state that acts to drive/guide behavior for the attainment of a specific outcome.

Pallial structures: layers of gray matter that develop from embryonic pallium and cover the outer surface of the vertebrate brain.

Pallium: a dorsal subdivision of the telencephalon (most highly developed and anterior part of the forebrain)

bad. In this context, emotion is often considered supramodal or **amodal**: emotion is experienced as either a background canvas that encompasses information from all sensory modalities, or as a cognitive state independent from sensation altogether. In these modality-general conceptualizations, emotion acts as a ‘common-currency’ [2,29] to evaluate objects and provide a framework to guide approach toward or avoidance of an object or situation [2,27,28,30]. In humans, most current theories addressing how emotional salience is assessed from, and subsequently modulates, sensory processing conceptualize emotion as centrally mediated information [31], processed in a privileged location in the information hierarchy, at a point of convergence for cortically processed sensory and cognitive signals [32]. Emphasis is on a feedforward volley of processed sensory information followed by subsequent feedforward projections guiding behavior and **re-entrant feedback** to sensory cortices to modulate perception [6,33].

In this framework (Figure 1A, Key Figure), derived from human work in the visual domain [34,35], processing begins in regions of primary sensory cortices defined by dominant entrant projections from sensory organs/receptors via a thalamic relay [36,37]. Subsequently, connections through secondary and tertiary sensory cortices propagate these sensory signals to frontotemporal structures, which, through dense connections back to sensory cortices, allows for interpretation and modulation of early sensory processing by affect-related information [31,33]. Such re-entrant feedback to the sensory cortices affords affective coloring of sensory data. Indeed, empirical work has identified a widespread network of subcortical and cortical structures [38,39] involved in evaluating and representing emotional content, including the anterior cingulate [40–42], insular [43,44], and orbital frontal [45,46] cortices, amygdalae [47], and ventral striatum [48]. Each of these regions serves a specific, yet interconnected, function in the appraisal of and response to emotional information [39,46]. In this framework, exteroceptive sensory information carried through these systems is without emotional content, forming internal representations of a viewer independent external world. The attribution of affect to sensation is instead dependent on centralized affective associations developed over a lifetime of environmental exposures and interactions [5,7,9]. Yet, if we broaden our view of human affect processing to include evidence from other sensory systems [12,14,17,49–51], we begin to see that a clear division between exteroceptive sensation and emotional appraisal may not exist (Figure 1B).

Peripheral Signals of Affective Information

For all sensory modalities other than the visual, there is direct or indirect evidence of distinct labeling of emotionally salient information (affect-coding) prior to entering the brain. Within proximal and chemical senses, we observe valence-coding indicating objective signals of environmental risk or benefit, either with direct relevance to internal homeostatic well-being (e.g., sweet versus bitter taste [12,19,20,24], odors of food/decay [51]), or indicative of social safety or threat (e.g., affiliative social touch and nociception [13,17,18,50,52–56]). For gustation, the response of individual receptors is inherently linked to nutritional profile [57,58], with receptors catered specifically to the dietary restrictions and requirements of an organism [12,59–61]. Representations of olfactory valence have been observed as early as the olfactory receptor [15], with receptor activity indicative of potential sources of chemical/biological threat and reward [22,51] or reproductive opportunity [62–64]. In somatosensation, positive and negative attributes of touch, corresponding to affiliative social interaction [21,65] and ongoing or potential tissue damage [52–54], are labeled as early as the sensory receptors themselves [66]. These affective sensations are then carried through peripheral nerves dissociable by physical characteristics in addition to receptive properties [13,52–54,56]. Even within the visual domain, recent work has refined and extended proposals that the thalamus performs rudimentary affect appraisal, focusing on the role of pulvinar and additional first-order extra-thalamic nuclei [67] with affective signals processed by these noncortical nuclei influencing adaptive ocular-motor responses, including pupil size and orienting responses.

common among vertebrates during embryonic stages. This term may also refer to structures in the reptilian and amphibian brains originating from this embryonic subdivision.

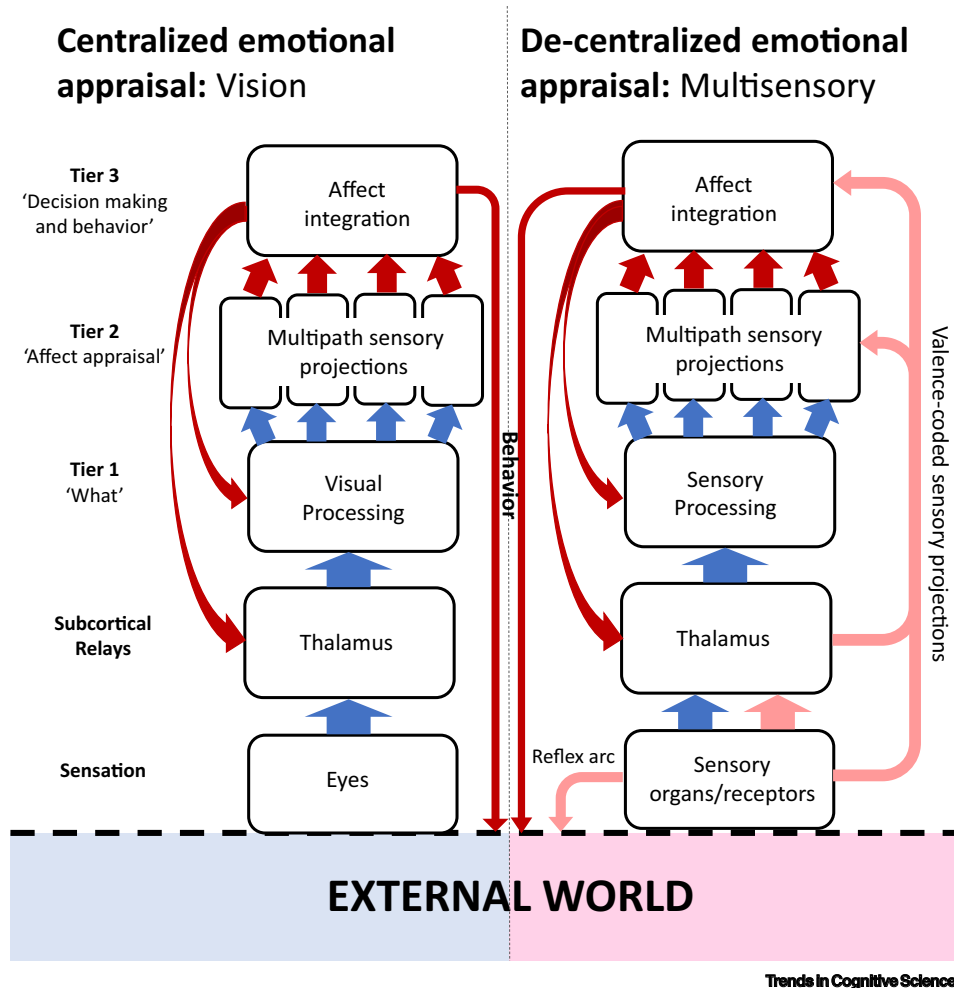
Re-entrant feedback: information conveyed by neural pathways that send signals against the feedforward flow of information. In sensory processing such information flows from association cortices back to primary and early sensory cortices.

Supramodal: information or experience that transcends sensory experience; a component of experience common across multiple sensory modalities.

Valence: value-related information about an object that is represented along a linear scale from good/pleasant to bad/unpleasant.

Key Figure

Emotional Appraisal of Sensory Information



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Figure 1. (A) Centralized appraisal. Many current theories of emotional appraisal of sensation, guided by evidence from the visual system, conceptualize emotion as a feature extracted from sensory information by an interconnected network of frontal and temporal structures. Information obtained through sensation does not contain emotional content (blue/blue arrows) and is propagated through thalamic relays and sensory processing areas. Signals indicating affective value (red/red arrows) only emerge as sensory information reaches association cortices and beyond. In this view, any mediation of sensory processing by affective salience preceding association areas are the result of re-entrant projections from structures involved in cortical emotional appraisal. (B) Decentralized appraisal. Responses in peripheral sensory systems indicate the adaptive value of the external world, thus rendering the environment directly informative of affect. These valence-coded signals (pink) propagate into the central nervous system in channels distinct from those for discriminative sensation and inform our representations of affect independent of their instantiation in sensory cortices.

Thus, the benefit of being able to assess objective sensory signals of biological importance prior to cortical instantiation is of critical importance to the survival of an organism.

Much of the observed valence-coding of sensation, be it olfaction [68,69], somatosensation [50,55,70], or audition [71–73], reflects objective characteristics of stimuli in a manner consistent

with a view of emotional valence as an objective feature of the environment. The utility of immediately identifying objective markers of threat and safety is clear: Receptors capable of hedonic appraisal allow rapid parcellation of sensation into signals informative of hedonic value, expediting the incorporation of such signals into behavior beneficial for survival. Indeed, in some of the simplest sensorimotor motor reflex arcs, (e.g., withdrawal reflexes) we can witness identification of, and response to, harmful events without the need for cortical input [74,75].

For organisms across the phylogenetic tree, peripheral sensation is used to identify external signals most relevant to well-being and behavioral strategies rapidly integrate this information to adjust action goals (e.g., [76–79]). For species with non-**corticate** nervous systems, affect-labeled sensory information can directly guide behavior. For example, behavior of *Caenorhabditis elegans* is dictated in part by tactile thermal receptors and nociceptors [80,81] and olfactory receptors signaling potential nutritive value [82,83], which subsequently promote avoidance and approach behaviors in a modularized fashion. This rapid integration of environmental signals into patterns of behavioral response allow the organism to quickly react to changing environments while minimizing the risk of harm and maximizing nutritive and/or social benefit. In species with more complex nervous systems, peripheral signals of valenced sensation maintain their role in guiding perception and behavior and are carried by nerve fibers distinct from those for discriminative sensation [13,15,20,84]. Distinct valence-related sensory signals remain trackable beyond their peripheral instantiation, projecting to neural structures mediating emotional response rather than sensory experience [12,19,21,85–87]. This pattern of cortical dissociation may provide critical insight into how these valence-labeled signals, crucial to the survival of less complex systems yet often neglected in theories of human emotional processing, adapted with evolutionary expansions of cognitive processing and cortical development.

Cortical Processing of Affect from Sensation

Accumulating evidence in humans suggests that, in addition to carrying valenced information from the point of contact, valence-labeled sensory afferents follow distinct trajectories from valence-independent afferents upon cortical entry [12,19,21,85–87] (for review, see Table 1).

Table 1. Coding of Sensory Affect in Mammals^{a,b}

Modality	PA coding	Adaptive feature	Primary SC location	Affect processing w/o SC representation	PA instantiation in the brain
Vision	No	n/a	pOC	No	n/a
Audition	Inconclusive	Species-specific frequencies [71–73]	STS	Yes [149,150]	Amy ^c [144,151,152]
Gustation	Yes [12,20]	Nutritive value/toxicity	Ins ^d	Yes [153]	Ins [24]
Olfaction	Yes [15]	Potential nutritive value [22,51], reproductive opportunity [62–64]	Piriform cortex ^e	Inconclusive, but likely reduced [22,99,101]	Piriform, Amy ^f , OFC ^g [99,102,154], striatum [22,99]
Somato-sensation	Yes [13,52–55,84]	Social presence [65,87], cutaneous damage [17,70]	postCG	Yes [21,155,156]	Ins, ACC, OFC [40,42,87,93]

^aAbbreviations: ACC, Anterior cingulate cortex; Amy, amygdala; Ins, insula; OFC, orbitofrontal cortex; PA, peripheral affect; pOC, posterior occipital cortex; postCG, posterior central gyrus; SC, sensory cortex; STG, superior temporal sulcus; vStr, ventral striatum.

^bThe framework of affective appraisal as a centrally mediated process has been challenged by recent evidence from nonvisual modalities outlining the existence of valence-labeled sensory signals. While some of these signals are represented in sensory cortices, their contribution to modality-general affect is often not dependent on sensory-specific structures. Above is a brief summary outlining the contribution of peripheral affect (PA) to the representation of modality-general affective states and the dependency of these processes on sensory-specific cortices.

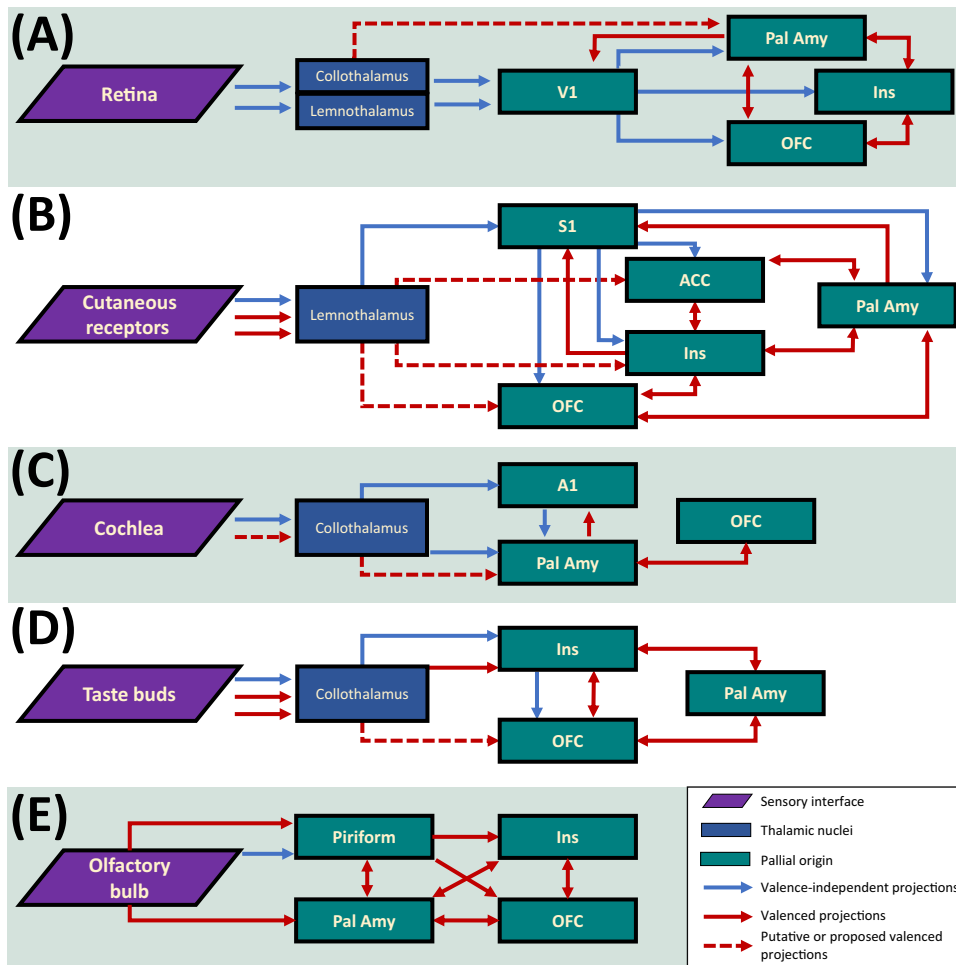
^cThe amygdalae are most responsive to the feature considered the most likely candidate for PA coding in audition (i.e., species-specific distress frequencies). It remains inconclusive, however, whether these features are isolated by cortical means, or at a precortical processing step.

^dThe putative primary gustatory cortex is a distinct subregion of the insula and has a notable role in multisensory integration, consistent with the overall role of the insula in processing modality-general affect. For review of multisensory integration in gustatory cortex, see [157].

^eSimilar to the putative primary gustatory cortex, piriform cortex has been highlighted for its role as an association cortex for nonolfactory sensory information. For review, see [158].

^{f,g}Evidence [102,154] suggests that olfactory valence is represented in the OFC, while affective intensity is represented in the amygdalae.

Valence-labeled signals propagate to structures typically associated with emotion evaluation, regulation, and interoception [1,43,88] in a manner dissociable from, or in the absence of, their representation in sensory cortices [21,66] (Figure 2). For example, suggested points of cortical entry for tactile signals of pain and pleasure carried by C- and C tactile-fiber afferents [18,52,53,56] are frontotemporal structures, including ventromedial prefrontal cortex (vmPFC)



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Figure 2. Projections of Sensory Information That Affect Processing Structures in Mammals. (A) Visual processing. (B) Somatosensory processing. (C) Auditory processing. (D) Gustatory processing. (E) Olfactory processing. A common organization can be observed across most sensory processing pathways: peripheral sensory afferents project to thalamic nuclei, which in turn project to primary sensory areas. Affect-related structures receive sensory input via projections from primary sensory cortices (via secondary sensory cortices and association cortices, not pictured) as well as additional projections independent of sensory cortices. A notable exception to this organization is observed in olfaction: the olfactory bulb does not relay through thalamic nuclei, but rather has direct projections to piriform cortex and, to a lesser extent, the amygdala. This reflects a unique evolutionary and functional history of this modality (for review, see [103–105]). Note: these schematics are not intended as an exhaustive description of pathways related to either sensory or affective processing. They focus solely on the propagation of unimodal sensory signals through cortical structures implicated in centralized affect representations. Notable omissions include pathways through secondary and tertiary sensory cortices, multimodal integration in sensory cortices, and pallial/nonpallial circuitry (including projections through the striatum, hypothalamus, periaqueductal gray, etc.). Abbreviations: A1, primary auditory cortex; ACC, anterior cingulate cortex; Amy, (primate) amygdala; Ins, insula; OFC, orbitofrontal cortex; Pal Amy, pallial amygdala; S1, primary somatosensory cortex; V1, primary visual cortex.

and OFC, insular cortex, and ACC. While each of these regions is implicated in a broad spectrum of cognitive, affective, and motivational functions, they are also consistently linked to specific affect-related processes. For example, vmPFC/OFC is typically associated with value-based decision making [89], insular cortex is often conceptualized as processing representations of aversion [42,90] as well as the ‘interoceptive self’ [91,92], and ACC represents both modality-specific and modality-general pain [40,93] among other functions [94]. Importantly, these regions mediate centralized representation of affective information rather than direct sensory processing. By contrast, the dominant point of cortical entry for nonhedonic tactile signals is primary somatosensory cortex [49]. Thus, hedonic and nonhedonic tactile signals, present from the point of cutaneous contact, inform distinct aspects of human experience: the former is represented as modality-general affect and the latter as modality specific exteroception.

Of note, some evidence suggests that hedonic and nonhedonic tactile signals may be integrated in part as early as the dorsal horn of the spinal cord [95–97], yet their cortical instantiation does not appear to depend on this integration. For example, dissociation of hedonic and discriminatory signals can be observed in patients lacking discriminatory touch ($A\beta$) afferents. Here, affective responses to tactile information persist in the absence of the experience of spatially discriminable touch [21,66] indicating that prototypical sensory representations are not required to process and experience valence-labeled sensation. Additional work may be needed, however, to further clarify dissociation versus integration of tactile signals.

As in the somatosensory system, valenced and nonvalenced gustatory and olfactory information are carried along distinct pathways. Human neuroimaging research has identified valence-sensitive gustatory modulation of insular cortices independent of primary sensory structures [19,24,41,98]. Valence-coded olfactory signals are projected to ventral striatum [22] and amygdalae [99,100] via pathways that are independent of those to primary olfactory cortex (i.e., piriform cortex [85,86]), which is itself responsive to valence information [86,101,102]. The ubiquitous presence of valence-labeled information in cortical areas processing olfactory information and the omission of a dominant precortical thalamic relay reflect a unique functional role and evolutionary history for olfaction (for review, see [103–105]).

Cortical instantiation of emotion-labeled sensation in insular, prefrontal, cingulate, and medial temporal structures is of particular interest given the intimate relationship between these regions and modality-general emotional processing. Such processing includes **interoceptive sensation** [91,106,107] (the representations an organism has of its own homeostatic well-being [92,106]) reward-motivated learning and behaviors [108,109], and salience detection [31,110–112], revealing a stark differentiation between affect-labeled and discriminative sensation. Valence-coded sensation can act to inform modality-general representations of internal affective states, independent of sensory-specific processing, while valence-independent sensation contributes to our perceptual experience of discriminative sensation.

Together, evidence from nonvisual modalities in humans suggests that even the supramodal and centralized processes for emotional appraisal that do occur may not rely solely on an initial feedforward volley of nonaffective information from sensory cortices to evaluate sensory experience. Rather, such processes are informed directly by signals of peripherally coded affect. Representations of valence-labeled sensation are not dependent on projections to traditional sensory regions but are instead instantiated in frontotemporal structures implicated in emotion appraisal and behavioral guidance. This process may allow peripherally valence-labeled information to have a more direct role in organizing the behavior and perceptual experience of an organism. Emotional responding may be explicitly driven by sensory activation of a specific modality. Yet,

in humans, these valenced sensations appear to contribute to a modality-general experience of emotion rather than exteroceptive perception of an external world [113].

Projections of sensory information to emotion-processing regions independent of traditional sensory cortices may provide a mechanism by which exteroceptive sensory information directly alters our motivational states, specifically those related to proximal threat and safety. Yet, given the utility of valenced sensation in guiding behavior (evidenced even in the simplest organisms) the independence of their representation from sensory-specific processing in human neocortex is striking. The possibility of neural regions evolving to represent modality-general representation of emotional state, as observed in humans [114–116], without any sensory-focused value-processing would appear rather remote.

Non-human Affect Processing

Evidence garnered from neural homologs of human emotion-processing structures in other tetrapods suggests an evolutionary history of these regions intrinsically linked to sensation. Human insular, cingulate, and orbitofrontal regions share an evolutionary origin with the avian Wulst and reptilian/amphibian **pallium**. Each of these regions is descended from the proto-pallium of a common ancestor [117–119] and develop in their modern form from the embryotic dorsal/dorsolateral pallium [120,121]. Notably, the precise organization and function of **pallial structures** diverges greatly across species, reflecting the unique history of evolutionary pressures each faced. Recent work has emphasized the extensive connectivity of pallial structures to thalamic, striatal, amygdalae (both pallial and subpallial components), and other pallial regions, observed in **amniotes**, indicating an evolutionarily ancient role for information integration in these regions (for review, see [122]). Interestingly, beyond amniotes, there is a much greater divergence among species regarding the integration of pallial signals across regions. For example, we can contrast pallial connections to the thalamus and optic tectum across species. Projections of sensory information from peripheral receptors to both regions, along with feedforward projections from these regions to affect-related pallial structures, are among the most conserved pathways across all jawed vertebrate species [123–126]. Interestingly, whereas amniotes, most notably mammals, display dense reciprocal connectivity between pallial structures and the thalamus [122,124,127], in amphibians and fish, it is the optic tectum that receives comparable pallial feedback with limited, if any, re-entrant projections observed from pallial structures to the thalamus [125,126]. However, stimulus-driven orienting responses mediated by optic tectum are observed across species [128,129] regardless of the level of pallial feedback. Conservation of unidirectional projections of sensory information, and their role in adaptive responses across vertebrate classes, suggests that these are likely features of a common evolutionary ancestor. By contrast, divergence in both the existence and strength of pallial projections to nonpallial nuclei suggest that neural architectural patterns affording extensive nonpallial integration of pallial signals (i.e., pallio-thalamic versus pallio-tectal feedback) are more recent adaptations to specific pressures faced by a species in later evolutionary stages. Thus, over an extended evolutionary timescale spanning beyond amniotic differentiation, processing of sensation, including valenced sensation, appears more conserved than widespread integration of processed information.

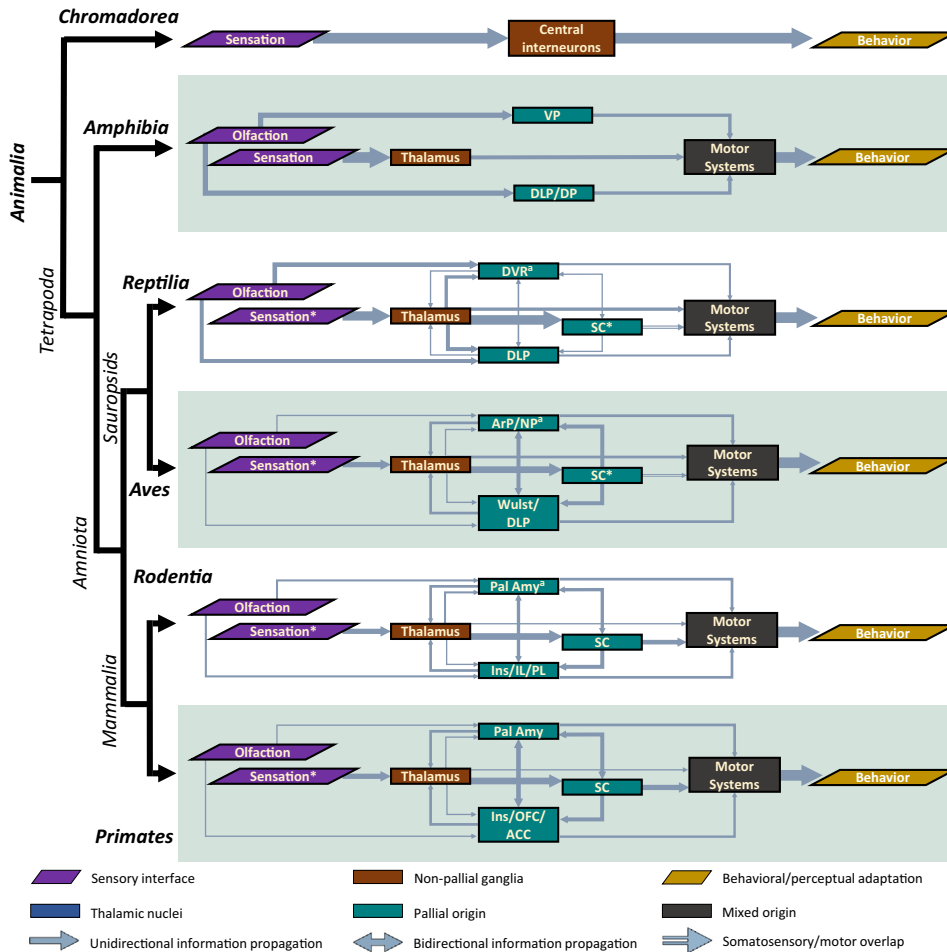
Even within amniotes, individual species diverge extensively in the dominant information integrated by emotion processing regions, as evidenced by patterns of pallio-pallial connectivity. For example, the amygdalae display many highly conserved patterns of connectivity and processing [119,130–132], yet diverge significantly in dominant inputs across species and phyla [133,134]. In species possessing pallial amygdalae or amygdala-like structures, there is evidence that sensory projections from both collothalamal nuclei [123,135] and the olfactory bulb are conserved. In reptiles and amphibians, these sensory projections provide primary input to putative

developmental homologs of pallial amygdala, specifically, the dorsal ventricular ridge [130,134,136], though the degree to which these structures are amygdalar homologs remains unclear. In mammals and birds, olfactory information comprises a very minor contributor to amygdala function [137]. Instead, this structure is characterized by broad connections to widespread regions of cortex [138] and its role as a central hub for multiple functional networks [112,137,139], though the organization of these networks varies greatly between mammalian and avian species. Even within classes, there is divergence in the contribution of sensory information to processing in pallial amygdala. For example, in some non-primate mammals, amygdalae homologs are preferentially responsive to sensory signals, with auditory, rather than olfactory signals acting as dominant contributors [140]. Thus, it appears that signals informing activity in brain regions processing affect have differentiated in step with the cognitive capacity of a species: unimodal and multimodal sensory projections to affective structures are conserved across species, yet the dominant contribution of these signals to affect processing has diminished in species with greater pallio-pallial connectivity.

Conservation of sensory projections to emotionally evaluative pallial/cortical structures observed in all vertebrates indicate that this feature is likely characteristic of a shared ancestral brain. Furthermore, conserved feedforward projections of these sensory signals to areas controlling motor response indicate they play an integral role in shaping behavior. However, the expansion of pallio-pallial and pallio-thalamic loops anchored in the OFC, insular and cingulate cortices, as well as the amygdala of amniotes, have allowed these species to co-opt behaviors once provoked by modal appraisal of sensory signals to function in a more generalized capacity: amodal appraisal of abstract cortically processed information. Thus, as cognitive capacity in some species has expanded over evolutionary time, valenced-sensory signals have become an ancillary feature to integrative higher order assessment and experience of emotion. They remain, however, an important window into their evolutionary development (Figure 3).

Abstraction of Sensory Experience

When we consider evidence obtained across all sensory modalities, the understanding of both the current manifestation and the evolutionary development of affect processing in humans moves beyond a singular focus on centrally appraised value. Objective signals of valenced sensation can be observed in afferent nerves across all nonvisual modalities and are highly conserved across the phylogenetic tree. These objective signals of value and harm guide the behavior of an organism in a manner critical for evolutionary fitness. Examination of the instantiation of emotional experience in the central nervous system, however, outlines a divergence across species. In nervous systems with less complex architecture, affective-processing occurs in a relatively modularized manner with a substantial contribution from unprocessed sensory signaling [130,133,134,136]. In organisms with simple trackable nervous systems, such as *C. elegans*, behavioral responses are often tied directly to modality-specific sensory experience, consistent with its value to survival [78,80,82]. In humans, while we can observe similar labeling of affect for non-visual sensory sensation [13,51–53,56–58,62,84], processing of this information can occur independent of sensory-specific representation. Valenced sensory signals project to structures mediating modality-general representations of affect, including vmPFC/OFC, amygdala, ACC, and insular cortex [12,87,113], where dominant inputs are cortico-cortico projections rather than raw sensation [112,137]. Thus, we argue that pre-existing structures dedicated to processing valence-labeled sensory signals provide the foundation of modern affect-processing regions. Evolutionary expansion of structures dedicated to translating affectively informative sensation into adaptive behavioral responses has allowed them to integrate processed cortical information, indirectly related to an organism's future well-being, into the affective state of species with increased cognitive capacity [141,142].



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Figure 3. Affect Processing from Sensation across Species. While a general flow of affective information, from sensation to behavior, can be observed across all species, the dominant mechanisms of affect appraisal vary greatly. *Caenorhabditis elegans* (Chromadorea): sensation codes the adaptive value of the external world and can directly guide behavioral responses. Amphibia: sensory information is often processed in a modular manner, with limited pallio-pallial integration; behavior is guided largely by response to sensory stimulation. Amniota: note a distinctive increase in pallial connectivity with subpallial, thalamic, and other pallial regions. Reptilia: olfaction is the dominant input into the DVR (a putative pallial amygdala homolog). Aves/Mammalia: limited direct sensory information projects to affect-related structures, including the avian Wulst/DLP, the mammalian Ins/ACC/OFC and putative amygdalae homologs in both species. Mammalia (most notably primates): the role of the amygdalae, and other affect related structures, is more dedicated to processing cortical than sensory signals. Arrow width indicates the relative influence of the projection to processing in the receiving structure. The anatomical overlap between somatosensory cortex and motor structures in reptiles and birds (double compound arrow) is also observed in marsupials [159], further substantiating the inter-related nature of sensory signals and adaptive behavior. Note: these schematics are not intended to be an exhaustive description of all structures nor accurate depictions of the precise anatomical pathways involved in affect processing. Rather, they highlight the general propagation and integration of sensory and affective signals thalamic and select pallial regions across species. Notable omissions include pallial circuitry with the basal ganglia, optic tectum, nonpallial amygdala, as well as the unique patterns of projections/interaction observed for individual sensory modalities. In addition, note that these schematics do not account for variability within each presented phylogenetic branch. Abbreviations: ACC, anterior cingulate cortex; ArP/NP, nido/arcopallium; DLP, dorsolateral pallium; DP, dorsal pallium; DVR, dorsal ventricular ridge; Ins, insula; IP, infralimbic cortex; OFC, orbitofrontal cortex; Pal Amy, pallial amygdala; PL, prelimbic cortex; SC, sensory cortices (mammalian); SC*, sensory cortical homologs (housed in reptilian/avian DP) [160]; Sensation*, nonolfactory sensation; VP, ventral pallium. ^aProposed homologs to pallial amygdala in primates.

Consistent with its path of evolutionary development, we argue that the overall role of a brain region in guiding sensory behavior and modulating perception remains true to its ancestral utility. The current role of human amygdalae in relevance detection and value assessment, a role spanning multiple cognitive and sensory domains [111,112,137,139], and subsequent sensory modulation via dense connections with visual cortices [33,143], comprise an expansion of a system originally processing salient sensory (e.g., olfactory and auditory) signals [133,134,144] to facilitate feature prioritization across other brain regions. The role of human insular cortex in processing threat and distaste [24,44,145], both in the abstract and concrete form [90,146], as well as internal interoceptive well-being [106,145] stems from differentiating and expanding this structure's original role in processing sensation from proximal space. Accordingly, strong representations of gustation and somatosensation can be observed in neural homologs across species [24,147] and residual valence-labeled gustatory [24] and tactile [18,21,56,87] projections to insula are observed in humans. Similarly, the value-based decision making and pain representation subserved by vmPFC/OFC [38,45,148] and ACC [40,93], respectively, may descend from ancestral processing of valenced sensation and subsequent rapid behavioral modification and perceptual experience. The evolutionary adaption of these structures favoring a diversification of input have allowed their sensory-specific functions to generalize, resulting in amodal emotion-sensitive regions with functions consistent with modality-specific behavioral modulation. Through evolutionary scaffolding, the perceptual experience of specific exteroceptive sensation of objectively valenced objects has become the abstract cognitive states we consider emotions.

Concluding Remarks

In this paper, we have outlined a proposal about the nature of emotional experience. We reviewed evidence indicating that the prevailing view of emotional appraisal systems as inherently supramodal is insufficient to accommodate evidence from all sensory modalities. Valenced labeling of nonvisual sensory signals from as early as the sensory receptor [53,71], and subsequent projections to affect-related regions [1,43,88], indicate that many emotional processes are not entirely centrally mediated. Current theories of emotion conceptualize central domain-general signals as mechanisms for privileged integration of relevant sensory information into mostly modality-general emotional representations [3,6,25,114–116]. By contrast, we argue that emotional appraisal in the modern human also depends on a series of structures descendent from sensory regions dedicated to processing valenced sensory input. Moving forward, we believe that additional work should track the precise propagation of valenced sensory signals, both in humans and across species, as well as determine the impact of these signals on the modality general experience of emotion during both healthy and disordered mood states (see Outstanding Questions).

In our view, representations of valence-labeled sensation in emotion-processing regions are not an ancillary feature developed to inform centralized affect representation. Rather, they reflect the ancestral role of these structures; they are relics of a time when the experiences of sensory information and emotional-motivational states were one and the same. Thus, the experience of emotion we associate now with an amodal cognitive state may well be how our evolutionary ancestors experienced specific sensory events evoked by the external world.

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Outstanding Questions

To what extent, if at all, do signals of peripherally labeled affective information, which propagate through distinct labeled lines in the peripheral nervous system, integrate with signals of discriminative sensation prior to their projection to central emotion-processing structures?

Do emotion-related structures receive direct anatomical projections of valenced sensory information from peripheral receptors/thalamic nuclei, or are these signals mediated by additional cortical/subcortical relays?

Do valenced sensory signals exclusively inform representation of affect, or do they also inform representation of discriminative sensation in early sensory cortices?

How can more fine-grained comparisons of the links between valenced-sensation and instrumental behavior across species help elucidate the evolutionary history of human emotion?

Are the sensation-emotion-behavior pathways common to tetrapods grounded in the conservation of adaptive motor plans (e.g., withdrawal from all threat/harm) independent of sensory input? Or are they modality-specific behavioral responses (e.g., physical recoil from nociceptive input), which have been co-opted by multimodal or cognitive processes?

To what extent do peripheral signals of affective information influence modality-general experience of emotional states?

Can targeted stimulation of receptors coding valenced sensation be used to assist with treatment of clinical mood disorders?

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