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Emotions: form follows function

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Emotion research has been divided by debate as to whether emotions are universal in form or cognitively constructed. We review an emerging approach that focuses on function rather than form. Functional affective science suggests that the particular origin of an emotion is relatively unimportant; instead, emotions can be understood in terms of a rapidly deployed set of mechanisms that structure perception, cognition and behavior to facilitate goal fulfillment. Evidence from this approach suggests at least three major functions of emotion: sensory gating, embodying affect, and integrating knowledge toward goal resolution. These functions appear to be universal and automatically activated, yet also moderated by conscious representation and regulatory efforts.

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Introduction

The study of emotion is divisive because of the two seemingly contradictory positions that emotions are both universal and individually constructed. Proponents of universality argue that emotions arise from low-level biological systems that support action tendencies which are common across mammalian species [1]. This view emphasizes the distinctiveness and adaptive value of these 'core' or 'basic' emotions [2,3]. By contrast, proponents of constructed emotion argue that emotions arise from the interaction of visceral drives and conceptually derived context. This perspective allows for the breadth of human emotional experience at the expense of universality and functional distinctiveness [4•,5]. Evidence for both positions is mixed: while emotion expressions are similarly categorized across cultures [6], their associated action tendencies often overlap and can only be differentiated by inference from social context [7,8].

One resolution to this debate is to focus on the functions of emotions rather than opining about their origins. This functionalist perspective seeks to establish the basic mechanisms by which emotion affects perception, cognition, and behavior. Functionalist research may also inform universalist and constructionist theories of a particular emotion: the more ubiquitous and automatic an emotion processes is, the more it supports a universalist claim, whereas the more variable or culturally specific a response is, the more it supports constructivism [9•,10]. Such research has already revealed at least three central functions of emotion (Figure 1). First, emotions have a sensory gating function, regulating the breadth and focus of attention. Second, emotions have an expressive function, creating observable, embodied representations of internal states. Finally, emotions have a knowledge integration function, distilling complex representations into concrete action tendencies that facilitate goal resolution. While there are doubtless additional emotion functions, the aim of this article is to demonstrate how prioritizing function over form allows affective research to progress without creating divisive theoretical camps.

Function 1: sensory gating

Emotional arousal appears to alter perception by regulating sensory access to cognitive representation. Generally, arousal increases sensory throughput: in a recent study by Todd *et al.*, participants rated emotionally arousing images as more perceptually vivid, even after controlling for objective stimulus vividness such as image contrast or complexity [11]. These effects were more than subjective: emotion-evoked vividness (EEV) accounted for greater eye fixations to the images and predicted greater recall of stimulus details. Neurally, emotion engaged a common brain network supporting perceptual vividness: EEG analysis revealed that both objective vividness and emotion-evoked vividness contributed to a posterior cortical P2 component at around 200 ms, which was localized to the lateral occipital cortex, posterior insula, and amygdala using fMRI. As this effect was observed for both positive and negative images, EEV appears to be a general consequence of emotional arousal.

While EEV enhances perceptual processing of eliciting stimuli, it does so at a cost. In particular, emotionally salient targets appear to attract attention at the expense of peripheral information, in both spatial [12] and temporal [13] dimensions. Corroborating this idea, a recent attentional blink study demonstrated that emotional arousal led to poorer second target detection at short time intervals between targets, but improved detection at longer intervals [14]. Emotional arousal thus appears to have

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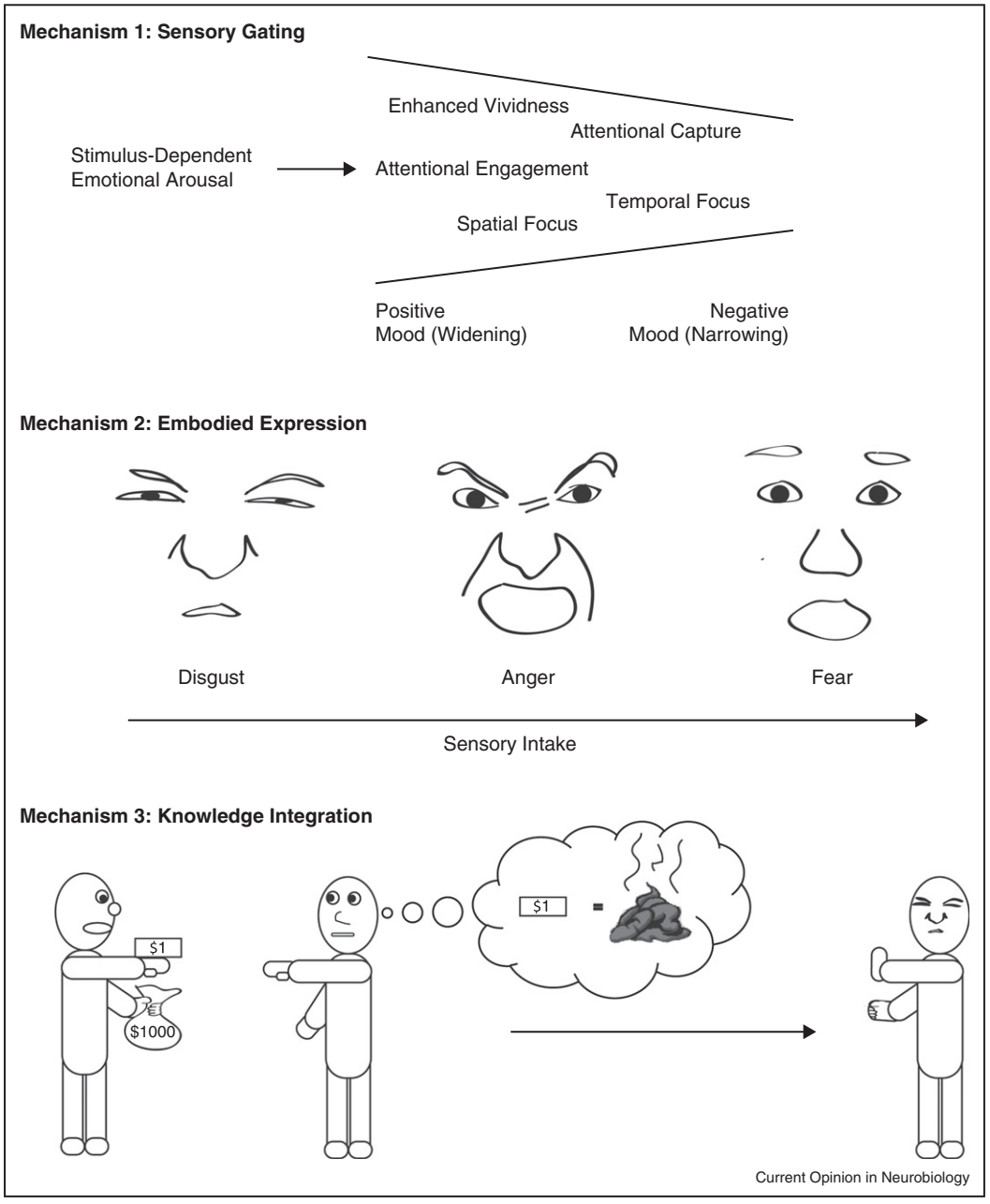
Figure 1



Three proposed universal functions of emotion. Top panel: emotions function to modulate spatial and temporal breadth of sensory input; both stimulus-dependent and stimulus independent, that is, mood, effects of emotion on sensory gating are apparent. Middle panel: emotions function to express internal states in a manner that facilitates other functions such as sensory gating, and such expression constitutes the emotional experience. Bottom panel: emotions serve to integrate complex social or conceptual representations into a single motivational context by relating these complex situations to concrete visceral action tendencies.

'targeting' effect on attention: it facilitates attentional capture in the presence of an appropriate target, and primes the attention system to engage with targets during periods of vigilance.

While peripheral details tend to be ignored in the presence of an emotionally salient stimulus, this effect is moderated by stimulus-independent valence, that is, mood. Behaviorally, positive and negative emotions appear to promote attentional broadening and narrowing, respectively [15•,16,17••]. Mechanistically, a recent fMRI study by Schmitz *et al.* demonstrated that peripheral encoding of scenes in the parahippocampal place area (PPA) was dependent on earlier exposure to positive or

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negative images [18]. While participants focused on centrally presented faces, positive mood was associated with increased processing of unattended peripheral scenes in the PPA, and increased connectivity between primary visual cortex and the PPA. Negative mood had the opposite effect, reducing PPA responses and visual cortex connectivity.

Mood-dependent gating of attention has important functional consequences. Consistent with the neural evidence, positive mood induction increases iconic memory storage [19], suggesting that positive emotions improve the ability to rapidly and stably represent perceptual details. While these positively evoked enhancements are adaptive for exploration or problem solving, they also allow for more incidental encoding of distracters in tasks optimized for vigilance and focus [20,21]. Conversely, negative mood may help individuals to resist such distraction, yielding greater attentional focus to threat stimuli such as a snake lying in the grass [22]. On the other hand, negative moods lead to greater self-focused attention, which may increase attention to distressing information such as negative physical symptoms [23]. The adaptive value of emotion-evoked sensory gating is therefore dependent on its fit with contextual demands.

Function 2: embodied expression

In addition to modulating sensory input, emotions are expressive, reflecting internal feeling states through observable embodied representations. By internal feeling states, we mean states that are cognitive and/or physiological in nature, whereas embodied representations take place at the level of musculature, posture, or behavior. Consistent with a connection between internal states and embodied representations, conceptual priming of emotion words has been linked to distinct expression-congruent EMG responses for happiness, anger and fear [24,25]. Furthermore, considerable evidence suggests that embodiment of emotions is constitutive of emotional experience rather than a downstream expressive byproduct. For example, nonverbal auditory emotional stimuli result in emotion-congruent facial expressions and subjective emotion, but inhibiting facial expression impairs recognition of emotion and induction of stimulus-congruent mood [26,27]. Reducing sensory feedback from the facial muscles via Botox injections appears to impair recognition of facial emotion in others, whereas increased feedback via a resistant gel mask enhances recognition [28••]. Voluntary facial muscle contraction modulates subjective emotion experience, with lowered eyebrows promoting more negative mood, raised eyebrows leading to more surprise at hearing unusual facts, and wrinkling one's nose leading to rating aversive odors as more unpleasant [29]. Subliminally presented facial expressions influence ratings of picture positivity or negativity, but such priming only occurs when movement of the observer's facial muscles is unobstructed, suggesting that embodiment may implicitly inform subjective emotional experience [30].

In addition to arguing that embodied expressions reflect and contribute to internal experience, the functionalist perspective posits that embodied expressions are not arbitrary — a smile looks different than a scowl because such diversity in expression promotes discrete adaptive functions [9•,31]. For example, Susskind *et al.* demonstrated that disgust and fear expressions support a second, more physical form of sensory gating [32••]. Fear expressions are constituted by a host of physical changes that increase sensory intake to aid in the detection of physical threats, such as increased visual field size, velocity of nasal inhalation, and speed of saccadic eye movements. Conversely, disgust expressions are characterized by opposing effects on vision and respiration, consistent with physically inhibiting the intake of noxious substances, consistent with theories positing that disgust is a disease-avoidance mechanism [33].

Anger is a third category of emotion with a relatively discrete expression and function. Like fear, anger increases attention toward a target [34]. However, anger is distinct from fear in that it focuses attention specifically on a target, whereas fear appears to focus less on the target itself, instead widening attention to take in the surrounding context. In its expression, anger is associated with a narrowing of eyes relative to fear, potentially supporting this attentional narrowing. Narrowed eyes may also have a social communicative function: where wide eyes, as in a fear expression, appear childlike and non-threatening, narrowed eyes in a dominant angry individual may make them seem more mature [35]. The approach orientation of anger gives it commonality with other emotions such as surprise and enjoyment, whose tonic elevations all appear to reduce defensive startle reactions to maintain fixation on sensory stimuli [36].

Thus, mounting evidence suggests that one reason emotions such as happiness, fear, disgust, and anger are consistently physically expressed is that they are functionally constrained. First, affective facial expressions appear to contribute to sensory gating effects on a physical level. Second, expression mimicry appears to occur automatically and facilitate emotion recognition. This embodiment of perceived emotion then influences affective judgments, helping to organize conceptual knowledge representation.

Function 3: adaptive knowledge integration

Affective processes that act upon perception and expression are complemented by organizational effects on cognition. By linking cognition to concrete action tendencies, emotions lend motivational relevance to complex or ambiguous situations [37]. For example, when one auditory tone is associated with reward and another with

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punishment, ambiguous tones tend to be treated as threatening rather than rewarding [38,39], suggesting an automatic prioritization of threat avoidance in the face of environmental ambiguity. Extending beyond cases of sensory appraisal, emotions ground higher order social and conceptual knowledge with a sense of motivational value [40]. For example, Chapman *et al.* observed that gustatory disgust, as elicited by unpleasant tastes, basic disgust, as elicited by photographs of contaminants, and moral disgust, as elicited by unfair economic offers, all activated the same facial muscle expression, namely the levator labii muscle region of the face responsible for the characteristic disgust nose wrinkle [41]. This finding suggests that the abstract notion of justice may be constituted by emotional processes for concrete, visceral disgust, an idea supported by behavioral studies demonstrating that disgust experiences prime moral judgments [42,43].

By shaping the motivational value of abstract knowledge to match concrete affective values, emotions allow for rapid responses to complex social situations. This functional perspective is distinct from hedonic theories of emotion which argue that emotions act simply to promote the pursuit of positive feeling states [44••]. It follows that adaptive cognition and behavior are determined by a person's ability to flexibly and accurately map complex situations onto emotions: people low in the ability to correctly identify affective expressions demonstrate a link between somatic stress sensations and subsequent depressive symptoms, whereas those high in discrimination ability do not [45]. Conversely, people with high stress resilience show greater ability to flexibly change emotional expressions to match environmental context than those with low stress resilience [46]. In a recent EEG study, flexible matching of expressive responses to auditory affective stimuli was only visible in participants with a left > right alpha asymmetry, associated with tonic positive or approach related affect [47], but not in those with a right > left asynchrony, which has been associated with a depressive 'affective style' [48]. Individual differences in flexibility may be partially determined by genetic factors: serotonin transporter mutations appear to predict greater emotional reactivity [49] with an inflexible negative attentional bias [50], which when combined with external life stressor may predict dyspohric affect [51]. Indeed, clinical psychopathology is in many instances characterized by inflexibility of emotion-induced processing heuristics: mania may be an inability to shift from a focus on immediate reward outcomes toward future expectations [52], sadness-induced rumination may predict relapse risk in depression [53], and anxiety has been shown to make police officers more threat-expectant and less responsive to actual threat information [54].

If flexibility in affective knowledge representation is important for well-being, then how is such flexibility facilitated? One possibility is that flexibility can be promoted through reconnecting with embodied expressions. For example, the act of physical cleansing may broadly embody absolution from both physical and mental corruption, leading to a reduction of competing emotional conflict [55•]. In a study by Farb *et al.*, depressive affect was related to reduced viscerosomatic body representations in the right insula following emotional challenge. Recovery of interoceptive tone following meditation training was associated with lower depressive symptoms [56•]. Indeed, interoceptive attention to the body's momentary sensations may serve to re-engage affective knowledge reorganization processes, reducing processing of negative stimulus as measured by EEG [57]. By appealing to interoceptive sensation, the activity of inflexible habitual cognitive systems may be supplanted by activation of an interoceptive attention network allowing for viscerosomatic feedback from embodied emotion expressions [58,59]. Interoceptive awareness itself may be improved through training practices such as dance or meditation [60], of which the latter appears to improve both tonic and phasic access to this interoceptive network [61]. Functionally, such training has been shown to attenuate negative appraisals associated with painful stimulation, allowing participants to disengage from conceptual appraisal that may lead to habitual negative emotional reactions [62]. In this way, voluntary access to embodied affective expressions may counter-intuitively lead to a shortened time course of negative emotion, allowing for immediate expression and resolution of negative emotional responses. Thus, adaptive emotion expression allows for both the efficient recruitment and release of motivationally relevant knowledge.

Concluding remarks

The functional approach offers a framework for investigating the form and function of emotion without assuming the universality or cognitive construction of emotion states. Focusing on particular functions of affective processing appears to fruitfully advance our understanding of emotion, introducing concepts such as sensory gating, embodied expressions, and motivated knowledge representations. While this approach is still nascent, it offers a common methodological discourse for human affective science, elucidating how emotions affect how we see the world, how we react to these perceptions, and how we learn to respond to complex feelings and ideas through reference to these basic perception-expression dynamics.

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