How Do Humans Perceive Emotion?

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Abstract

Emotion carries crucial qualities of the human condition, representing one of the major challenges in artificial intelligence. Research in psychology and neuroscience in the past two to three decades has generated rich insights into the processes underlying human emotion. Cognition and emotion represent the two main pillars of the human psyche and human intelligence. While the human cognitive system and cognitive brain has inspired and informed computer science and artificial intelligence, the future is ripe for the human emotion system to be integrated into artificial intelligence and robotic systems. Here, we review behavioral and neural findings in human emotion perception, including facial emotion perception, olfactory emotion perception, multimodal emotion perception, and the time course of emotion perception. It is our hope that knowledge of how humans perceive emotion will help bring artificial intelligence strides closer to human intelligence.

Keywords

emotion perception; faces; smells; time course; neural basis

1 Introduction

While computers and artificial intelligence have assumed the supreme power of computation and "reasoning" (in some aspects such as chess and go) that excels even the finest human mind, they crumble at the simplest task that a toddler can instinctually perform—emotion perception. Whether they are purposeful products of evolution to serve adaptive functions or mere vestiges as energy spillover during physiological shifts [1], [2], emotional expressions are salient social cues in everyday interactions, communicating one's emotional states and action tendencies to conspecifics [3]– [5]. Social bonding and communal behavior via emotion (known as "emotional contagion"; Hatfield, 1993) have the capacity to reach millions of people and last over decades [6], [7]. Simply put, emotion is a critical ingredient of the human condition, imbuing it with richness and sensibility [8]. Such importance and utility of emotion has compelled artificial intelligence to incorporate emotion and feelings into neural networks and robotic systems [9].

To the extent that such efforts are encouraging and some promises are on the horizon, emotion communication is such a complex system that all endeavors so far have fallen short. While artificial face recognition has advanced greatly in the field, reaching remarkable accuracy and speed, artificial emotion perception still lags behind. Emotional expressions are often transmitted and synchronized with such potency and speed that any other stimuli would pale in comparison [10], [11]. For instance, encoding of facial expressions or emotional gestures in the receiver can consummate as early as 100 ms [12]–[17], preceding the latency for structural encoding of faces (~ 170 ms) [18], [19].

This paper will discuss how this seemingly extraordinary feat is achieved, quite effortlessly, in humans, in hopes that such knowledge will inform and inspire the research of artificial emotion perception. Given its obvious advantage and dominance in emotion communication, the discussion will focus on facial emotion perception. Nevertheless, emotion is communicated through multiple sensory channels. Chemical information, such as smells and pheromones, may provide pivotal and sometimes indispensable information to mediate emotion communication. Therefore, the review will discuss emotion perception via the olfactory channel and how multiple modal cues are combined in emotion perception. To account for the remarkable speed of emotion perception, the time course of emotion perception will be described with a special focus on early processes. The review will end with a discussion of sensory cortical encoding of emotion, which could provide particularly useful insights into computation modeling of emotion perception.

2 Visual Emotion Perception

Faces are inherently salient, emotion-relevant stimuli such

that even "neutral" faces would be emotionally charged due to its race, gender, eye gaze, attractiveness, and so on. Accordingly, faces often attain preferential perception compared to other objects [20]. Highlighting an innate advantage in face perception, human newborns prefer tracking faces to non-face objects [21], [22]. Infant monkeys reared with no exposure to any faces also prefer looking at human and monkey faces than non-face objects [23]. Notably, these stimuli are controlled for basic visual properties, such as contrast, complexity and spatial frequency, to exclude any possible confounds due to physical disparities.

Dubbed as the "face in the crowd" effect [24], faces containing threat emotions such as anger and fear receive particularly privileged perceptual analysis, often "popping out" from a crowd of faces containing neutral or happy emotions, showing faster reaction times and higher accuracy in face detection and discrimination [25], [26]. This effect is particularly consistent across studies using schematic faces but relatively controversial when photos of real faces are involved [27], which could be ascribed to the fact that schematic faces are generally deprived of information related to race, gender, attractiveness and so on, i.e. the factors that are rich in real face photos but impoverished in schematic faces [27]. Indeed, studies that attempt to reduce such effects tend to support this face in the crowd effect [28] as opposed to studies lacking such face control [29], [30].

Recent studies further suggest that this acute emotion perception not only differentiates threat from non-threat (neutral or positive) stimuli (along general dimensions of affective valence/arousal; Russell, 1980), but is also capable of dissociating individual basic emotions (Ekman, 1992), even within the domain of threat (e.g., fear, disgust and anger). During basic perception, fear purportedly elicits an immediate "stop-look-and-listen" response to facilitate sensory acquisition in order to guide action (e.g., fight or flight; Gray, 1987), while disgust provokes instant sensory rejection to prevent poison or contamination from entering the organism [31]. These opposing sensory tendencies align with the contrary biomechanical properties in facial expressions of fear and disgust. That is, wheareas fearful faces are characterized by widened eyes and nostrils, which augment visual and olfactory sensory intake, disgust faces are represented by narrowed eyes and nostrils, which restrict sensory intake (Susskind et al., 2008). Critically, these opposing sensory responses have been repeatedly demonstrated in our lab [32]–[34] and others (Liu et al., 2015); fear-evoking scenes/faces enhance whereas disgust-evoking scenes/faces suppress visual event-related potentials (ERPs; e.g., the P1 component, an early visual ERP peaking around 100 ms) and concomitant extrastriate cortical activity.These findings highlight the ecological adaptiveness inherent in emotion perception, promoting biologically appropriate actions with minimal delay.

Neuroscience research in the past few decades has provided important insights into mechanisms and processes involved in encoding and recognizing emotional expressions. As summarized in recent meta-analyses of neuroimaging studies, substantial evidence implicates limbic/paralimbic structures, especially the amygdala and, to a lesser extent, the anterior cingulate cortex and ventral medial prefrontal cortex/orbitofrontal cortex, in processing facial expressions [35], [36]. These regions appear to be nodes shared by the emotional brain [37] and the social brain (Adolphs, 2009), akin to their roles in processing socially relevant emotional information. Notably, these regions are also responsive to emotional vocalization (e.g., laughter and screams [38]; and emotional touch [39], [40], representing a core system supporting amodal, abstract emotion analysis and evaluation. As for the processing of specific (vs. general) emotions, data to date are not as conclusive. Nevertheless, fairly clear consensus has emerged for fear and disgust facial expressions, which reliably activate the amygdala and insula, respectively [35], [36]. In keeping with that, perception of fear and disgust vocalizations also depends on these same structures [41], [42].

While emotion research has focused primarily on limbic/paralimbic structures, accruing evidence also isolates a highly associative, heteromodal sensory cortex—the superior temporal sulcus (STS) [43]; STS is a conventional multisensory zone, involved in vision, audition and somatosensation [44]. Importantly, it has been implicated in the social neural network [45], processing sophisticated social cues to infer other people's mental states (e.g., theory of mind) [46], [47]. Accordingly, the STS is found to play a critical role in the perception of facial expressions, especially dynamic ones [48]−[50]. Furthermore, the STS exhibits specialized response patterns for facial expressions of the basic emotions (anger, disgust, fear, sadness, happiness, and surprise; Ekman, 1992) and supports highly integrated analysis of subtle differences in emotional expressions [47]. Representing a key voice-processing area [51], the STS also participates in assessing emotional vocalizations [52]. Lastly, the importance of the sensory cortex in supporting emotion perception, independently of limbic input, has been increasingly recognized [53]−[55].

3 Olfactory Emotion Perception

As summarized above, emotional expressions are typically considered to be transmitted through faces and (to a lesser extent) posture, vocalizations, and touch, with research interest predominantly dedicated to facial expressions. However, are chemical senses involved in emotion communication as well? Are chemical signals (chemosignals) of emotion processed similarly as physical signals?

A large body of literature documents emotion communication via chemical stimuli (odors and pheromones) in non-primate animals [56], [57]. In these animals, olfaction is the most crucial sensory channel, purportedly principally involved in effectively detecting, locating, and identifying reward and threat

in the environment [58]. Accordingly, vital biological information is transmitted among conspecifics via olfaction, informing food or poison, mate or predator. In humans, olfaction is deemed as a minor sensory system, and humans are considered microsmatic [59], presumably due to Lamarckian disuse of the olfactory sense. Nevertheless, this microsmia notion has been challenged by recent work, documenting the remarkable capacity of human olfaction at both neuronal and behavioral levels [60]−[63]. Furthermore, the olfactory system is intimately associated with the emotion system: odors provoke potent emotional responses in people [64], [65], and the neuroanatomy of olfaction and emotion is intricately connected as in macrosmatic animals [66], [67]. Indeed, infinitesimal amounts of odors (as low as 7 ppt) can be processed by the human olfactory system (albeit subliminally), thereby modulating affective processing of faces [68], [69]. Lastly, the human body constantly secretes chemicals, which vary in intensity and chemical composition with internal/endocrine states and interactions with resident bacteria (primarily, in axillary areas and genitalia [70]. Owing to this close association with the host's emotional and physiological states, these chemical excrements can carry potent information about momentary emotion and intended/prepared action. Overall, the special faculty of olfaction promises the significance of this chemical sensory system in social communication of emotion.

Accruing evidence indeed suggests that humans perform similar chemical communication of emotion as other animals. Human body odors and fluids carry certain genetic information such that by smelling these chemicals, the receiver can determine his/her genetic compatibility [71], [72] and kinship [73]−[75] with the sender, thereby preventing inbreeding while enhancing nepotism. Similar to chemosensory-based avoidance of sick conspecifics in other mammals [76], a new study shows that when people are sick, their body odors change, becoming more unpleasant and unhealthy to other people [77]. In addition, people can detect or differentiate elevated arousal [78], [79] as well as specific emotions (happiness, fear, disgust and anxiety; Ackerl, Atzmueller, & Grammer, 2002; Chen & Haviland‑Jones, 2000; de Groot, Smeets, Kaldewaij, Duijndam, & Semin, 2012; Pause, Ohrt, Prehn, & Ferstl, 2004; Prehn-Kristensen et al., 2009) by smelling axillary sweat. Interestingly, familiarity between the sender and the receiver enhances recognition of emotion conveyed in body odors (Ackerl, Atzmueller, & Grammer, 2002; Chen & Haviland‑Jones, 2000; de Groot, Smeets, Kaldewaij, Duijndam, & Semin, 2012; Pause, Ohrt, Prehn, & Ferstl, 2004; Prehn-Kristensen et al., 2009).

In terms of underlying neural basis of chemosignaling of emotion, evidence is fairly scarce. Nevertheless, the extant neuroimaging data largely converge on limbic participation in emotion communication via chemosignals [80], conforming to emotion communication via other sensory signals. Specifically, body odors conveying potential threat evoke strong response in the amygdala [78], [81]−[83]. In general, the extant literature

combined with long-standing animal research suggests that human olfactory emotion communication represents a highly valuable research subject and, potentially, an emerging frontier of the field.

4 Multisensory Integration of Emotional Signals

As emotional expressions are communicated via multiple senses, and very often simultaneously (e.g., a terrified face being accompanied by a shaky voice, tense posture, and quite likely, a particular body odor), a natural question becomes how multisensory emotional signals are integrated in social communication. For either neural activity or consequent behavior, an organizing principle is that inputs from multiple senses converge and interact in a variety of brain structures, supporting highly coordinated responses [84], [85]. In fact, organisms as primitive as a progenitor cell integrate information from multiple senses to optimize perception; moreover, this synergy is especially prominent with minimal sensory input, facilitating signal processing in impoverished or ambiguous situations (known as the principle of "inverse effectiveness" [86]. Conceivably, multisensory integration of emotional expressions would afford a special ecological advantage by facilitating communication of salient information, especially when such activity is impeded by various sensory barriers (e.g., darkness, distance or background noise) or suppressed in special situations (e.g., communicating with a hostage under close watch). While pertaining primarily to integration between visual and auditory senses, research in the past decade has shed some first light on the mechanisms underlying multisensory integration of emotional expressions [87], [88]. Akin to its role in processing of emotion and its multimodal connections (via dense bidirectional fibers linking all sensory cortices) [89], the amygdala has emerged as a key convergence/integration area in this literature. Furthermore, the STS (particularly, the posterior STS) has also been isolated as a key site for multisensory convergence of emotional expressions [87], [90]. As mentioned above, the posterior STS is long known as a key multisensory convergence zone, largely due to the multimodal (visual, auditory and somatosensory) neurons in this region and dense fibers connecting it to different sensory cortices [84], [91]−[93]. Also, functional connectivity analysis suggests that the STS not only engages in integrating emotional expressions across modalities (between faces and voices) but also gates synthesized sensory input to the amygdala [94]. Given the modest size of this literature, however, it remains unclear whether multisensory integration of discrete emotional expressions would recruit distinct or shared convergence areas and mechanisms.

Another problem yet to be explored is integration of emotional expressions between physical and chemical senses. A wealth of behavioral data evinces active visual and olfactory interaction in information processing [95]−[98]. Evidence further

suggests that synthetic or body odors can improve perception of visual social signals including facial expressions [14], [99]–[101]. However, neural evidence in this regard is rather limited, and preliminary evidence suggests that the insula and orbitofrontal cortex are involved in integrating emotional signals in faces and synthetic or body odors [102]–[104]. However, due to the relative anatomical segregation between the physical and chemical sensory systems, it is likely that a fairly intricate neural network would be recruited in integrating social signals of emotion between these two systems. Indeed, in contrast to crossmodal auditory-visual integration that may takes place at early sensory corticies [105], visuo-olfactory integration of emotion favors a top-down (vs. bottom-up) account of crossmodal integration in higher-order brain areas [104].

5 Stages of Emotion Perception

As aforementioned, emotion perception is marked by its extraordinary speed, taking as little as 100 ms to isolate facial expressions. How does the process of emotion perception unfold over time? Starting from a highly prominent two-stage model of early "quick-and-dirty" and delayed, elaborate processing of threat information [106], the emotion literature has expanded to support a complex system involving multiple stages and processes, mediated by distributed, parallel neural pathways [11], [107], [108]. Several influential cognitive theories converge on a parsimonious model of three stages—an orienting mode, a primal mode and a metacognitive model—operating in sequence over time [109], [110]. In general, predominant charges for these three stages are feature detection, significance evaluation, and conscious threat perception, respectively [111], [112]. During the first stage, an external stimulus registers with the "feature detectors" in a nonconscious, automatic fashion. These detectors isolate signal features of biologically significant stimuli, which then triggers the nonconscious "significance evaluator." Confirmation from the significance evaluator turns on the third stage: controlled, strategic processing of the stimulus, generating conscious threat perception. Notably, Ohman's model also emphasizes that autonomic arousal is directly activated by feature detectors, which provides input to facilitate significance evaluation and conscious threat perception.

Empirical evidence from human neuroscience research aligns with this multi-stage view. Brain electrophysiological (mainly ERP) research has leveraged on its precise temporal resolution to delineate the time course of information processing of emotional stimuli on the scale of milliseconds. Findings from this research implicate three temporal stages of emotion processing [11], [107], [113], [114]. The first stage, indexed by the P1 component, represents sensory processing of emotional stimuli in the low-level, occipital visual cortex. The second stage, indexed by the N1/N170 components (onset ~170 ms), entails intermediate-level, configural perceptual analysis in

the temporal visual cortex. The third stage, indexed by the P3/P300 and late positive potential (LPP) components (~300 ms and beyond), reflects high-level, cognitive and motivational processes. During this stage, emotion processing engages memory-based, goal-oriented operations, often culminating in conscious perception of the stimuli and volitional behavioral response. Broadly speaking, this sequence of electrophysiological events corresponds really closely to the three main stages of the cognitive models above.

Pertinent to the perception of threat specifically, a recent study in our lab acquired fear detection rates and ERPs to parametrically varied levels of fearful expressions along a morphing continuum [115]. To provide further insights into the specific cognitive mechanisms involved at different stages in threat perception, we decomposed the threat processing by combining psychometric and neurometric modeling. Building on the psychometric curve marking fear perception thresholds (e.g., detection, sub- and supra- threshold perception), neurometric model fitting identified four key operations along the information processing stream (**Fig. 1**). Unfolding in sequence following face presentation, these four psychological processes are: 1) swift, coarse categorization of fear versus neutral stimuli (~100 ms, indexed by the P1), 2) detection of fear by picking up minute but psychologically meaningful signals of fear (~320 ms, indexed by the P3), 3) valuation of fear signal by tracking small distances in fear intensity, including subthreshold fear (400–500 ms, indexed by an early subcomponent of the LPP), and lastly 4) conscious awareness of fear supporting visibility of suprathreshold fear (500–600 ms, indexed by a late subcomponent of the LPP). Furthermore, as the processes became progressively refined over time, they were also increasingly linked to behavioral performance (i.e., fear detection rates; Fig. 1d, bottom row). Specifically, from the first to the last operations, within-subject brain-behavior association grew from no association, to weak, then moderate, and finally strong, respectively.

Overall, these findings provide specific descriptions and temporal profiling of threat processing stages. The first operation—broad threat-non-threat categorization—would correspond to the orienting mode in threat processing, which automatically tags the stimuli as threat or non-threat. Such gross categorization (at the P1 window) concurs with standard object categorization (e.g., natural vs. domestic scenes) [116]. This finding also aligns with the notion that emotional stimuli can elicit rapid emotion categorization based on automatic, bottom-up sensory input [117], [118], coinciding with Ohman's idea of "feature detectors" that isolate threat-relevant signal features [111], [112]. This significance detection then activates salience-driven bottom-up attention and the brain's salience network, which switches on other networks to start resource allocation (via attention and working memory) and goal-driven processes in the subsequent stages [119]–[121].

The second and third operations—threat detection and valuation—would largely fall into the primal mode as the interme-
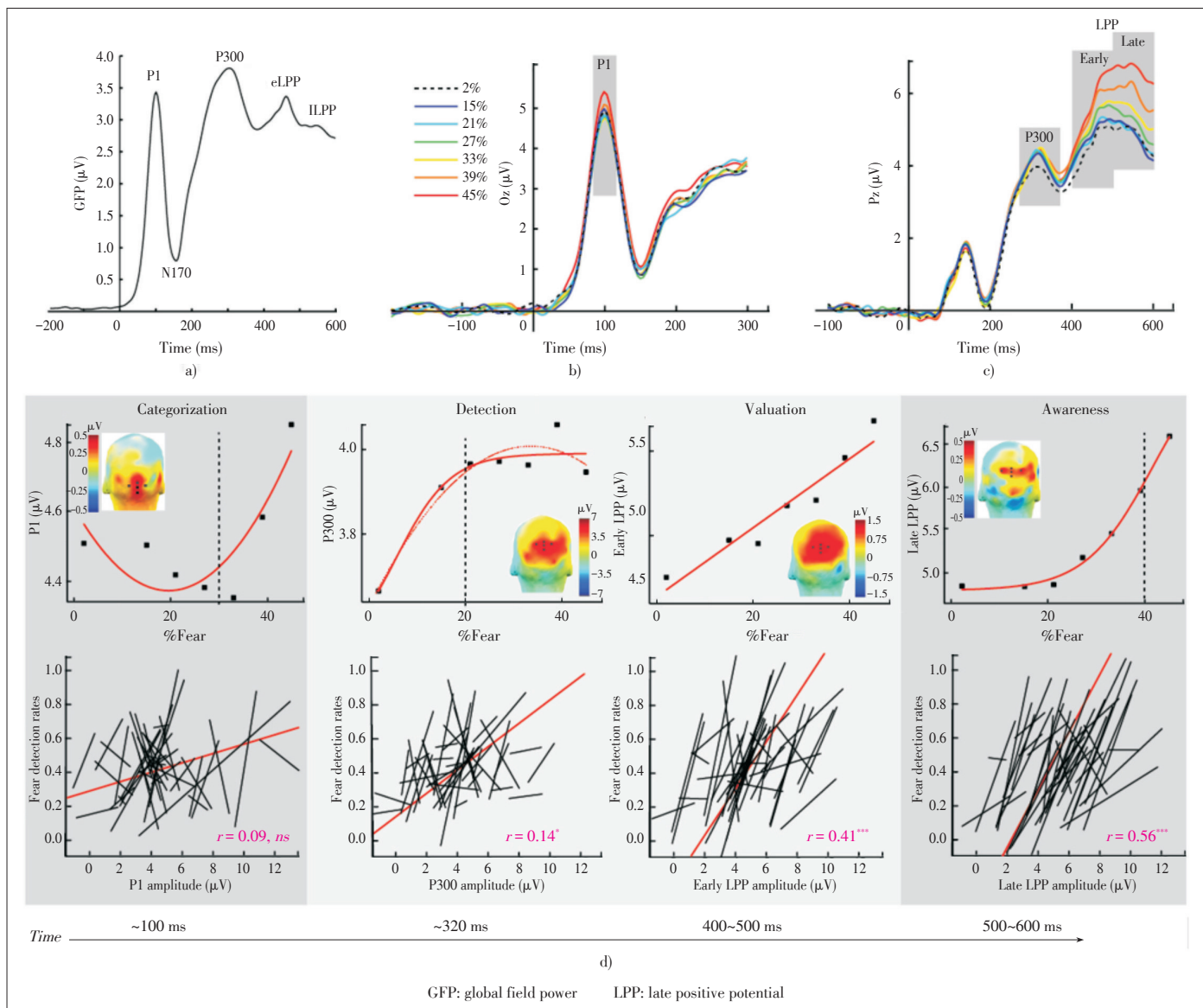
▲Figure 1. The time course of human emotion perception. a) The GFP demonstrates five critical ERPs evoked by faces. b) Evoked P1 at the occipital midline by the neutral face and six levels of fear (15%−45% in increments of 6%). c) Three ERPs evoked at the parietal midline by the faces. d) Psychometric and neurometric modeling of fear detection performance and ERPs in a fear detection task maps out four key operations unfolding in sequence, emotion categorization, detection, valuation and conscious awareness. Adapted from Forscher et al., 2016.

diate-level threat analysis. As illustrated in Fig. 1, the neural detection threshold aligns with the inflection point (25% fear) of the psychometric function, and the strength of this neural response is significantly (though only weakly) predictive of fear detection rates, suggesting somewhat reliable threat detection at this stage. The third operation is more sophisticated and advanced, linearly tracking the intensity of fearful expressions and directly predicting behavior performance ($r = 0.41$). The last operation brings about conscious awareness, corresponding closely to the metacognitive mode, where consciousness of threat emerges and conscious processes ensue. In keeping with that, this last operation accounts for a remarkable 31% of the total variance of the behavioral output.

Compared to the later operations (especially threat valuation and awareness), the first operation (threat tagging) does not show a relation with the behavior. This finding underscores the idea that the orienting mode is likely to be elusive to behavioral observation. Many creative paradigms (e.g., emotional Stroop, dot-probe, visual cueing, and visual search) have been used to isolate early operations in threat processing, but as pointed out early in the field, behavioral measures from these tasks are inevitably confounded by operations from multiple stages [122]. By virtue of the rapid development of neuroscientific methods, especially brain electrophysiology technologies,

relatively pure measures of the orienting mode have become viable.

6 Conclusions

The field of artifical intelligence has progressed in leaps and bounds over the past decade. How artifical intelligence can become truly intelligent, taking possession of the human condition, has been the holy grail of the field. In the search of the human psyche, knowledge of reasoning and cognition had preceded the understanding of emotion. Now, growing insights into human emotion and emotional processes, such as emotion perception, have issued cordial invitaitons to computer scientists to adopt emotion-related models and paradigms into artifical intelligence. The future is ripe, tarry not.

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Biography

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