

Emotion in the perspective of an integrated nervous system¹

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1. Neglecting emotion and missing the integrated view

It would not be possible to discuss the integrative aspects of brain function without considering the operations that arise in large-scale neural systems; and it would be unreasonable not to single-out emotion among the critical integrative operations arising in that level. Yet, throughout the twentieth century, the integrated brain and mind have often been discussed with hardly any acknowledgment that emotion does exist, let alone that it is an important function and that understanding its neural underpinnings is of great advantage. There are numerous reasons behind the benign neglect of emotion and I cannot mention them all and much less discuss them. In general, however, it seems fair to say that emotion must have seemed both too elusive and too subjective to attract the interest of neuroscientists or cognitive scientists concerned with researching that which appeared most concrete and objective.

It seems clear now that there is nothing more elusive about emotion than about, say, perception or memory—in fact less so, in my opinion—and it is equally clear that emotion is also no less objective. In the event, however, it did seem more elusive and less objective than other cognitive and behavioral phenomena. Perhaps this was so be-

cause, in post-Cartesian and especially post-Kantian approaches to mind, emotion came to be regarded as the very antithesis of one good thing called reason. And who would want to spend a lifetime attempting to understand the very opposite of one good thing? Many nineteenth century creative thinkers actually did, as it turns out, and many others do again, now, but only a handful did, in between. Of those who did, one hundred and some years ago, Charles Darwin, William James, and Sigmund Freud, loom large.

The neglect suffered by emotion during most of the twentieth century has some curious parallels. The first parallel is the lack of an evolutionary perspective in the study of brain and mind. By and large neuroscience and cognitive science have proceeded as if Darwin never existed. The situation is now changing remarkably, in the neurosciences, and some would say that it is changing far too much and not too well within cognitive science itself. It is one thing to try to illuminate a theory by looking at a possible evolutionary account for a given phenomenon, it is another to explain current aspects of cognition in exclusive evolutionary terms, especially when the explanations cannot be subject to any empirical verification.

The second parallel concerns the disregard for the notion of homeostatic regulation in the sciences of mind and brain. This does not mean, of course, that there were not numerous scientists preoccupied with understanding the neurophysiology of homeostasis; the neuroanatomy and

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the neurochemistry of the autonomic system; the mechanisms of neuroendocrine regulation; or the interrelation between nervous system and immune system. But the scientific progress made in those areas was not used to modify the prevailing views of how mind or brain worked. The importance of this point is probably best made by considering the recent exceptions to this state of affairs, for instance in the role accorded to homeostatic value in Gerald Edelman's neural models [7,8], or in my own somatic marker hypothesis [4,5].

A third parallel is the prevalent absence of a notion of organism in the sciences of mind and brain. It is not just that the mind remained linked to the brain in a rather equivocal relationship, but that the brain remained consistently separated from the body and thus not part of the deeply interwoven mesh of body and brain that defines a complex living organism. Again, the notion of organism was available, e.g., Goldstein [9]; Weiss [11], but it was rarely used.

Has anything been missed by the neglect of emotion? The answer is yes, unequivocally. Let us consider the following:

1. First, emotion and the experience of emotion, are the highest-order direct expressions of bioregulation in complex organisms. Leave out emotion and you leave out the prospect of understanding bioregulation comprehensively, especially as it regards the relation between an organism and the most complex aspects of an environment: society and culture.
2. Second, emotion is critical for survival in the complex organisms equipped to process it. Since disorders of emotion can kill, in animals or humans, would one not wish to know how emotion works?
3. Third, emotion plays a role in memory and understanding memory happens to be one of the main goals of neuroscience and cognitive science. Memory is a property of living systems that are bent on survival and, in complex organisms, these two functions, emotion and memory, are so closely coupled that one cannot fully understand the latter without the former.
4. Fourth, emotion plays a role in reasoning and decision-making, from the simple decisions that animals make to avert danger or to endorse an advantageous encounter, to the more complex decisions that we humans can consider. Making sense of the mechanisms behind the finest human achievements —high-reason, ethics, law, artistic, scientific and technological creativity— cannot proceed without an understanding of emotion.

In terms of fundamental science, we probably cannot develop a comprehensive, integrated view of the human brain and mind, if we do not turn emotion into an important topic of investigation. In practical terms, it pays off to understand emotion better — disorders of emotion are a leading cause of human suffering, from those conditions triggered by acquired brain damage to those, such as mood disorders, whose genetic and developmental origin is less

well elucidated. Fortunately, the entire attitude towards emotion has begun to change.

In the pages ahead I provide a brief summary of recent theoretical and factual progress in the neurobiology of emotion. Because so many new findings are being reported, from varied approaches, I will focus my comments on work in humans and only at the large-scale systems level.

2. Emotion and feeling

The terms emotion and feeling are usually used interchangeably but I have suggested that they should not be. From a research perspective it is advantageous to use separate terms to designate separable components of this enchainned process. The term emotion should be rightfully used to designate a collection of responses triggered from parts of the brain to the body, and from parts of the brain to other parts of the brain, using both neural and humoral routes. The end result of the collection of such responses is an *emotional state*, defined by changes within the body-proper, e.g., viscera, internal milieu, and within certain sectors of the brain, e.g., somatosensory cortices; neurotransmitter nuclei in brain stem.

The term feeling should be used to describe the complex *mental state* that results from the emotional state. That mental state includes: (a) the representation of the changes that have just occurred in the body-proper and are being signaled to body-representing structures in the central nervous system (or have been implemented entirely in somatosensory structures via 'as-if-body-loops'); and it also includes (b) a number of alterations in cognitive processing that are caused by signals secondary to brain-to-brain responses, for instance, signals from neurotransmitter nuclei towards varied sites in telencephalon.

Both emotions and feelings are amenable to investigation, all the more so if their sequential and concurrent functional components can be relatively individualized for analysis along the model suggested by the above distinction. Emotion is somewhat more accessible than feeling because the triggering stimuli and sites are easier to identify, and because so many of the responses are externalized and thus easier to measure. But once the neural systems which can support feelings are identified, feelings are also accessible, especially in humans, using modern neuroimaging tools.

3. Neural systems underlying emotion

Discussions on the neurobiology of emotion at systems level tend to revolve around the notion of limbic system, a collection of cortical and subcortical structures defined quite circularly by their very involvement in emotion. Prominent among those structures are the cingulate cortex

(usually used as shorthand for the anterior cingulate cortex), the amygdaloid nuclei (known collectively as the amygdalae), and the hypothalamus (for those authors who include the hypothalamus in the limbic system, which is not always the case). Although the term limbic system is often criticized I have no particular problem with retaining it. The notion of limbic system is helpful provided the term is seen as a convenience for communication and not as a suggestion that this odd collection of structures has a single function. But I do have a problem with the notion that *only* limbic system structures are seen as relevant for emotion; or that emotion and feeling are seen as *happening within* the limbic system; or that the results of emotion and feeling are thus relevant only within the limbic system.

Numerous structures outside of limbic system are involved in processing emotion and feeling. The list includes: (a) the prefrontal cortices, especially those in the ventral and medial sectors and, more broadly, in the orbital sector; (b) it also includes the somatosensory cortices, by which I refer not just to S_I in the rolandic region but also to S_{II} and to insular cortices; (c) monoamine nuclei in the brain stem; (d) periaqueductal gray; and (e) other nuclei both in the brain stem and spinal cord involved in both

afferent and efferent signaling relative to viscera and internal milieu.

Analysis of the flow diagram in Fig. 1 reveals the problem I have with the notion that emotion and feeling happen within limbic system and that their consequences affect limbic system alone. Not only are the emotion processing structures far more numerous than the collection described as limbic system, but even the actions of those within the limbic system are observable throughout the organism, in both body-proper and elsewhere in the brain, via neurons and blood stream.

The ultimate results of emotion are of two kinds. First there are *behaviors* —the expressing of joy, or anger, or disgust— which affect interactions with other living creatures. Second, there are *experiences* of emotional states, that is *feelings*, which affect the ongoing thinking of the subject and by so doing can alter future thinking, future planning and future behavior. The limbic system is very much in the loop of this entire process but it serves neither as its beginning nor as its end.

Equally problematic is the widespread view that the limbic system is the neural basis for all emotions. A rich body of evidence tells us that this is just not the case. Both

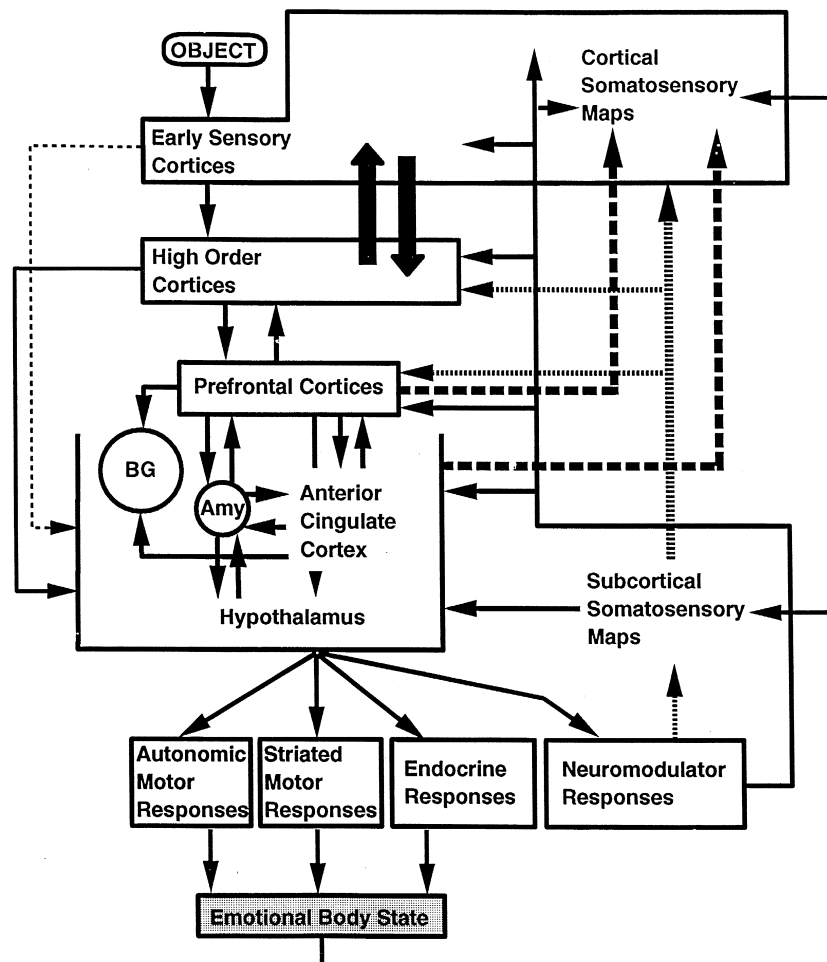


Fig. 1.

within and around the limbic system, circuitry connecting varied neural sites supports the operation of different emotions. For instance, work on aversive conditioning in rodents has shown that the amygdala is certainly involved in negative emotions such as fear [10,6]. Work in humans, on the other hand, has not only confirmed the amygdala's involvement with negative emotions such as fear and anger but also shown that the amygdala is not involved in the processing of positive emotions such as happiness, or negative emotions such as disgust. Studying patients with surgical damage to both amygdala, and with Urbach–Wiethe disease (a condition in which total and gradual depositions of calcium leads to the circumscribed damage and functional inactivation of both amygdala), we have been able to show, for instance, that the recognition of facial expressions of fear and anger but not of any other emotions are selectively impaired [1,2]. This selective involvement of the amygdala in some but not all emotions is even noticeable at non-conscious level, as shown in functional imaging experiments by Whalen et al. [12]. Moreover it is clear that some cortical structures are required for the processing of fear—for instance, the right somatosensory cortices—but those same structures are not needed for the processing of primitive emotions such as happiness [3]. Ongoing functional neuroimaging studies at our laboratory demonstrate that there are varied critical sites, both within and outside the limbic system, relative to distinct emotions.

4. The rationality of emotions

Emotion is the most complex expression of homeostatic regulatory systems. The results of the emotions serve the purpose of survival even in nonminded organisms. The emotions operate along the dimensions of approach or aversion, of appetite or withdrawal. The emotions protect the subject organism by avoiding predators or scaring them away, or by leading the organism to food and sex. As such, the emotions often operate as a basic mechanism for making decisions without the labors of reason, that is, without resorting to deliberated considerations of facts, options, outcomes, and rules of logic. But the emotions have other roles to play in conscious, minded, knowledgeable organisms such as our own. In human organisms, appropriate learning can pair emotion with all manner of

facts (for instance, facts which describe the premises of a situation, the option taken relative to solving the problems inherent in a situation, and, perhaps most importantly, the outcomes of choosing a certain option, both immediately and in the future). The pairing of emotion and fact remains in memory in such a way that when the facts are considered in deliberate reasoning when a similar situation is revisited, the paired emotion or some aspect of it can be reactivated. The recall allows emotion to exert its pairwise qualification effect. This can happen either as a conscious signal, e.g., a 'gut feeling', or as nonconscious bias, or both. In both types of action the emotions and the machinery underlying them play an important regulatory role in the life of an organism. This higher order role for emotion is still related to the needs of survival albeit less apparently. But it should be noted that beyond survival the impact of emotion in the process of reason affects the quality of survival and can help guide the creative process that best characterizes the human mind.

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