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Introduction

Understanding human emotion and the mechanisms underlying its generation or expression has been a central preoccupation of thinkers for millennia. Yet, its scientific study, particularly from a biological perspective, is quite recent, especially in comparison to that of other mental processes, such as vision, language, attention, or memory. Despite this late start, neuroscientific approaches to emotion have experienced a dramatic growth over the past decade. This has led to the birth of the new area of affective neuroscience, which has extended the field of cognitive research initiated in the previous decade. This new development was in large part due to important advances in the use of noninvasive functional neuroimaging techniques – such as positron emission tomography (PET), electroencephalography (EEG), magnetoencephalography (MEG), and, particularly, functional magnetic resonance imaging (fMRI). Together with refinements in more traditional methods, such as lesion studies, behavioral measures, and physiological recordings, the new techniques helped scientists make subjective and "private" affective processes more "visible" and amenable to experimental research in humans.

Largely building on previous research in neurophysiology, human affective neuroscience research began by focusing on the so-called basic emotions, particularly fear, mostly through visual stimuli (e.g., facial expression). However, as illustrated in the wide range of topics covered here, emotion research now covers different sensory modalities, processes, interactions with other systems, as well as individual differences. Emotion is now an accepted component of many "unrelated" disciplines, such as social psychology, economics, marketing, politics, and philosophy.

This book is intended to provide a wide yet comprehensive, up-to-date, and authoritative review of the cognitive neuroscience of human emotion that is both rigorous and accessible. Naturally, to keep the book manageable and of a reasonable size, we had to make some difficult choices in terms of its contents. Rather than choosing a few snippets from the entire field of affective neuroscience, we decided to focus on a specific area within the field. With this in mind,

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we explicitly left out nonhuman animal work. This does not mean in any way that we underestimate the importance of this research. Indeed, as stated in many of the chapters, research in experimental animals has been critical in providing the framework in which human affective neuroscience has developed; the authors were encouraged to highlight corresponding links with animal and biological sciences whenever possible. However, adding this perspective to the book would have required substantial coverage of molecular and cellular techniques that go beyond the aims of a single book. We also left out more clinically oriented research, such as emotional dysfunction in psychiatric and neurological disorders, although several of the chapters, especially those in the *Individual Differences* section, are highly relevant to this important area of knowledge.

One of the key features of this volume is that all the invited authors are established, yet young researchers – the Generation X of human affective neuroscience research – representing more than 20 institutions across three continents. They are some of the most active researchers who have contributed to the field and are still doing so.

The volume's 28 chapters are organized into seven independent yet complementary sections. We believe that this organization of topics will help readers gain a broad and structured view of the field.

Section I provides an introduction to the study of emotion from a cognitive neuroscience perspective. It is followed by a methodology section (Section II) that presents some of the most effective and widely used approaches to measure emotional responses. It describes the various techniques in a rigorous yet accessible manner, with particular emphasis easy-to-follow on affective neuroscience research – highlighting the advantages and limitations of each approach and providing concrete examples to help the reader appreciate these issues.

Section III consists of six chapters covering emotional perception and expression across different modalities (visual, auditory, olfactory, and somatosensory) and different domains within a given modality (e.g., auditory: voices and music; vision: faces and bodies). We decided to take this approach rather than, say, dividing the section according to the basic emotions, because most researchers, and thus their work, tend to focus on one of these domains but often encompass several emotions and/or processes. Thus, this structure, although somewhat arbitrary (because emotion is typically multimodal) will be most helpful to readers and reflects the current mainstream directions in human affective neuroscience.

Section IV follows with a description of how emotion and cognition interact. In this large and ever growing field, we focus on some of the most studied topics; namely emotion-attention interactions, emotion regulation, and decision making. Because of its importance and the large literature associated with it, interactions between emotion and learning and memory are covered in a separate section (Section V); its three chapters cover implicit and explicit aspects of memory, aversive learning, and reward learning. Chapters in Section VI address recent research in the so-called higher emotions, including morality, empathy, and other social emotions. Finally, Section VII covers some of the most studied individual differences – namely sex and gender, anxiety, age, and genotype – in emotional processing.

This book is particularly aimed at scientists and students of all levels (undergraduate, graduate, and postdoctoral) from psychology, neuroscience, and cognitive science, as well as people from other disciplines – including medicine, biology, computer science, economics, sociology, and political science – who have an interest in the relation between emotion and their area of study or research. In addition, this book should be useful to more clinically oriented professionals, including physicians and therapists, who are interested in gaining a better understanding of the neurobiological bases of human emotions.

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Section I

INTRODUCTION TO HUMAN AFFECTIVE NEUROSCIENCE

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CHAPTER 1

Models of Emotion

The Affective Neuroscience Approach

David Sander

Since its emergence in the 1990s (e.g., Davidson & Sutton, 1995; Panksepp, 1991), affective neuroscience has considerably extended our knowledge of the emotional brain. However, affective neuroscience research has only started to influence interdisciplinary models of emotion. The scientific object of affective neuroscience is "affect," which many disciplines share. Yet the way that affective neuroscience approaches affect and emotion is unique. For historical reasons and because of epistemological boundaries, psychological, neuroscientific, computer-based, and philosophical models of emotion have developed relatively independently from each other during most of the 20th century. Today, however, there is hope that the interdisciplinary nature of affective neuroscience will be able to constrain such varied models of emotion by bridging the gaps among different disciplinary approaches to emotion. Various debates that exist between and within disciplinary approaches to emotion could also benefit from the search for converging behavioral, computational, and neural evidence that is characteristic of affective neuroscience.

In this context, the overall aim of this chapter is to consider major current models of emotion by using an affective neuroscience approach. It provides a global survey of historical and conceptual issues that have guided scientific inquiries about emotion and presents the major theoretical foundations for more experimental work described in the following chapters. Although the scope of affective neuroscience research is not limited to emotion but includes other affective phenomena such as moods, preferences, and affective dispositions, this chapter examines models of emotion because they are more typically the focus of affective neuroscience research.

After having introduced what is implied by an affective neuroscience approach to models of emotion, I address terminological and taxonomy-related issues and suggest what seems to be a relatively consensual definition of emotion. Next, I outline the major models of emotion in modern research and the contrast in their focus on different phenomena: expression, action tendencies, bodily reaction, feeling, and cognition. Finally, as a brief conclusion, I illustrate the potential

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of the affective neuroscience approach to constrain theoretical models of emotion by considering more particularly the case of the amygdala.

The Affective Neuroscience Approach

In this chapter, affective neuroscience is defined in reference to cognitive neuroscience, similarly to the way in which cognitive sciences have been used as a reference for the development of affective sciences (see Sander & Scherer, 2009, for an overview of affective sciences).

Affective sciences can be seen as either integrated in or as complementary to cognitive sciences, depending on how one conceives the relationship between affect and cognition (see Forgas, 2008; Hilgard, 1980; Moors, 2007). Indeed, a traditional conceptual debate is whether affective processes are a type of cognitive process or whether they are qualitatively different in nature. This controversy is fundamental for contemporary models of emotion and is therefore addressed in this chapter. However, this debate seems to be quite independent from the approach of affective neuroscience. Indeed, there does not seem to be any reason for thinking that consideration of affective neuroscience either as a discipline on its own or as a "cognitive neuroscience of affect" modifies its approach.

In fact, the very reason for the growing importance of affective neuroscience was the recognition that emotion can be usefully studied by using the concepts and methods of cognitive neuroscience, leading to the "cognitive neuroscience of emotion" (for discussion see, e.g., Lane & Nadel, 2000; Ochsner & Schacter, 2000; Sander & Koenig, 2002). For instance, when Davidson and Sutton (1995) pointed to affective neuroscience as an emerging discipline, they argued that studies on emotion require a careful dissection of emotional processes into elementary mental operations, which is similar to the approach of cognitive neuroscience.

With respect to models of cognition, one strength of cognitive neuroscience is that it relies on the so-called cognitive neuroscience triangle (see, e.g., Kosslyn & Koenig, 1992). Indeed, rather than relying on a single approach to cognition (e.g., brain mechanisms) or even on two approaches (e.g., brain and psychological mechanisms), cognitive neuroscience also relies on a third approach – the computational approach – to constrain models. Computational analysis has been important for the development of models of traditional domains of cognitive neuroscience such as perception, attention, memory, and action (Kosslyn & Koenig, 1992; Marr, 1982) and has also, more recently, been considered as important for models of social cognition (see Mitchell, 2006) and emotion (see Moors, 2007; Sander & Koenig, 2002). Inspired by David Marr's seminal work on levels of analysis (Marr, 1982), cognitive neuroscience defines computational analysis as a logical exercise aimed at determining what processing subsystems are necessary to produce a specific behavior, given specific input (Kosslyn & Koenig, 1992). Such computational analysis is important for producing explicit models of the mind in the form of functional architectures that could, in principle, be simulated by artificial neural networks or other computer-based models.

The view that incorporating emotion in computational models would be beneficial to our understanding of the mind has preceded the emergence of affective neuroscience, and very influential scholars in artificial intelligence such as Herbert Simon and Marvin Minsky have strongly emphasized the importance of taking emotion into account in models of the mind (e.g., Minsky, 1986; Simon, 1967). For instance, Minsky (1986, p. 163) strongly emphasized the critical role of emotion in models of artificial intelligence by arguing that "the question is not whether intelligent machines can have any emotions, but whether machines can be intelligent without any emotions." Such a pioneering perspective, according to which emotion should be modeled in artificial intelligence, was instrumental in creating a new field of research called "affective computing" (see Picard, 1997).

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Affective computing can be defined as the type of computing that relates to, arises from, or deliberately influences emotion and other affective phenomena (Picard, 2009). In that regard, a close consideration of affective computing can be viewed as being the basis for the implementation of emotions as adaptive mechanisms in autonomous agents (e.g., Caňamero, 2009), not only in robotics but also for software agents such as embodied conversational agents (e.g., Pelachaud, 2009). The basis of affective computing resides in the establishment of computational models of emotion (Fellous & Arbib, 2005; Petta & Gratch, 2009) that are based on both psychological (Gratch & Marsella, 2005) and neuroscience (Taylor & Korsten, 2009) constraints. For instance, with respect to connectionist models of emotional processing (see Roesch, Korsten, Fragopanagos, & Taylor, 2010), the most classic example is the work of Armony and colleagues. In their pioneering work, Armony and colleagues proposed a computational connectionist model of fear conditioning, constrained by what was then known about the neuroanatomy and neurophysiology of fear learning, in particular by modeling both cortical and subcortical pathways to the amygdala (Armony, Servan-Schreiber, Cohen, & LeDoux, 1995). However, this model was strongly inspired by the functional neuroanatomy of fear learning, and it is therefore unclear how it could be extended to other emotions and to aspects other than emotional learning.

Affective neuroscience and affective computing converge toward the importance of considering biological, psychological, and computational constraints in modeling emotion (see, e.g., Roesch et al., 2011). This convergence is consistent with the notion outlined earlier that the task of affective neuroscience is the same as that of cognitive neuroscience; namely, to "map the information-processing structure of the human mind and to discover how this computational organisation is implemented in the physical organization of the brain" (Tooby & Cosmides, 2000, p. 1167). A critical advantage of adopting a complete affective neuroscience approach is that it invites affective scientists to develop functional architectures that are sufficiently explicit to derive competing hypotheses that can be subject to computational simulations, conceptual analyses, and empirical experiments. As discussed in the next section, this advantage brought by explicit models is particularly salient in emotion research where definitional issues are still highly debated.

What Is an Emotion?

Fehr and Russell (1984) highlighted the difficulty in producing an explicit definition of emotion when they wrote that "everyone knows what an emotion is, until asked to give a definition. Then, it seems, no one knows" (p. 464). Definitions of emotion vary not only as a function of disciplines or approaches but also across history and culture. Scholars have emphasized the need to consider whether there is a history of emotion; that is, an understanding as to how emotions and the concept of emotion may have changed over historical time (see Konstan, 2009). As Konstan described it, the English term "emotion" is relatively recent and has only been used more often than, for instance, "passion," "affection," and "sentiment" in the past 200 years. Long before this period, other terms that closely correspond to "emotion" can also be found, such as the ancient Greek term *pathos*. In fact, Aristotle's definition of *pathê* as "those things on account of which people change and differ in regard to their judgments, and upon which attend pain and pleasure" (Rhetoric, Book 2, Chapter 1, 1378a) can be considered as one of the first influential explicit definitions of emotion (see Konstan, 2009). This definition was influential not only because it suggested a link between emotion and judgments but also because it already contained the dimension that almost all current models consider necessary: *valence* (here, "pain and pleasure"; see Colombetti, 2005, for a review). A history of emotion can be drawn from the time of Aristotle's definition (see, e.g., Konstan, 2009) that considers how

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definitions have evolved and whether emotions have changed over historical time; for example, whether today's emotions of "shame" or "anger" are the same as those described by ancient Greeks, Mesopotamians, or other civilizations.

Of course, the difference mentioned here in terms of time can also be investigated in terms of space. Although the differences found over the centuries cannot be directly investigated by affective neuroscience, the cultural differences that are observed today are a classical topic of emotion psychology (see e.g., Tsai, Knutson, & Fung, 2006) and have begun to be investigated from an affective neuroscience approach – as suggested, for instance, by the publication of a special issue on *Cultural Neuroscience* in the journal *Social Cognitive and Affective Neuroscience* (see Chiao, 2010). Reviewing historical and cultural effects on emotion would go far beyond the scope of this chapter, but, as it will be discussed later, the question of whether emotions are a universal phenomenon or whether they vary as a function of time and space is fundamental for many theories in affective sciences.

The Variety of Definitions of Emotion

"What is an emotion?" is not only the title of one of the most widely cited articles on emotion (James, 1884) but is also a current conceptual question in emotion research that seems to correspond to a never ending attempt to define emotion (see, e.g., Duffy, 1934; Frijda, 2007; Gendron & Feldman Barrett, 2009; Kleinginna & Kleinginna, 1981; Russell & Barrett, 1999; Scherer, 2005). Certainly, what affective neuroscience can significantly contribute to this effort is an understanding of emotion as a scientific concept, in particular by offering functional architectures of emotional processes in the form of explicit models.

A necessary step in modeling emotion is to acknowledge the variety of definitions that scholars have given to emotion. In a tour de force, Kleinginna and Kleinginna (1981) reviewed almost 100 definitions of emotion found in the literature and categorized them in 10 specific lists that emphasized various aspects of emotion: (1) affective definitions (emphasizing feelings of arousal and/or hedonic value); (2) cognitive definitions (emphasizing appraisal and/or labeling processes); (3) external stimuli definitions (emphasizing external emotion-generating stimuli); (4) physiological definitions (emphasizing internal physical mechanisms of emotion); (5) expressive behavior definitions (emphasizing externally observable emotional responses); (6) disruptive definitions (emphasizing disorganizing or dysfunctional effects of emotion); (7) adaptive definitions (emphasizing organizing or functional effects of emotion); (8) multiaspect definitions (emphasizing several interrelated components of emotion); (9) restrictive definitions (distinguishing emotion from other psychological processes); and (10) motivational definitions (emphasizing the relationship between emotion and motivation).

In affective neuroscience, scholars also disagree on how to define an emotion. For instance, let us consider the definitions offered by two of the most influential scholars of current research on the emotional brain, Damasio (1998) and LeDoux (1994). LeDoux (1994, p. 291) highlighted the fact that emotions cannot be unconscious when stating that "in my view, emotions are affectively charged, subjectively experienced states of awareness. Emotions, in other words, are conscious states." According to Damasio (1998, p. 84), "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." Therefore, Damasio certainly does not exclude the possibility that what he calls an emotion can be unconscious. Distinguishing between emotion and feeling, Damasio (1998, p. 84) also stated that "the term feeling should be used to describe the complex mental state that results from the emotional state." It is likely that such a *mental state* is conceptually closer to what LeDoux called an emotion,

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although Damasio called it a feeling rather than an emotion.

The Specificity of Emotion

The distinction between *emotion* and *feeling* mentioned earlier is just one of many conceptually useful distinctions that can be made in the category of affective phenomena. In fact, the term "emotion" is often considered in a framework that includes other less studied affective phenomena such as mood, motivation, drive, desire, preference, attitude, valenced reaction, passion, sentiment, affect, core affect, arousal, affective style, or affective reactivity. Some of these concepts are more scientifically defined because they have been coined to refer to a specific new concept and therefore suffer less than others from having a "folk" meaning (e.g., *affective style*, see Davidson, 1992; *core affect*, see Russell & Barrett, 1999). Attempts to define these constructs have sometimes led to extreme positions. For instance, Duffy questioned the specificity of emotion and argued that "for many years the writer has been of the opinion that 'emotion' as a scientific concept is less than useless" (Duffy, 1941, p. 283). She argued that, because emotion can be reduced to other constructs, there is no need to create a specific term for emotional states.

More recently, Brehm (1999) argued that emotion can be reduced to motivational states. Indeed, some question the boundaries between emotion and motivation. For instance, because Rolls (1999) included thirst or sexual behavior as emotions in his book *The Brain and Emotion*, Phillips (1999) proposed that it might have been more appropriate to title this book "The Brain and Motivation."

Motivation is typically considered as being related to emotion, but most scholars would agree on the need to distinguish between these two constructs (for discussion, see, e.g., Frijda, 1986, 2007). For instance, motivation can be considered both as a determinant and as a constituent of emotion. As a determinant, motivation is often considered causal for the elicitation of emotion because events that are relevant for major motivations of the individuals (e.g., needs or goals) are indeed those that typically elicit emotions (see Moors, 2007). As a constituent of emotion, motivation is often considered as being expressed in action tendencies (e.g., approach or avoidance) that indeed motivate a change in the relation between the individual and the event (see Frijda, 1986). A definition highlighting the specificity of emotion is suggested later.

Taxonomies of Emotion

Not only can emotion be distinguished from other affective phenomenon but also within the category of "emotion," various subcategories have been proposed. To the best of my knowledge, no full taxonomy of emotion has achieved consensus, but some categories are recognized as conceptually useful. Taxonomies of emotion are based on various features, and categories often overlap so that they should not be seen as describing mutually exclusive categories of emotion, but rather as describing ways in which emotions are categorized in various research traditions. Indeed, a given emotion (e.g., anger) can belong to many categories.

Basic Emotions

As an example of a category that is defined by the type of emotion, the so-called basic emotions category is very common in current affective neuroscience research (for review, see Ortony & Turner, 1990). This category, which is conceptually similar to the categories of "primary," "discrete," or "fundamental" emotions, acknowledges the fact that, according to many researchers, a small set of emotions – typically between 2 and 10 – are more elementary than others. This concept of "basic emotions" is key to the development of the basic emotion theory that is discussed later (see the section, "Is Emotion an Expression?"). The following emotions are often considered as being "basic": anger, disgust, fear, enjoyment,

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sadness, and surprise (see Matsumoto & Ekman, 2009).

In this theory, the adjective "basic" is used to express three postulates (see Ekman, 1992). First, it is used to convey the notion that "there are a number of separate emotions which differ one from another in important ways" (Ekman, 1992, p. 170). Second, it is used to indicate that "evolution played an important role in shaping both the unique and the common features which these emotions display as well as their current function" (Ekman, 1992, p. 170). Finally, the term also often refers to the notion that nonbasic emotions are made up of blends of basic emotions (e.g., Tomkins, 1963).

Of note, the notion of basic emotions is anchored in the philosophical history of psychology; for instance, Descartes (1649, Art. 69) distinguished among six primary emotions (admiration, love, hatred, desire, joy, and sadness) and assumed that all other emotions either belonged to these families or were blends of these primary emotions.

Most of the work in affective neuroscience in the last decade has consisted of searching for discrete dedicated brain systems underlying each and every basic emotion, using as evidence either neuropsychological double dissociations (see Calder, Lawrence, & Young, 2001) or brain imaging results (see Vytal & Hamann, 2010). As discussed later (see the section, "Is Emotion an Expression?"), this view has been strongly challenged by both conceptual analyses and empirical results.

Positive versus Negative Emotions

Another example of a category that is defined by the type of emotion is the common valence-based distinction between "positive" and "negative" emotions. For instance, Tomkins' (1963) influential contribution to affective sciences was a book divided into two volumes, the first volume concerning *positive affects* and the second one on *negative affects*. Although the type of valence used to distinguish between so-called positive emotions and negative emotions is often not clear (see Colombetti, 2005), it is often the feeling component that is considered: An emotion is positive when "it feels pleasant" or negative when "it feels unpleasant." This valence-based distinction has been key to the development of the circumplex/bidimensional theories of emotion that are discussed later (see in particular the section, "Is Emotion a Feeling?"). Of course, the valence dimension is not restricted to the feeling component; eliciting events are sometimes categorized as positive or negative in terms of their appraised intrinsic pleasantness or goal conduciveness (e.g., Scherer, 2001). There is not always congruence between the appraised valence of an event and the valence of the feeling. For instance, although the emotion of "interest" is considered as positive in terms of feeling, it can also be elicited by appraised negative stimuli (e.g., disgusting stimuli can elicit interest; see Silvia, 2006b).

Although feelings are often considered to be either positive or negative, some scholars have argued that evaluations of events can be ambivalent (see Cacioppo & Berntson, 1994). This means that one can feel *both* good *and* bad about an event, rather than good *or* bad about it (see Larsen, 2007). Depending on the aspect of the event that is appraised, the very same event can be appraised as positive or negative, meaning that if two aspects are appraised simultaneously by two dissociated evaluative channels, both positive and negative feelings could be elicited (for discussion, see Cacioppo & Berntson, 1994). For instance, having a sexual relationship with someone else than one's significant other can be appraised as positive in the sense that it elicits pleasure, but as negative because it interferes with moral concerns of the individual. Ambivalent attitudes have been considered as evidence for the separability of positive and negative substrates and the view that mixed emotions could be jointly elicited. For instance, it has been suggested that individuals can feel *both* happy and sad at the same time while viewing tragicomic movies (Larsen, McGraw, & Cacioppo, 2001).

In affective neuroscience, the notion that brain systems could be differentially

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