Prologue

What William James once said about attention could also be said about emotion: “Everyone knows what it is.” And, like attention, replacing this intuitive understanding with operational definitions and theoretical constructs—admitting it into the domain of scientific study—is far from a trivial task. Indeed, it sometimes seems that there are as many definitions as there are investigators (see Panksepp 1982 for a representative set). One aspect of emotion that is generally agreed upon, however, is that it is associated with physiological reactions: in emotional situations, the body acts. The heart pounds, flutters, stops, and drops; palms sweat; muscles tense and relax; blood boils; faces blush, flush, frown, and smile. We note these reactions in ourselves, and we make inferences about the emotional life of others based on visible bodily responses.

The link between emotion and bodily action is evident in the derivation of the word “emotion,” which stems from the Latin movere, meaning to move. In emotional situations, people move: they act and they react. It is informative that the word “motivation” also stems from the same verb; a motive is, literally, “something that moves one.” Whereas the term “emotion” is usually reserved for describing stimuli that move people, “motivation” is often used to describe animal behavior. Under conditions of high motivation, animals move: they act and they react. Both emotion and motivation are fundamentally related to action.

Those studying motivated behavior in animal subjects have consistently agreed that action is controlled by two basic parameters of direction and intensity (see e.g. Hebb 1949; Schneirla 1959). That is, even in the simplest organism, stimuli that promote survival (e.g., food, nurturance) elicit approach behaviors, whereas those that threaten the organism prompt withdrawal, escape, or avoidance. All these behaviors can occur with varying strength, speed, and vigor. The motivational parameters of direction (i.e., towards or away) and intensity map well onto parameters of hedonic valence (i.e., pleasant or unpleasant) and arousal that are recognized as central in emotion. Emotional events can be differentiated on the basis of whether they are good or bad (Arnold 1960), appetitive or aversive (Dickinson & Dearing 1979), agreeable or disagreeable (MacLean 1993), positive or negative (Cacioppo & Berntson 1994), pleasant or unpleasant (Lang, Bradley, & Cuthbert 1990), hospitable or inhospitable (Cacioppo, Berntson, & Crites 1996). These valenced events differ in the degree to which they arouse or engage the individual.

Based on these observations, a number of theorists have advocated a biphasic approach to emotion, which posits that emotion fundamentally stems from varying activation in centrally organized appetitive and defensive motivational systems that have evolved to mediate the wide range of adaptive behaviors necessary for an organism struggling to survive in the physical world (Davidson et al. 1990; Dickinson & Dearing 1979; Konorski 1967; Lang et al. 1990). Neuroscientists have begun to determine how the relationship between stimulus input and behavioral output is mediated through specific, largely subcortical, neural circuits that have evolved to organize and direct adaptive actions (Davis 1989; Fussel 1994; LeDoux 1987, 1996). A biphasic approach to emotion suggests that its psychophysiological study should assess physiological responses as they vary with systematic variations in hedonic valence and arousal.

Another approach, and one more commonly thus far in the psychophysiological study of emotion, conceptualizes emotion in terms of a set of discrete states such as fear, anger, sadness, and so forth. Lists of basic emotions have typically varied from theorist to theorist. Descartes (discussed in Panksepp 1982) listed wonder, love, joy, desire,
hate, and sadness as fundamental, and it is interesting that this is the last time positive emotions outrepresented negative and that love was included on the list. Watson (1924), showing allegiance to definitions based on observable behavior, had a short list of fear, rage, and sexual activity. More contemporary lists include surprise, enjoyment, interest, disgust, shame, distress, fear, contempt, and anger (Izard 1972); surprise, acceptance, desire, fear, rage, panic, and disgust (Plutchik 1980); and others. The question of whether specific physiological responses are characteristic of different emotional states has been pursued for almost a century by psychophysicists, prompted primarily by James's hypothesis regarding the relationship between physiology and specific feelings.

This chapter will begin with a discussion of James's influence on the psychophysiological study of emotion over the course of the last century, reconsidering its implications in light of recent advances in thinking in neuroscience, cognitive psychology, and psychophysiology. A brief review of theory and data relevant to a biphasic approach to emotion will then be presented. Current models of emotional processing at both anatomical and cognitive levels of description will be reviewed, particularly as they describe potential links between stimulus input, motivational activation, and response output. It will then be suggested that three methodological factors loom large when designing or comparing across studies of emotion: (i) the definition of the affective cue, (ii) the determination of the task, and (iii) the description of the response. A brief review of empirical findings in the psychophysiology of emotion will highlight these crucial elements in experimental studies of emotion. It will be suggested that comparisons across studies in which the cues, tasks, or response measures differ have led to a number of difficulties in making sense of the data from psychophysiological inquiries of emotion. Specific issues regarding inter- and intrapersonal differences, conscious experience of emotion, and discrete states will be raised briefly and considered within the context of a biphasic motivational approach to the psychophysiological study of emotion. It will be concluded that inferences about the relationship between emotion and psychophysiological response will be, at first, highly context-dependent.

**HISTORICAL BACKGROUND**

The psychophysiological study of emotion has been preoccupied for roughly a century with assessing James's hypothesis that physiological responses form the basis of emotional experience. Given the many advances in thinking about the mind and behavior since the time of James, it is not surprising to see that modern viewpoints are somewhat different from those of James, a turn-of-the-century introspectionist whose interest in physiological processes was secondary to his primary goal of explaining feelings—that is, conscious emotional experience. His radical proposal that feelings followed the physiological response elicited by an emotional stimulus represented a nonintuitive reversal of traditional folk wisdom, and provoked the scientific imagination of the psychologist: Is a person afraid because he runs rather than running because he is afraid?

The Jamesian hypothesis defined the central question in the study of emotion as whether specific feeling states were associated with a specific pattern of physiology. To the extent that physiological changes do not uniquely specify different feelings, the Jamesian hypothesis would be disconfirmed. The answer to this question is clearly within the purview of psychophysicists, who began pursuing answers in investigations spanning the last 100 years using a variety of methods to determine whether specific physiological patterns are associated with specific emotions such as fear and anger (e.g. Ax 1953; Ekman 1971; see Cacioppo et al. 1993 for a review).

Empirical support for the Jamesian hypothesis has not been strong. As noted in a recent review of this literature by Cacioppo et al. (1993), part of the problem stems from inadequate experimental designs in which different studies include different types or numbers of specific emotions than others, do not include appropriate comparison conditions, utilize different dependent measures, or, importantly, investigate emotion in very different experimental contexts. Nonetheless, Cacioppo et al. (1993) selected studies that met a number of important criteria for assessing the question of whether specific physiological patterns accompany specific states of emotional feeling. The data were quite disappointing, with "little evidence for replicable autonomic differences in pairwise comparisons of the emotions on the measures of bodily temperature, systolic blood pressure, facial temperature, respiration, skin conductance level, and cardiac stroke volume" (p. 125). Although heart rate was found to be a relatively effective discriminator, a number of methodological problems led Cacioppo et al. (1993) to conclude that even the meager support provided by this measure was probably an overestimate of actual effect sizes.

In addition to a disappointing lack of empirical confirmation for the Jamesian hypothesis (despite a century of experimentation), there are conceptual difficulties with the question of whether specific emotional states are associated with a specific physiological pattern. These include the facts that (1) physiology varies with specific actions and (2) specific actions can vary both within and across specific emotions. Regarding the link between physiological response and action: it is a truism that most, if not all, peripheral (and, to some degree, central) indices of physiological activity vary as a function of the amount and type of somatic involvement and the accompanying demand for metabolic support. Put bluntly, running will produce a very different configuration of physiological activity than sitting, with activity in one system (e.g. cardiovascular) dependent, to some degree, on activity in another system.
(e.g., somatic). In addition to these obvious relationships, more subtle interdependencies noted between physiological systems — such as cardiac—somatic coupling (Obrist 1975) and respiratory sinus arrhythmia (Porges 1992) — rule out simple statements about physiology in the absence of specifying a particular action set.

It is also a truism that specific actions can vary in the same emotional state, as well as (more obviously) across different emotional states. For example, both animal and human research indicates that a cue signaling threat can lead to fight, flight, or freezing, as well as a variety of specific idiosyncratic behaviors (see Mackintosh 1983) depending upon available contextual support and the organism’s learning history. The physiology of fear in the context of headlong flight will be different from the physiology of fear in the context of freezing, particularly in somatic and cardiovascular systems. Predicting identical physiological patterns in the context of these disparate activities highlights the inappropriateness of the initial question regarding the physiology of fear. At the least, it will be necessary to specify whether the target emotion involves fleeing fear or freezing fear or fighting fear.

Attempts to define emotion’s physiology in the absence of information specifying both the context in which it is elicited and the actions it evokes neglect the important context-dependent aspects of emotional actions. To address the role of context in emotion, Lang and his colleagues (1990) distinguished between strategic and tactical aspects of emotion. Whereas strategies define the dominant motivational state (i.e., appetitive or defensive), a variety of different tactics — diverse, specific, context-bound patterns of action — can be employed in a situation eliciting defense, for example. Thus, a male rat’s response to an aversive shock is various: if administered to the rat’s feet in a bare chamber, the animal freezes; if delivered by a prod from outside the cage, the rat flees; if suitable material is present, the rat will attempt to bury the shock apparatus; if another male is in the vicinity, a fight ensues (see Mackintosh 1983 for a discussion of these data). This variability in specific emotional behaviors has been a major source of frustration when attempting to extrapolate across instances of the same emotion or to differentiate individual emotions, particularly in terms of assessing their psychophysiological signatures. Tactical variation negates physiological similarity.

Thus, from a modern perspective, the Jamesian question of whether a specific emotion will result in a specific physiological pattern is psychophysiological naive. For James, however, physiological responses were important only insofar as they provided the ingredients from which conscious experience could be built — he was not explicitly invested in the study of psychophysiological processes per se. Yet Lange, whose ideas are closely linked with James’s owing to a similar focus on the role of physiology in emotion, was in fact a physiologist (see Lang 1994b for a thorough discussion of James—Lange theory). For Lange, however, physiological response was the emotion — whether a conscious feeling subsequently arose from physiology’s activity was not an issue that concerned him. Rather, Lange’s goal was simply to characterize similarities and differences in emotion based on empirical patterns of physiological (primarily cardiovascular) response. For psychophysicists, a shift in emphasis from the study of conscious feelings to the study of physiological pattern- ing redefines the central question from the Jamesian, “Are specific states associated with specific physiology?” to the Langean, “How do physiological patterns vary in different emotional situations?”

Whereas both James and Lange believed that at least some physiological events differentiated among emotions, Cannon (1928) and later Bard (1934) argued that physiological responses, particularly those mediated by the autonomic nervous system, were too general, too diffuse, and too slow to provide a basis for distinguishing different emotional states. Cannon proposed that physiological responses, particularly in aversive contexts, resulted from a general activation of the sympathetic nervous system that he termed the “emergency” reaction. Modern viewpoints again clarify the relevance of the Cannon—Bard theory for current researchers. First, the focus on autonomic responses, particularly those mediated by the sympathetic branch, is quite narrow considering the number and extent of methodologies available to the modern psychophysologist. In addition, whereas some aspects of autonomic functioning are slow and diffuse, others are more precise and rapid, and the addition of new measures of emotional reactivity in somatic (e.g., reflex), central (e.g., ERP, EEG, fMRI), and neurochemical systems can be profitably employed. Second, the focus on aversiveness renders Cannon’s view silent with respect to physiological responses elicited in the context of pleasant, appetitive stimuli.

In this chapter, Lange’s empirical approach to the study of emotion is advocated. According to this view, the goal of the psychophysiological study of emotion is the assessment of physiological responses in multiple response systems (unlike Lange’s focus on vasomotor) as they vary in well-defined emotional contexts. Perhaps the experimental legacy of the many investigators that pursued the Jamesian hypothesis in the twentieth century will be that these studies highlighted, however indirectly, the context-dependent and tactical nature of emotional response. The data compellingly show that physiological patterns are not the same for a given emotional state, especially if it is prompted in different contexts (Cacioppo et al. 1993; Lacey 1967; Lang et al. 1990).

**Pleasure and Arousal in Emotion**

James clearly advocated a discrete emotion view, particularly for what he called the “coarse” affects — which
included fear, anger, and so on. Because of his influence on psychological research, this theoretical view has received considerable attention in terms of physiological assessment. The simpler dimensional view, however, has not been tested as thoroughly. One benefit of the dimensional view is that it is parsimonious; furthermore, extending back at least to Wundt (1896), there has been agreement among theorists that the basic organizational dimensions of emotion are pleasure and arousal. Moreover, a clear bridge to animal motivation exists, with many scientists equating pleasant events with those that elicit approach behavior and unpleasant events with those eliciting withdrawal or avoidance. For instance, Schneirla (1959) defined the two responses of approach and withdrawal as the only basic patterns “applicable to all motivated behavior in all organisms.” According to his view, approach behaviors (i.e., A-type mechanisms) are elicited in situations such as acquiring food, obtaining shelter, mating, and other activities that promote survival of the individual and the species. Withdrawal (W-type mechanism) behaviors include defense, huddling, flight, and other protective reactions. Schneirla focused on physical intensity as the important parameter eliciting A-type or W-type behaviors, with low-intensity stimuli associated with approach and high-intensity stimuli evoking withdrawal. However, he noted that, for complex organisms such as humans, basic biphasic responses could permeate through evolution to provide a basis for more varied types of emotional elicitors (for adult humans, object meaning tends to outweigh stimulus magnitude as the eliciting cue) and emotional activities (e.g., active seeking or avoiding).

Based on a sorting of unconditioned reflexes, Konorski (1967) agreed that a biphasic organization was fundamental, dividing response classes into those that are either protective or defensive. Dickinson and Dearing (1979) developed Konorski’s dichotomy into two opponent motivational systems, aversive and attractive, each activated by a different but equally wide range of unconditioned stimuli. These systems were held to have “reciprocal inhibitory connections” (p. 5) that modulated learned responses and reactions to new, unconditioned input. More recently, Davidson and colleagues (1990; Davidson 1992) and Lang and colleagues (1990) have embraced a biphasic organization, assuming that emotion stems from activation in basic appetitive or defensive motivational systems. In the simplest case, biphasic motivation is defined as a behavioral tendency to approach or withdraw from a stimulus.

There are a number of other factors supporting a simple biphasic organization of emotion. Whereas Schneirla’s assertion was based on the behavior of simple creatures such as planaria, Hebb (1949) also concluded – on the basis of studies of higher organisms including rats, cats, dogs, and primates – that a primary parameter of behavior was direction (towards or away). Human developmental data are consistent with the idea that ontogeny recapitulates phylogeny in this sense, as newborns immediately evidence both protective (oral rejection) and appetitive (e.g. sucking) reflexes, indicative of a basic biphasic chassis. Whereas only unconditioned stimuli at first reflexively activate appetitive and defensive systems, experience allows new (conditioned) stimuli to activate these same systems. Thus, infants evidence fear of heights only after they are able to crawl (Campos, Bertenthal, & Kermoian 1992), suggesting that the visual cliff cue activates the defensive system only after experience has forged a connection between it and aversive consequences (i.e., the child has taken a tumble).

Empirical support for a fundamental biphasic organization of emotion is also clearly seen in studies investigating how adults (as well as children) categorize the world. Osgood’s (1969) seminal research demonstrated that, when asked to rate words on attributes that included physical dimensions (heavy–light, thick–thin, hot–cold), psychological descriptors (honest–dishonest, brave–cowardly, kind–cruel), and emotional scales (good–bad, pleasant–unpleasant), factor analyses consistently found that the dimension of hedonic valence was primary in organizing these data and clearly accounted for the most variability in these judgments. A second factor – labeled activation, arousal, or intensity – also accounted for substantial variance. He later found these dimensions were primary for linguistic stimuli in non–English-speaking cultures, as well as in organizing judgments for stimuli ranging from sonar signals to aesthetic paintings (Osgood, Suci, & Tannenbaum 1957). Mehrabian (1970) extended the analysis to nonverbal behavior and again found that hedonic valence and arousal were the basic factors underlying judgments concerning facial expressions, hand and bodily movements, and postural positions.

In short, the world appears to be categorized, fundamentally, in terms of hedonic valence, which can be related to the extent that an event promotes (pleasant) or threatens (unpleasant) life in some way. The fact that human experience, verbal and nonverbal, can consistently be organized in terms of basic appetitive–aversive evaluation provides support for the idea that this dimension is fundamental in human emotion.

**Intensity, Arousal, Activation**

As just noted, factor analyses of emotional judgments consistently identify a second factor – degree of arousal or activation – as organizing semantic judgments. If, in simple organisms, hedonic valence is directly coupled with behavioral dispositions toward or away from appetitive or aversive stimuli, then its intensity can be measured as the strength or speed of the movement (e.g. Duffy 1962; Hebb 1949; Miller 1959; Schneirla 1959). That is, movement toward or away from a stimulus can be implemented with more or less vigor, energy mobilization, or activation. In simple organisms, behavioral intensity was initially linked
to stimulus intensity, with the strength (Miller 1966) or speed (Schneirla 1959) of a withdrawal response varying directly with the degree of shock intensity, for example.

Thus, in its earliest (and simplest) form, intensity characterized the vigor of a response. Subsequently, response vigor was theoretically linked to a central drive state, which was proposed as a primary motivator underlying observed behavior (Hull 1943). The vigor of a response was presumed to directly reflect the intensity of the underlying drive state, allowing response vigor to be used as an index of central motivation. In the Hullian view, stimulus intensity increased motivation (drive), measured in the strength of the resulting (approach or avoidance) behavior. In this view, arousal is conceptualized as a nonspecific, energizing force that intensifies and strengthens either approach or withdrawal.

This nonspecific, activating conception of drive was refined in the late 1950s and early 1960s by a number of theorists who emphasized the activating effects of emotion (Duffy 1962; Lindsley 1951; Malmo 1959). In their view, behavior was conceptualized as varying along a dimension of activity, with coma and death anchoring one end and emotional excitement anchoring the other. Increased activity in cortical, sympathetic, and behavioral systems was predicted as one moved from the calm to excited end of this behavioral dimension, a prediction supported in a number of different studies (see Duffy 1962 for a review).

Activation theory clearly linked increases in arousal to unilateral and monotonic increases in the strength of responding in numerous systems, including cortical (e.g., alpha-band EEG), sympathetic (e.g., heart rate, blood pressure, etc.), and somatic (e.g., muscle tension, motor activity). Lacey (1967) challenged this notion on the basis of data indicating that responses in all systems do not uniformly increase together. For instance, somatic deactivation can be obtained in states of high cortical activation, and pupillary dilatation (a sympathetic response) can occur with cardiac deceleration (a parasympathetic response; Libby, Lacey, & Lacey 1973), effects he termed "directional fractionation." A centerpiece of Lacey's argument was the finding that electrodermal and cardiac responses showed directional fractionation as a function of specific tasks: perception and mentation both result in electrodermal increases, but perception generally involves cardiac deceleration whereas mentation is accompanied by cardiac acceleration.

Modern thinking clarifies different aspects of Lacey's (1967) criticism. First, the notion that cortical activation and somatic or sympathetic activation are necessarily coupled is less reasonable, given current conceptions of the brain. When envisioned as a computational device, it is clear that the brain can be quite busy (i.e., active) when inhibiting somatic or autonomic output, for example, depending upon the goal at hand. Second, the comparison between cardiac responses in different tasks (i.e., perception and mentation) actually violated Duffy's (1962) caveat that comparisons between differentially arousing contexts could be satisfactorily assessed only with "all other things being equal." That is, tests of arousal theory are more appropriately conducted by varying the level of intensity within the same task context.

Nonetheless, two aspects of activation theory remain untenable today. First is the assumption that increasing arousal uniformly increases activity in physiological and behavioral systems. As noted before, behaviors appropriate to a highly arousing, aversive context can include active somatic responses (such as fleeing or fighting) or relatively inactive responses (such as freezing). The degree of somatic activation will depend to a large extent on the specific behavior selected in a particular context. Thus, increases in intensity will not necessarily or uniformly increase somatic and autonomic activation; instead, they will depend upon the response appropriate for the current context and its somatic and metabolic requirements. In this view, arousal amplifies the strength of the associated behavior, which could involve (depending upon the context) decreases rather than increases in activity.

A second unsatisfactory outcome of activation theory is the notion that arousal can be conceptually separated from behavioral direction — that is, the idea that one can consider arousal in the absence of behavior. As noted earlier, arousal was first proposed as a parameter of directed behavior: an organism approached or avoided a stimulus with more or less vigor or strength. The idea that vigor could be removed from the specific behavior, or studied separately, is not a clear corollary of this view. In advocating a unidimensional activation process that energized and amplified all behaviors, regardless of direction, activation theories unwittingly encouraged explorations in which arousal was manipulated (through drugs, motor activity, etc.) in the absence of directed behavior. In fact, Duffy (1962) was quite clear on the centrality of direction (valence) as the main parameter of behavior; her focus on activation was an attempt to deal with the intensive aspects of emotion.

Konorski (1967) clearly advocated activation as a parameter operating within separate appetitive and aversive systems, as did Lang et al. (1990, 1997). In these formulations, arousal is conceived as a hypothetical construct linked with increasing activation in centrally organized appetitive or defensive motivational systems. From this viewpoint, the task of psychophysiologists is to determine how variations in intensity within appetitive and aversive systems affect somatic and autonomic responses in well-defined experimental contexts.

**Modes of Biphasic Activation**

Assuming that emotion is organized by activity in separable appetitive and aversive systems, one central issue concerns their relationship. An assumption shared by
Defensive motivation

Figure 1. Modes of biphasic activation. Activation in hypothetical appetitive and defensive motivation systems can vary from uncoupled activation in each system to coactivation. Adapted with permission from Cacioppo & Berntson, "Relationships between attitudes and evaluative space: A critical review with emphasis on the separability of positive and negative substrates," Psychological Bulletin, vol. 115, pp. 401–23. Copyright © 1994 by the American Psychological Association.

many is that these systems are reciprocally inhibited: as activity in one system increases, activity in the other is inhibited (Konorski 1967). Bipolar measures of affective valence reflect this assumption in that a stimulus can be rated as either pleasant or unpleasant, but not both simultaneously. A more flexible conceptualization of biphasic activation was advocated by Cacioppo and Berntson (1994; see also Cacioppo, Gardner, & Berntson 1997), who presented a comprehensive model that allows all possible modes of activation. Figure 1 illustrates this scheme, in which appetitive and defensive activation can vary from being mutually reciprocal to simultaneously active to separably active. Different points in bivariate space identify instances when aversive and appetitive activation are highly coactive when they reciprocally related.

Defining critical parameters that contribute to reciprocal versus concurrent (or separable) activation of appetitive and aversive systems remains to be worked out. Reciprocal activation is certainly plausible at the stage of actual behavioral output: a specific effector is not always able to respond to two concurrent demands in parallel (i.e., one cannot run both toward and away from a stimulus at the same time). To the extent that one behavior is controlling the organism, it is less likely that another can be simultaneously active. For this reason, Grossman (1967) proposed a central integrator that "decided" which neural system could control behavior at any specific moment. It is also plausible that, at extremely high levels of arousal in either system, the relationship is typically reciprocal – as, for ex-
ample, when the search for food is actively inhibited in a situation involving high threat (see McNaughton 1989).

Conversely, coactivation in both the appetitive and aversive systems may be more probable in moderate or low arousal situations, or in situations that involve multiple independent stimuli or complex unitary (i.e. multifaceted) stimuli that simultaneously activate both the appetitive and defensive systems. Cacioppo and Berntson (1994) originally proposed the bivariate space to deal with attitudes, which are often based on multiple sources of information that have separable appetitive and defensive elements. For instance, when investigating blood or organ donorship, aspects associated with appetitive motivation (e.g., desire to help society) as well as defensive motivation (e.g., fear of pain) are readily elicited from subjects (Cacioppo & Gardner 1993).

A similar instance of coactivation occurs in studies of appetitive behavior, which are often conducted in a context of deprivation (presumably an aversive event) reinforced with food (appetitive motivation). Avoidance learning and active coping paradigms also represent instances of motivational coactivation, since they typically involve an aversive stimulus (e.g. shock) that can be successfully avoided, resulting in a melange of positive and negative cues. Mixed states of appetitive and aversive activation may be the most difficult to understand from the perspective of studying emotion, yet these tasks have been widely used in the study of emotional learning and behavior. To begin with, however, it may be more useful to understand emotional reactions in situations where reciprocal or separable activation is dominant.

System Dominance

A biphasic approach to the study of emotion also raises the issue of whether one or the other system is customarily more dominant or at an advantage in terms of mobilizing the energy and behavioral focus of the organism. When a system is proposed as primary, it is usually the aversive system (Taylor 1991). The adaptive importance of dealing with threats (e.g., defending against a predator) before satisfying appetitive urges lies in the fact that, if the threat is not dealt with, eating may no longer matter: annihilation is a clear bottom line. Therefore, defensive responses seem to take precedence over appetitive.

In a classic situation designed to assess the strength of appetitive and defensive motivation and their relationship to one another, Miller (1966) measured the strength of an animal's approach toward or retreat from a goal box associated with food and/or shock. He found that the slope of the function relating force to distance was steeper for aversive stimuli: as distance to the goal decreased, the strength of withdrawal was greater than approach. Cacioppo and Berntson (1994) characterized this steeper aversive gradient as supporting the idea of an inherent negativity bias in which responding to aversive events has primacy over those
that are appetitive. In a recent meta-analysis, Cacioppo and associates (in press) found empirical support for this proposition, with the data demonstrating stronger physiological reactions in the context of negative emotional cues compared with positive ones. We will re-examine this issue later in the chapter.

Physical Context

ANATOMICAL SUBSTRATE

Physiological responses associated with processing appetitive or aversive stimuli in the human psychophysiological laboratory include those in many of the systems discussed in this volume, including electrodermal, cardiovascular, electrocortical, electromyographic, and reflex systems. The reader is encouraged to refer to these chapters for specific information regarding the pertinent anatomical substrates.

NEUROANATOMICAL SUBSTRATE: DEFENSIVE AND APPETITIVE SYSTEMS

In a biphasic approach to the study of emotion, separable motivational systems mediating appetitive and defensive responding are posited. Whether these systems are implemented in the same or different brain structures—and how appetitive and aversive cues come to selectively activate appropriate outputs—are the critical questions when contemplating the neural substrates of emotion. To date, research has tended to focus more on the neural circuitry involved in the defensive motivational system. This is due, at least in part, to the relative ease of presenting intense aversive (compared with appetitive) stimuli in a laboratory setting (but see Ashby, Isen, & Turken 1999; Davidson & Irwin in press).

It is widely agreed that emotion is mediated in subcortical, particularly limbic structures, based mainly on lesion and stimulation studies in animal samples. As LeDoux (1987) noted, “studies of the neural substrates of affective behavior and its autonomic correlates seem always to lead to brain regions traditionally described as components of the limbic system” (p. 425). Knowledge regarding the neural substrates of emotion in humans is still quite cursory, owing to obvious limitations in research investigating the neural circuitry involved. However, new methodologies for studying the human brain in action (e.g., dense electrode arrays, fMRI, PET) promise to greatly accelerate progress in this area.

The Peripheral Nervous System

Because the psychophysiological study of emotion has traditionally focused on autonomic and somatic outputs (e.g., heart rate, blood pressure, electrodermal and muscle tension changes), it is reasonable to start an exploration of its neural substrates from these indices and work backward. Both autonomic and somatic responses are proximally controlled by the peripheral nervous system (see Guyton & Hall 1996 for an overview). In the autonomic system, anatomical and functional distinctions between the parasympathetic and sympathetic branches have been important in the study of emotion. The sympathetic nervous system is characterized by postganglionic fibers, which are quite lengthy and which branch and divide as they make their way to specific target organs. Functionally, this means that a single sympathetic fiber activates a number of different effectors and so provides an anatomical substrate for Cannon’s emergency reaction, which proposed a volley of responses—heart rate and blood pressure increases, electrodermal reactions, increase in respiration rate and depth—on the basis of sympathetic activation. Conversely, the postganglionic fibers in the parasympathetic branch are short and hence more likely to target a specific effector.

Most organs are innervated by nerves from both the parasympathetic and sympathetic divisions, which tend to exert opposite effects. Figure 2 lists effects of parasympathetic and sympathetic activation on a variety of different systems typically measured in the study of emotion. The reciprocal effects of these two systems on different organs are mediated by the release of different neurotransmitters at the neuroeffector junction, with acetylcholine released by parasympathetic fibers (cholinergic) and noradrenaline released by sympathetic fibers (adrenergic). Subsequent actions (e.g., increase or decrease in heart rate) are also temporally differentiated by the fact that noradrenaline dissipates slowly whereas acetylcholine dissipates more rapidly. Thus, parasympathetic control will tend to activate specific organs with rapid, phasic effects, whereas sympathetic control is not only more diffuse but also somewhat longer-lasting.

Although sympathetic activity has been associated with mobilization for responding to aversive events, as Cannon originally proposed, some theorists have associated pleasant affect with parasympathetic dominance (Arnold 1960; Gellhorn & Loofbourrow 1963; Schneirla 1959). According to this view, pleasure was presumed to be related to the vegetative, homeostatic controls implemented by the parasympathetic system, because appetitive situations (by definition) do not involve stress and its sympathetic manifestations. Current thinking does not support such a simple relationship. First, rather than simply responding to aversive stimulation, the sympathetic nervous system is more generally designed to prepare and instantiate action, a nonspecific demand. Sympathetic activation clearly occurs in appetitive contexts, such as sexual behavior (Guyton & Hall 1996) and adventure seeking (Zuckerman 1982). To the extent that sympathetic activity is involved in facilitating action, it may play a role in those that subserve either appetitive or aversive motivation.
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<thead>
<tr>
<th>Organ</th>
<th>Effect of Sympathetic Stimulation</th>
<th>Effect of Parasympathetic Stimulation</th>
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<tr>
<td>Heart Muscle</td>
<td>Increased rate and force of contraction</td>
<td>Decreased rate and force of contraction</td>
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<tr>
<td>Blood Vessels</td>
<td>Most often constricted</td>
<td>Most often little or no effect</td>
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<tr>
<td>Sweat Glands</td>
<td>Copious sweating (cholinergic)</td>
<td>Sweating on palms of hands</td>
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<tr>
<td>Skeletal Muscles</td>
<td>Increased strength &amp; glycogenolysis</td>
<td>None</td>
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<tr>
<td>Apocrine Glands</td>
<td>Thick, odoriferous secretion</td>
<td>None</td>
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<tr>
<td>Pupil of Eye</td>
<td>Dilated</td>
<td>Constricted</td>
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<tr>
<td>Ciliary Eye Muscle</td>
<td>Slight relaxation (far vision)</td>
<td>Constricted (near vision)</td>
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<td>Gut (Lumen)</td>
<td>Decreased peristalsis and tone</td>
<td>Increased peristalsis and tone</td>
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<td>Increased tone (usually)</td>
<td>Relaxed (usually)</td>
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<td>Lung Bronchi</td>
<td>Dilated</td>
<td>Constricted</td>
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<td>Penis</td>
<td>Ejaculation</td>
<td>Erection</td>
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<tr>
<td>Adrenal Medulla</td>
<td>Increased secretion</td>
<td>None</td>
</tr>
</tbody>
</table>

Second, the notion that the aversive system is associated with sympathetic activity and the appetitive with parasympathetic activity suggests a mode of consistent reciprocal activation between the sympathetic and parasympathetic branches that is no longer tenable. This notion has been replaced by the comprehensive view that these systems can be coactive, as illustrated in Figure 3. Berntson, Cacioppo, and Quigley (1991; see also Berntson et al. 1994) proposed a theory of autonomic control in which physiological measures of a dually innervated end organ (e.g., the heart) may differ as a function of the weighting of activation in the parasympathetic and sympathetic systems: systems can be independently active, reciprocally controlled, or coactive. Quigley and Berntson (1990) further demonstrated that heart rate acceleration to an aversive stimulus (in the rat) is larger than to a low-intensity stimulus not because of differential sympathetic activity but because parasympathetic activity decreases with high-intensity stimulation. Similarly, Wenger, Averill, and Smith (1968) concluded that autonomic responses measured when males processed erotic texts indicated coactivation rather than parasympathetic or sympathetic dominance. This approach suggests that independent measures of sympathetic and parasympathetic autonomic system activation may be essential in understanding peripheral physiological response measured in emotional contexts.

**Cortical and Subcortical Controls of Autonomic and Somatic Activity**

If activation of the peripheral nervous system is important in modulating the responses in many of the autonomic and somatic systems measured in the psychophysiological study of emotion (e.g., heart, skin, muscles, gut), then
PARASYMPATHETIC RESPONSE

<table>
<thead>
<tr>
<th>SYMPATHETIC RESPONSE</th>
<th>Increase</th>
<th>No Change</th>
<th>Decrease</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Increase</strong></td>
<td>Coactivation</td>
<td>Uncoupled Sympathetic Activation</td>
<td>Reciprocal Sympathetic Activation</td>
</tr>
<tr>
<td><strong>No Change</strong></td>
<td>Uncoupled Parasympathetic Activation</td>
<td>Baseline</td>
<td>Uncoupled Parasympathetic Withdrawal</td>
</tr>
<tr>
<td><strong>Decrease</strong></td>
<td>Reciprocal Parasympathetic Activation</td>
<td>Uncoupled Sympathetic Withdrawal</td>
<td>Coinhibition</td>
</tr>
</tbody>
</table>

Figure 3. Modes of autonomic control. Activation in the parasympathetic and sympathetic branches of the autonomic nervous system are proposed to vary from coactivation to independent activation. Adapted with permission from Berntson, Cacioppo, & Quigley, “Autonomic determinism: the modes of autonomic control, the doctrine of autonomic space, and the laws of autonomic constraint,” *Psychological Review*, vol. 98, pp. 459–87. Copyright © 1991 by the American Psychological Association.

Understanding the neural circuits involved in emotion will depend to some degree on determining which brain structures are important in controlling autonomic and somatic activity. Not surprisingly, control systems occur at every level of the central nervous system: from the spinal cord to the brainstem to subcortical and cortical structures (for more extensive discussions see Gellhorn & Loebfornow 1963; Guyton & Hall 1996; LeDoux 1987). Thus, for instance, mechanisms in the spinal cord can affect the level of activity in sympathetic and parasympathetic fibers in the absence of supraspinal controls.

Among the more important brainstem control structures is the medulla oblongata. Electrical stimulation of the rostral portion of this structure evokes sympathetic reactions throughout the body, including heart rate and blood pressure increases, pupil dilation, inhibition of gastrointestinal activity, secretion of sweat, and so on. Conversely, activation of the vagal nucleus of the medulla oblongata causes a decrease in heart rate and blood pressure and an increase in gastrointestinal activity—reactions associated with parasympathetic activity. Because of its ability to control many elements of autonomic function, the medulla oblongata has been proposed as the final common pathway for autonomic responses associated with defense reactions (LeDoux 1987).

Control of the autonomic as well as the somatic nervous system is clearly tied to activity in brain structures more advanced than either the spinal or brainstem mechanisms. The neural structures proposed to mediate the emotional reactions subserved by the peripheral nervous system continue to evolve, as more information becomes available about the brain from both animal and human research. In general, the neural substrates in emotion are not usually discussed with the goal of assessing whether there is evidence for separable appetitive and aversive systems; rather, many theoretical schemes have lumped appetitive and aversive motivation together as involving “emotion” or have implicitly described a system involving aversiveness, since this has proved more amenable to study. Nonetheless, an effort will be made in the following review to highlight research that concerns evidence for or against the notion of separable appetitive and defensive systems. What is clear is how rapidly the views of brain structure in emotion have changed in the last 50 years.

**Hypothalamic Focus**

Instead of focusing on peripheral physiological changes in emotion, Cannon advocated a more central approach. He maintained that key structures in the brain, particularly the hypothalamus and thalamus, were important in controlling emotional reactions. His view anticipated modern theorizing in that activity in neural circuits was held to affect neurohumoral and neurochemical events that impact on peripheral reactivity. A focus on the hypothalamus as central in emotion was supported by a number of animal studies which demonstrated that electrical stimulation of the hypothalamus produced physiological reactions associated with sympathetic activation—and even full motor sequences indicative of emotion, including freezing, piloerection, hissing, and attack (collectively termed the “defense reaction”; Hess & Burgger 1943) as well as grooming, mating, and feeding or drinking. Lesions of the hypothalamus (Bard 1934) effectively eliminated these reactions.
Many prominent theorists at this time (e.g. Hess 1957; Morgan 1937; Stellar 1954) confidently subscribed to the notion that the hypothalamus was the main structure implicated in emotion, the “hub” of the limbic system (Gellhorn & Looffbourou 1963), the “driver at the wheel” (MacLean 1954). Stimulation studies suggesting that the anterior and posterior portions of the hypothalamus were differentially associated with parasympathetic and sympathetic reactions (see Grossman 1967 for a review) led some theorists (e.g. Bovard 1962) to suggest that the anterior (and lateral) hypothalamic region was a “positive reward system” whereas the posterior (and medial) region constituted a negative system – a view not widely held today. Despite proposing a much more extensive neural circuit, Papez (1937) also focused on the hypothalamus as a central structure in mediating emotion, particularly bodily responses. In addition to important thalamic-hypothalamic connections, Papez’s circuit included the cingulate cortex and hippocampus. This circuit is generally considered incomplete today, mainly because it neglects to include structures currently thought important in emotion (e.g. amygdala) and includes structures (e.g. hippocampus) that are now recognized as more important for memory (LeDoux 1987). Nonetheless, certain key structures in Papez’s circuit, such as the thalamus and cingulate cortex, have been implicated in recent neuroimaging explorations of emotional processing (Breiter et al. 1996; George et al. 1995; Lane et al. 1997a,b).

Periaqueductal Central Gray

Grossman (1967) argued that the focus on the hypothalamus was misleading because data showed that hypothalamic lesions are not irreversible and that stimulation or damage to other parts of the limbic system (e.g. amygdala) can affect emotional behaviors as well. His view was that the hypothalamus was part of a larger, more complex system and that the “apparently unique effects of hypothalamic damage or stimulation may be a ‘geographic’ artifact” (p. 608) due in part to the fact that the “hypothalamus, because of its peculiar anatomical configuration, seems to act as a funnel for most afferent and efferent impulses to the cortex” (p. 612). Support for his view was provided by studies demonstrating that defensive behavior can be elicited by stimulating the central gray, even after the hypothalamus has been lesioned (Hunsberger, cited in LeDoux 1987), and that lesions in the hypothalamus that destroy cell bodies but not fibers of passage do not disrupt conditioned emotional behavior (Coyle & Schwartz 1983) whereas lesions of the central gray do (LeDoux 1987).

A series of studies conducted by Fanselow and his colleagues (1995; Fanselow 1991, 1994) demonstrated that different regions in the periaqueductal central gray of the rat control freezing and active defense, with lesions and stimulation of the ventromedial portion affecting defensive freezing behaviors and those involving the dorsolateral region affecting defensive actions such as attack and escape. It is interesting that distinct actions appear to have anatomical counterparts that are organized longitudinally within the periaqueductal gray region; for example, jumps are elicited by stimulation in caudal regions whereas defensive upright posture and withdrawal are elicited by stimulation in more rostral regions. Based on these and other data, LeDoux (1987) suggested that projections to the central gray may be the important link in the descending motor pathway for defensive behavior. Nonetheless, the hypothalamus remains central in mediating many of the autonomic responses measured in emotion.

Amygdala

Another limbic structure, the amygdala, has more recently become a focus in neuroanatomical models of emotion – particularly in terms of its role in mediating associations involving motivationally relevant events, positive and negative (Amaral et al. 1992; Gaffan 1992). Not surprisingly, the nature and type of data supporting the role of the amygdala in emotion are very similar to those originally invoked to support the hypothalamus as the center of the emotion system: lesion and stimulation studies have indicated that specific nuclei in this structure mediate specific emotional phenomena, both appetitive and defensive. Stimulation of the amygdala produces rage, attack, and defense reactions similar to those earlier elicited by activation of the hypothalamus. Moreover, bilateral lesions of the amygdala are, in part, responsible for the observance of the Klüver–Bucy syndrome, in which monkeys lose fear behaviors, become hypersexual, and are indiscriminate with respect to mouthing food and nonfood stimuli. Lesions of the amygdala eliminate the fear-potentiated startle response (Davis 1986) and have been implicated in disrupting appetitive behaviors such as mating, food acquisition, and reward learning (Gaffan 1992). An extensive review of research involving effects of amygdala lesion and stimulation is available in the volume edited by Aggleton (1992).

Geschwind (1965) earlier suggested that the amygdala was particularly necessary for associating stimuli with affective or motivational labels. Amaral and co-workers (1992) elaborated on this by suggesting that “the amygdaloid complex might have widespread ... roles ... that might range from facilitating the selection of an appropriate food or mate, to insuring the avoidance of dangerous situations or substances, to facilitating the aesthetic appreciation of art or music” (p. 2). Clearly, this structure is seen as potentially able to mediate a wide range of behaviors relevant in defensive and appetitive motivation.

A primary reason for considering the amygdala a central component in emotion is that, relative to other limbic structures, it includes multiple afferent and efferent connections to cortical, subcortical, and brainstem structures, which allows it to receive inputs from – and control outputs to – many parts of the brain, including those that have
been implicated as important in mediating the autonomic and somatic responses involved in emotional behaviors (Amaral et al. 1992). Thus, the amygdala contains much of the basic architecture necessary for evoking a wide range of behavioral and physiological responses on the basis of multiple types of input cues (i.e., both internal and external). Figure 4 illustrates some of the afferent, efferent, and intra-amygdaloid connections based on a variety of sources, including Amaral et al. (1992), Davis (1989), Fanselow (1994), LeDoux (1987), and Nieuwenhuys, Voogd, and van Huijzen (1988).

A number of general points can be made about the amygdala. First, it is composed of several different nuclei, each of which receives and sends information to a wide variety of different structures. It is no longer reliable to refer to “the amygdala” as having one function or another; rather, different nuclei have both specific inputs and specific outputs. Whereas some nuclei (e.g., the central nucleus) seem to be predominantly output structures, others (e.g., lateral nucleus) are primarily input structures. Second, the various nuclei within the amygdala are extensively interconnected, with the organization of these connections reflecting the input–output function of different nuclei. Nuclei that primarily serve input functions, such as the lateral and basal nuclei, receive many fewer intra-amygdaloid projections than nuclei that primarily mediate output functions – for example, the central nucleus, which is extensively interconnected with all amygdaloid nuclei (Amaral et al. 1992).

In order to mediate effectively both appetitive and defensive reactions to the variety of potential stimuli encountered in the world, a neural system implementing motivation would need to receive extensive perceptual and memorial information. In fact, inputs to the lateral nucleus of the amygdala (see Figure 4) include those from unimodal cortical sensory areas – including visual, auditory, and somatosensory (via the insula) information – as well as from polysensory association cortex. Olfactory input is relayed to the periamygdaloid (rather than lateral)
nucleus, and gustatory information may be relayed to this nucleus via its thalamic input. Information arriving from the senses is in most cases fairly well processed; whereas inputs from primary sensory cortex are few, the presence of multiple unimodal and polymodal inputs suggest the amygdala in general receives information that has received considerable cortical processing. Note especially that inputs representing information on physiological functions are also available to the amygdala, with input from the hypothalamus relayed to the medial nucleus as well as directly to the central nucleus and with visceral information from the brain stem relayed via the thalamus to the lateral nucleus.

The presence of thalamic inputs to the lateral as well as central nuclei indicates that some relatively raw sensory information is probably also available to the amygdala, although this information would presumably be processed only to the level of gross physical features (loud, bright, etc.). As LeDoux (1996) emphasized, these alternative pathways to the amygdala, thalamic and cortical, may play an important role in understanding emotional processing of different sensory stimuli. It is worth emphasizing, however, that (i) complex stimuli (e.g., pictures) that require higher-level perceptual processing for encoding are probably not processed via direct thalamic-amygdaloid input, and (ii) simple unconditioned stimuli are the best candidates for direct activation of the amygdala through thalamic relays.

In the nonhuman primate, the amount of visual information relayed to the amygdala appears to be greater than auditory or somatosensory information (Amaral et al. 1992), which might reflect the fact that, for primates as well as for humans, much behavior is elicited on the basis of visual cues. Consistent with the idea that amygdaloid inputs reflect species-specific perceptual preferences, olfactory-amygdaloid connections are so central in the rodent that Gellhorn and Loofbourrow (1963) concluded the amygdala's role in emotion was only as "a secondary olfactory center."

Outputs from the amygdala are extensive as well, and they include almost all of the structures highlighted as important in emotional processing — with direct connections to the hypothalamus, the central gray, the brainstem, the striatum, and cortical structures including the cingulate gyrus, frontal lobe, visual cortex, and more. Interestingly, a rough division in amygdaloid outputs can be made between the central and basal nuclei. As Figure 4 illustrates, the central nucleus of the amygdala mediates outputs to many of the hypothalamic and brainstem structures involved in emotional responses, whereas outputs from the basal nucleus consist primarily of cortical targets, including visual areas of temporal and occipital lobes as well as frontal, anterior cingulate, and so on. This organization makes it possible for different amygdaloid nuclei to be involved in activating information relevant to physiological response or associative meaning.

An additional output from the basal nucleus is to the nucleus accumbens, which — together with the ventral striatum and other dopaminergically innervated structures — has been implicated as important in modulating appetitive behaviors (Koch & Schnitzler 1997) and in reward learning (see Everitt & Robbins 1992). Activation of both the nucleus accumbens and amygdala have been found in studies investigating the rewarding properties of cocaine use in humans (Breiter et al. 1998), lending support to the notion that the amygdala is a contender as a key component of both appetitive and defensive motivational systems.

**Neurohumoral Control**

In addition to engaging specific effectors, activation of the sympathetic nervous system has significant implications for release of a number of blood-borne substances that also affect physiological reactivity (for overviews see e.g. Baum, Grunberg, & Singer 1992; Grunberg & Singer 1990). One pathway, emphasized by Cannon, begins with sympathetic activation of the adrenal medulla (in the kidney), which releases catecholamines such as epinephrine and norepinephrine that have the same influence on anatomical structures as direct sympathetic innervation — that is, increasing heart rate, blood pressure, and respiration while redirecting blood flow to active muscles. These sympathetic effects of catecholamines on physiological systems can be longer-lasting than direct sympathetic activation and can also affect organs not directly innervated by sympathetic fibers. A second pathway involves pituitary-adrenocortical activation, a focus of Selye's (1950) work on stress. This path is from the pituitary to the adrenal cortex (also in the kidney), which leads to production of corticosteroids, including the commonly measured substance cortisol. Release of cortisol is stimulated by adrenocorticotropic factor (ACTH) from the brain and functions to increase energy mobilization (see Levine 1986).

Although biochemical measures of catecholamines (e.g., epinephrine, norepinephrine, and cortisol) are common in research investigating both brief and sustained stressors (e.g. Cacioppo et al. 1995), inclusion of these indices of sympathetic activation is less typical in emotion research. Part of the difficulty may lie in obtaining assays (e.g., in blood, urine, or even saliva) at the frequency and rate at which different emotional stimuli are typically presented in emotion research. In addition, early hypotheses (e.g. Ax 1953) that epinephrine and norepinephrine may be differentially associated with fear and anger were disconfirmed, suggesting these biochemical indices could not differentiate among discrete emotions. Rather, catecholamines in particular appeared to be sensitive to the arousing aspects of a situation, increasing in environments that are novel or complex as well as in those that are emotionally arousing (Frankenhaeuser 1975). Such a pattern is clearly informative if the psychophysiological investigation seeks to understand effects of pleasure and arousal on physiological
response. Hence, it would be useful to include these measures more routinely in studies of emotion.

**Cognitive Models**

Neuroanatomical models propose that inputs from a number of different sources converge on sub cortical structures such as the amygdala, which controls outputs to the somatic and autonomic nervous system as mediated through various structures, including the central gray and the hypothalamus. This same type of neural network can be described at a cognitive level, where a model of the functional relationship between input and output is provided without identifying specific anatomical structures.

One popular type of cognitive model is instantiated in various forms of “appraisal” theory (Lazarus 1991), in which stored information (appraisals) regarding the stimulus (Arnold 1970) or physiological response (Schacter & Singer 1962) is the critical variable determining the emotionality of an experience. When physiology is the focus of the appraisal process, it is usually conceptualized as involving undifferentiated arousal (Schacter & Singer 1962). Appraisal theories seek to provide a mechanism by which the same stimulus (input) can produce different reports of emotion (output) and by which different situations can produce reports of the same emotion. This is enabled by allowing appraisals – stored interpretations of stimuli and responses – to control emotional experience.

More explicitly information-processing models of emotion propose that emotional representations code multiple types of information, including stimulus characteristics, response features, and stored associations (e.g. Bower 1981; Lang 1979). Lang’s bioinformational theory (1979, 1984, 1994a) conceives of emotion as a cognitive network that includes stimulus and response units that are linked by associations (see Figure 5). Lang distinguishes between inputs that are perceptually based (stimulus) and those that are conceptually based (meaning). Whereas “stimulus units” code information regarding sensory and perceptual features (e.g., the visual, acoustic, and tactile features of a snake and the current context), “meaning units” provide semantic information previously learned about the stimulus (e.g., snakes are dangerous). Meaning units are an associationist interpretation of what might typically be termed appraisals (see Lang 1994a). That is, semantic information – previously learned and associated with specific stimulus and response contexts – is part of the memory representation for emotional (and nonemotional) events.

An important feature of Lang’s (1979) bioinformational theory is its inclusion of response units in the representation of an emotional stimulus. A number of cognitive models focus almost exclusively on the representation of stimulus and semantic information in memory without considering the coding of relevant behavioral outputs. In bioinformational theory, on the other hand, emotion is instantiated primarily via response units, which code associated actions (e.g., running) and reactions (e.g., heart rate acceleration) that are part of the associative structure of an emotional event. Response information is linked to input cues on the basis of both unconditioned and conditioned associations. Consistent with the use of these terms in the learning literature, unconditioned responses are innate, hard-wired links between stimulus features (e.g. sudden movement) and a particular action (e.g. startle response), whereas conditioned associations reflect links forged through experience.

Network models (e.g. Anderson 1983; Lang 1979) and more recent distributed models of cognition (e.g. McClelland & Rumelhart 1986) view cognitive processing as an iterative process in which information in an input cue initially controls the level of activation in memory. Associated units are activated, and this information is subsequently fed back into the system as a new input cue, allowing different types of information (e.g., stimulus, response, or meaning) to further affect the level of network activation. Thus, whereas physiological responses are often considered outputs of emotional processing, they can also serve as input cues (consistent with James’s earlier suggestion). The iterative nature of emotional processing, in which current information regarding both stimulus and response is repeatedly re-entered as input to the processing system, is also highlighted in Cacioppo and colleagues’ somato-visceral affective model of emotion (SAME; Cacioppo, Berntson, & Klein 1992a; Cacioppo et al. 1993).

From a methodological perspective, these theories suggest that the nature, quality, type, and amount of information in the input cue is important, since these parameters have implications for the degree of associative activation and physiological output (see e.g. Lang et al. 1980). Because stimulus, response, or meaning information can serve as input that initiates or maintains a processing episode, the bioinformational framework can accommodate theories that identify the primary input to emotion as physiological (e.g., the Jamesian hypothesis or facial feedback theories) as well as more traditional views that focus on sensory stimulation.

All events can be considered as coded and processed in associative structures of the type described here, so what is it that makes a particular cognitive representation “emotional”? Lang (1994b) and LeDoux (1996) agree that it is specific associations to the motivational systems mediating appetitive and defensive behavior (e.g. limbic structures) that are the defining feature of an emotional representation. To the extent that input cues activate these subcortical motivational systems, the resulting cognitive processing can be considered to be emotionally engaging. It is because of associations to these basic biphasic motivational systems (and the resulting activation of relevant autonomic and somatic responses) that physiological activity is a hallmark of emotional processing.
Figure 5. Top panel. A cognitive representation of an emotional event includes information relevant to (1) the stimulus and environmental context, (2) learned semantic associates, and (3) appropriate behavioral and physiological responses. Connections to primitive appetitive and defensive motivational systems define an "emotional" event. Bottom panel. Example of a cognitive representation coding an encounter with a snake in the woods. Adapted with permission from Lang, “Cognition and emotion: Concept and action,” in Izard, Kagan, & Zajonc (Eds.), Emotion, Cognition and Behavior. Copyright 1984 Cambridge University Press.
Inferential Context

BIOMETRICS: MENSURATION AND QUANTIFICATION PROCEDURES

Because emotional responses can be measured in many of the physiological systems addressed in this volume, the reader is referred to chapters on specific response systems for information concerning current measurement and quantification techniques. Assessments of changes in electrodermal, somatic, respiratory, reflex, cardiovascular, or cortical activity assessed in the context of emotional (appetitive or aversive) stimulation should be measured, quantified, and mapped to system changes in ways that are consistent with those recommended in this volume.

PSYCHOMETRICS: THE PSYCHOPHYSIOLOGICAL STUDY OF EMOTION

According to the view expressed here, one goal of psychophysiological studies of emotion is to determine the nature of the relationship between inputs (that vary in hedonic valence and arousal) and outputs (measured in a variety of different response systems) as they vary in specific experimental contexts. Making inferences specifically about the psychophysiology of emotion will rely on clearly (1) defining the affective nature of the stimuli, (2) determining the task context, and (3) defining the measured output.

Defining Affective Stimuli

In order to study emotion, it is necessary to manipulate the affective characteristics of experimental stimuli. Research prompted by a biphasic view of emotion suggests that experimental stimuli should systematically vary in terms of pleasure and arousal; a view that sees emotions as discrete, on the other hand, seeks stimuli that vary in terms of eliciting specific emotional states (e.g., fear, anger, sadness). With either paradigm, some type of bootstrapping operation is needed to initially identify stimuli that differ in terms of emotionality.

In human subjects, verbal reports of emotion (e.g., pleasure and arousal ratings; Lang et al. 1990) are often used to classify stimuli a priori. Over the past ten years, our laboratory has developed different sets of experimental stimuli (pictures — Lang, Bradley, & Cuthbert 1998; sounds — Bradley & Lang 1999a; words — Bradley & Lang 1999b) that groups of subjects have rated in terms of both pleasure and arousal. The resulting stimulus collections allow one to select materials that systematically vary in valence and arousal while controlling for other potentially relevant factors (e.g., semantic category). Defining affect in this way allows one to begin to assess the impact of the emotional variables of pleasure and arousal on physiological, behavioral, and subjective report measures.

It is important to include neutral stimuli (i.e., neither highly pleasant nor unpleasant) when investigating emotion in order to assess the physiology associated with the task itself. As discussed more fully in what follows, specific processing tasks can affect the direction of physiological change; the inclusion of neutral stimuli allows one to assess this facet of the experimental procedure. The physiology of the task (imagery, anticipation, etc.) can be determined by assessing each measured response system (cardiovascular, electrodermal, etc.) in the context of processing neutral stimuli. Then, physiological responses associated specifically with emotion will rely on obtaining differences between processing neutral stimuli and those that are affectively engaging.

At the least, then, investigations of emotion should include three groups of affective stimuli, consisting of pleasant (high-arousal), neutral (low-arousal), and unpleasant (high-arousal) stimuli. Use of this minimal affective set allows one to assess effects due to differences in: (i) hedonic valence, where measurable differences are obtained between pleasant and unpleasant stimuli; and (ii) arousal, where significant differences are obtained between arousing (i.e., pleasant or unpleasant) and neutral, calm stimuli. Studies including only two of these three conditions (e.g., aversive–neutral) make it difficult to disassociate effects of stimulus arousal from effects of stimulus valence on physiological and behavioral response.

A more complete experimental design that is consistent with a biphasic view involves manipulating the level of arousal within both pleasant and unpleasant stimulus sets (Cuthbert, Bradley, & Lang 1996); this allows one to assess biphasic reactions at varying levels of intensity. If the goal is further to study whether physiological responses differ in terms of discrete emotions (e.g., fear, anger), it is important to include at least two emotions at each level of valence (e.g., two pleasant emotions; see Cacioppo et al. 1993) — preferably balanced for level of arousal. Otherwise, it is impossible to conclude that obtained differences are due to the physiology associated with the specific emotional state and not simply due to valence or arousal differences.

Determining the Task Context

Comparisons are often made between widely different paradigms of instigation. For example, the physiology during fear has been assessed in contexts as diverse as hearing loud noises, anticipating shock, imagining an intruder in the house, looking at a picture of an amputated leg, viewing a scary film, giving a speech, putting one’s hand in cold water (“cold pressor” test), or hearing an anguished scream. Conversely, positive reactions are compared across such diverse contexts as receiving money, listening to joyful music, looking at a picture of puppies, viewing an erotic film, imagining a day on the beach, receiving a good grade, thinking about winning the lottery, or anticipating a vacation.

Making comparisons across very different contexts has led to some confusion when trying to extrapolate effects
of emotion on psychophysiological response. For instance, cardiac reactions are often more different when processing affectively similar events in different tasks (e.g., heart rate decelerates during unpleasant picture viewing yet accelerates during unpleasant mental imagery; Lang et al. 1990) than when processing affectively different events in similar tasks (e.g., heart rate accelerates during imagery of pleasant and unpleasant events; Levenson 1992). In this case, the task context of perception or imagination has a strong influence on the direction of heart rate change. Making sense of cardiac patterns as a function of variations in hedonic valence and arousal will require careful consideration of the physiology of the task itself. In addition, whereas both perception and anticipation often produce triphasic cardiac waveforms that include an initial deceleration followed by acceleration and a secondary deceleration, the appearance and weighting of each component can vary with motor requirements (Jennings et al. 1970), ease of stimulus categorization (Bull & Lang 1972), or stimulus familiarity (Bradley, Cuthbert, & Lang 1993a). Thus, individual components of cardiac reactivity can be affected by task variables not particularly relevant to differences in emotion.

The task contexts typically used to induce affective reactions in the laboratory can be roughly sorted into the four categories of perception, anticipation, imagination, and action. In perception, the task is to process sensory information that varies in emotion (e.g., hedonic valence and arousal) and that can be presented in various modalities, such as visual (pictures, words, films), acoustic (sounds, music), tactile (shock, cold pressor), olfactory (odors), or gustatory (foods). In imagination, the primary task is to generate mentally an emotional stimulus or event. This task relies heavily on the human's ability to internally retrieve and elaborate information relevant to a particular object or event. In anticipation, the task is simply to await the presentation of a sensory appetitive or aversive stimulus, usually signaled by a neutral cue (e.g., tone or light). Most classical conditioning paradigms fall into this class. In contexts involving action, the task involves a specific overt activity, such as giving a speech or posing facial actions.

Careful attention to the task context should help to terminate comparisons between reactions elicited during presentation of a speech and anticipation of electric shock, for example, on the basis that both may elicit fear or that both are aversive. Rather, the psychophysiological study of emotion will need, at least at first, to restrict comparisons to data obtained in similar contexts. Emotional reactions in perception may differ both quantitatively and qualitatively from emotion in imagination, owing to the requisite physiology of these different tasks as well as to differences in the nature and type of information available in the affective cue. Clearly, the psychophysiology of emotion in action can differ from vigilant anticipation. Parameters need to be identified, within the context of each task, that have implications for motivational activation—that is, the ease with which hypothetical appetitive and aversive neural systems are activated—as well as for the nature of elicited physiological responses that are related to task but not emotion.

**Perception.** Perceptual cues can vary in a number of ways that may influence their ability to activate basic motivational systems or the degree of physiological response. Among these are: (1) the sensory modality of the cue (e.g., visual, acoustic, tactile), (2) the degree to which the sensory cue is an unconditioned or conditioned stimulus, (3) the duration of the cue, and (4) whether the information in the cue is static or dynamic.

For instance, cues in different modalities may have differential access to motivational circuits. As noted earlier, visual input to the amygdaloid complex in nonhuman primates is more extensive than auditory input (Amaral et al. 1992), suggesting that modality could be important in activating motivational dispositions. Whether a cue is unconditioned or conditioned reflects the presumed contributions to emotional reactivity of both learning and hard-wired associations. Whereas intense physical stimuli such as painful shocks or loud noises reflexively (and unconditionally) prompt defensive reactions, symbolic stimuli such as the pictures, films, and verbal scripts often used in emotion research rely on learning for motivational activation and may be expected to be more variable.

The importance of stimulus duration in affecting physiological reactions was highlighted in Selye's (1974) general adaptation syndrome, in which a brief stressor was proposed to produce a phasic alarm reaction followed by bodily exhaustion and system collapse after prolonged exposure. More generally, the duration of a specific appetitive or aversive stimulus may control whether sensitization (increased responding) or habituation (decreased responding) is a factor contributing to the pattern of physiological reactivity. Finally, a sensory cue can differ in the amount of information that it provides over time, ranging from a relatively static cue (e.g., a picture) to one that is quite dynamic (a film); see Simons et al. (1999). Physiological systems engaged by novel stimulation (i.e., orienting responses) may contribute substantially to the measured physiology in dynamic processing. Taken together, a keener appreciation of variables that may affect reactivity will help us more clearly interpret effects of emotion on psychophysiological response.

**Imagination.** Imagery (emotional reliving) paradigms have been used extensively in psychophysiological investigations of emotion. In these tasks, participants are instructed to mentally generate an emotionally evocative event based on either a text cue (i.e., a narrative script) or a perceptual cue (e.g., using a picture or film as an
imagery prompt). Important parameters in studies of emotional imagery include: (i) the nature of the information in the imagery cue, (ii) whether the imagined responses are passive or active, and (iii) whether the events imagined have been personally experienced or are fictional.

A number of studies have indicated that the nature of information in the cue affects emotional reactions. Lang and his colleagues (Lang et al. 1980; Miller et al. 1987) have demonstrated that physiological reactions differentiating fearful and neutral imagery are accentuated when response information (e.g., “imagine that your palms are sweaty”) is included in the prompt compared to when the imagery cue describes only information related to the stimulus context. Jones and Johnson (1978) demonstrated that imagery cues describing action produced more cardiac reactivity during imagery than cues describing passive scenes. Taken together, these data are consistent with the notion that physiological reactions during imagery reflect activation of response-related information in memory, cued in part by information present in the input prompt. Additionally, when subjects imagine events that they have personally experienced, more appropriate skin conductance and heart rate changes occur than when scripts are imagined that are not personally relevant (Miller et al. 1987), suggesting that motivational and physiological activation is more successful when an existing associative network can be activated. The parameters affecting physiological reactions during emotional imagery are discussed more fully in Cuthbert, Vrana, and Bradley (1991).

**Anticipation.** Waiting for an unpleasant or pleasant event to occur is the hallmark of classical conditioning studies, in which a neutral cue signals the upcoming occurrence of an unconditioned aversive or appetitive stimulus. Studies of anticipation (and, to some extent, conditioning) focus on physiological reactions during the warning interval—that is, before an emotional stimulus is actually presented. Numerous temporal and associative parameters have been noted as critical in obtaining conditioning effects (Mackintosh 1983; Stern 1972) and are potentially relevant when assessing emotional reactions during anticipation (see Putnam 1990). Critical variables in terms of motivational and physiological activation include: (i) the modality of the warning cue, (ii) whether the warning cue is continuous or discrete, and (iii) whether the warning cue signals a specific (e.g., snake) or nonspecific (e.g., “something bad”) target.

The sensory modality of an anticipated perceptual event has been important for theorists such as Graham (1992), who proposed differential modulation of physiological responses (e.g., the acoustic startle reflex) depending upon the modality to which attention is directed. Thus, stimulus modality can affect certain physiological reactions independent of, or in addition to, emotional variables. Whether the warning cue is continuous or discrete has implications for the amount of orienting (perceptual intake) activity that is occurring concurrent with anticipation, which again can affect the type of physiological reactions during the anticipatory period independent of effects due to affective parameters. Finally, the specificity of the warning cue affects the nature and type of information that can be retrieved or imagined during the anticipatory period, which can affect the pattern of physiological response.

**Action.** Contexts involving overt action are employed less often in psychophysiological investigations of emotion, and for good reason. Gross motor activity can saturate amplifiers, produce artifact in cardiovascular and electrodermal records, and generally interfere with recording the often smaller physiological effects related to emotional parameters. The main variable in an action context will generally be the required activity: giving a speech will be more physiologically demanding than a simple button press, for example. Assessing changes due to emotional parameters such as pleasure and arousal will be most difficult in contexts that involve considerable activity. Ambulatory monitoring studies, which attempt to study emotional reactions such as panic as they occur in the natural environment, fall within this class of paradigms. These investigators must cope with issues involved in trying to separate the physiology of emotion from the physiology of the ongoing action (see e.g. Turpin 1990; Wilhelm & Roth 1996).

**Response Measurement**

Most theorists have recognized that the data base of emotion—indices that can be measured and quantified in the laboratory—includes three systems: (1) subjective report, (2) overt action, and (3) physiological response (see e.g. Lang 1968). Subjective reports of affective experience include verbal descriptions (e.g., “I’m afraid”), ratings of emotion (e.g., ratings of fear on a scale of 1 to 10), reports of physiological responses (e.g., identification of bodily responses that occurred), and other methods that elicit reports from subjects regarding their awareness of affective reactions. Overt behaviors—such as running, jumping, fighting, freezing—used extensively in studies of motivated behavior in laboratory animals are somewhat less commonly measured in human studies. Representative overt behaviors in the human laboratory include expressive language (e.g., “I hate you”), vocalization measures (see Scherer 1986), performance measures (e.g., reaction time), and observable facial expressions (Ekman 1971). Physiological responses comprise bodily events that can be assessed using psychophysiological instrumentation and methods yet are not necessarily observable. In emotion research to date, these have included responses in cardiovascular, electrodermal, gastric, somatic, reflex, central, and neurohumoral/ neurochemical systems.

There are a number of interesting relationships among three-system measures of emotional responses. First, it is clear that affective reactions can be assessed solely through
two measures of overt behavior (e.g. freezing) and physiological (e.g. cardiovascular) response in the absence of verbal reports, as animal studies clearly demonstrate; motivational systems operate independently of a link to a developed language system. Second, when behavior is observable, changes in associated physiological measures will also occur. To the extent a person is overtly smiling, for example, changes will be detected in EMG measures over the appropriate muscles. Thus, behavioral and physiological measures of emotion can be distinguished by whether the response is observable: overt behaviors are visible to an observer, whereas physiological measures can further tap covert, unobservable bodily events. Because of their interdependence, behavioral and physiological measures will not be discordant in the same sense that reports of affective experience and physiology may be. Determining the relationships among three-system responses in specific affective contexts is an important step in the task of understanding human emotional response.

**AFFECT, TASK, AND MEASUREMENT: EMPIRICAL FINDINGS**

Perceptual information (in some form) is an ingredient in almost all experimental paradigms. Processing a sensory stimulus – as when instructed to look at a picture, listen to a noise, receive a shock, smell an odor, or taste some substance – is here considered to be a prototypical perceptual task. In emotional perception, instructions to simply process sensory stimuli often result in a relatively passive (i.e., physiologically inactive) intake posture.

Earlier investigations exploring emotion in perception assessed autonomic reactions such as vascular changes, electrodermal reactions, and heart rate (Epstein 1971; Roessler, Burch, & Childers 1966; Turpin & Siddle 1983) as a function of differences in stimulus intensity, because this variable was considered critical in eliciting orienting or defense responses. Sensory stimuli of low intensity were held to prompt orienting activity, associated with a pattern of peripheral and cephalic vasconstriction and heart rate deceleration, whereas intense stimuli prompted a defense response, associated with peripheral vasconstriction, cephalic vasodilation, and heart rate acceleration (see Graham 1979; Sokolov 1963; Turpin 1986).

Empirical support for a relationship between stimulus intensity (e.g., shock or noise) and predicted patterns of cardiovascular responses was generally good (but see Turpin 1986). Notable exceptions were found, however, particularly when the perceptual stimuli involved pictures. In the picture context, stimulus intensity was generally operationalized as involving variations in hedonic valence, and comparisons were made between pictures that depicted aversive (e.g., car accidents, mutilations) or neutral events. Work by the Lacey’s (e.g. Libby et al. 1973), Klorman (Klorman, Weissberg, & Austin 1975; Klorman, Weissbert, & Wiesenfeld 1977), and Hare (e.g. Hare et al. 1971a,b, Hare 1973) consistently found that the heart decelerated when people viewed pictures of unpleasant emotional events, contrary to the notion that such aversive stimuli should prompt defensive heart rate acceleration. Based on these kinds of data, Lacey (1967) introduced the concepts of directional fractionation (i.e., not all physiological responses uniformly increase with increasing arousal) and stimulus specificity (i.e., specific stimuli and tasks are associated with specific patterns of physiological response). That is, although the heart decelerates in a perceptual (sensory intake) context such as picture viewing, increased electrodermal reactions are consistent with sympathetic activation and increasing arousal.

However, pictures differ from the physical stressors (i.e., shock and noise) originally utilized in studies of orienting and defense on a number of the dimensions described earlier. In addition to the obvious modality differences (visual vs. tactile or acoustic), pictures differ from shocks or noises in terms of learning: simple stressors such as painful shock or loud noise are unconditioned stimuli, eliciting defense responses in animals as well as in newborn humans. Pictures, on the other hand, are highly symbolic stimuli whose encoding along affective dimensions requires prior learning as well as cognitive sophistication.

Furthermore, defining stimulus intensity in terms of differences in picture valence (i.e., comparing unpleasant to neutral pictures) confuses the issue of how the intensity of symbolic versus physical stressors affects physiological response. A more systematic approach is to assess how emotional reactions vary with changes in the valence and arousal of picture stimuli. One benefit of using pictures as affective cues is the ease of including pleasant exemplars: when shock serves as an aversive stimulus, for example, it has proven difficult to find an unconditioned tactile stimulus that is as pleasant as shock is unpleasant. Pictures also have the advantage of representing many of the events and stimuli people find affectively engaging in the environment, and these stimuli are experimentally tractable in terms of control and presentation.

**Affective Space: Pleasure and Arousal**

Recently we collected a set of pictures depicting a wide variety of objects, events, and situations into the International Affective Picture System (IAPS; Lang et al. 1998) with the goal of providing a set of standardized materials for use in studies of emotion. When human subjects are asked to judge the pleasure and arousal of these pictures, an affective space such as that depicted in Figure 6 (top panel) results. In this figure, each symbol represents a picture, plotted as a function of its mean judged pleasure and arousal rating.

The shape of affective space provides support for a fundamental organization of emotion in terms of appetitive and defensive motivation. First, it is clear that stimuli vary
Distribution of Pictures in Affective Space
(International Affective Picture System, 1998)

in hedonic valence: proceeding vertically in each direction from the center of the space (where neutral events cluster), stimuli are rated as progressively more pleasant or more unpleasant. Second, as ratings of hedonic valence change in either direction, ratings of arousal tend to increase. The boomerang shape of this space is very similar for sets of words or sounds (Bradley & Lang 1999a,b, respectively), instrumental music (van Oyen Witvliet & Vrana 1996), and films (Detenber, Simons, & Bennet 1998), suggesting a common organization for these perceptual stimuli.

The arrows in the top panel of Figure 6 illustrate activation in the hypothetical underlying appetitive and defensive systems. When activation in each system is minimal (neither pleasant or unpleasant), arousal is correspondingly low and events are usually labelled “unemotional” or “neutral.” From a motivational perspective, this suggests only a weak tendency to approach or withdraw from the stimulus, with little energy mobilization required for what is essentially a minimal behavioral response. As activation in the defensive system increases (stimuli are rated as increasingly more unpleasant), arousal increases as well, presumably indexing the metabolic requirements required for anticipated and

Figure 6. Top panel. Pictures from the International Affective Picture System (CSEA 1999) are plotted in a two-dimensional space defined by the mean ratings of judged pleasure and arousal by a large group of subjects. The arrows in the upper and lower portions of affective space indicate varying activation in hypothetical underlying appetitive and defensive motivational systems. Bottom panel. The slope of the arousal functions for pleasant and unpleasant pictures (excluding pictures rated in the neutral valence range, i.e., from 4.5 to 5.5 in upper plot), based on subjective reports of pleasure and arousal, closely parallel the approach and avoidance gradients based on direction and intensity of behavior originally noted by Miller (1959; inset) in his classic animal studies. Adapted with permission from Miller, “Liberalization of basic S-R concepts: Extensions to conflict behavior, motivation and social learning,” in Koch (Ed.), Psychology: A Study of a Science, vol. 2, Study 1. Copyright 1959 The McGraw-Hill Companies.
actual action (e.g., withdrawal, escape, defense). Similarly, increasing activation in the appetitive system is associated with increases in rated arousal, reflecting energy allocated to fueling behaviors involving approach and consummation.

The separate arousal gradients obtained for pleasant and unpleasant pictures in the top panel of Figure 6 are overlaid in the bottom panel of Figure 6. It is striking how well these gradients map onto Miller’s classic schematic illustrating differences in approach and avoidance behavior in the rat (inset, bottom panel of Figure 6), since Miller’s data were based not on verbal reports but on the strength of the animal’s pull toward or away from an appetitive or aversive stimulus. Miller found a prototypical pattern of responding in which withdrawal from an aversive stimulus increased with proximity to it whereas approaching a proximal appetitive stimulus was somewhat less intense. Despite the drastic difference in the measures used to index direction (i.e., withdrawal or approach vs. valence judgments) and degree of activation (behavioral strength vs. arousal judgments), it is clear that reports of arousal for pleasant and unpleasant perceptual stimuli closely parallel Miller’s classic motivational gradients. Emotion is fundamentally organized by motivation.

Drawing on data like these, Cacioppo and associates (Berntson, Boysen, & Cacioppo 1993; Cacioppo et al. 1997; Ito, Cacioppo, & Lang 1998) concluded that the positivity offset (i.e., the larger constant for positive motivation) indicates that a weak tendency for activation in the appetitive system exists when neither system is strongly active. They suggest that this tendency to approach, functioning at low levels of motivation, provides a basis for understanding the orienting and exploratory reactions that constitute daily interactions with environmental stimuli that are neither highly threatening nor highly appealing. The negativity bias—the steeper gradient for defensive behaviors—reflects a propensity to respond more strongly to aversive stimulation.

As Figure 6 (top panel) illustrates, the steeper slope for aversive pictures arises from a closer coupling between the degree of (un)pleasantsness and arousal: the relationship between valence and arousal ratings for unpleasant pictures is highly linear. For pleasant pictures, on the other hand, reported pleasure and arousal are less tightly coupled—primarily owing to stimuli that are rated as highly pleasant but low in arousal (e.g., clouds, nature scenes). The uncoupling in reports of hedonic valence and action for pleasurable stimuli may reflect the cognitive sophistication underlying aesthetic appreciation.

**Physiological Reactions and System Covariation**

Stimulus evaluations support the notion that dimensions of pleasure and arousal can be used to organize emotional reactions to picture stimuli. As noted earlier, however, these judgments are not exhaustive in tapping the subject’s affective data base. Using stimuli from the IAPS set, the nature of physiological reactions and their covariation with subjective reports have been assessed in a number of different studies (Greenwald, Cook, & Lang 1989; Lang et al. 1993; for a review see Bradley & Lang in press a). In these experiments, physiological responses such as heart rate, skin conductance, facial EMG activity (e.g., corrugator and zygomatic), blood pressure, respiration, eye movements, and event-related potentials have been measured while subjects simply view emotional and neutral IAPS pictures. Ratings of pleasure and arousal (and, in some cases, of interest, complexity, or familiarity) are obtained after the termination of each picture. Patterns of physiological reactivity as a function of picture valence and arousal have been assessed on the basis of the a priori groupings of pictures (i.e., determined by IAPS norms) as well as by each participant’s own reports of pleasure and arousal obtained during the psychophysiological assessment session.

In the latter, covariation method, individuals’ reports of experienced pleasure and arousal are related to physiological response by ranking the picture stimuli from lowest to highest on the basis of each subject’s own affective judgments. The mean activity in each physiological system is then assessed at each rank, across subjects. This strategy optimizes the opportunity to observe unit changes in physiology coincident with changes in affective judgments, and it provides a meaningful index of affective covariation. The method also allows one to determine whether systematic variations in pleasure or arousal (or their interaction) are associated with systematic changes in physiological response—and, if so, which measures are sensitive to which dimension. On the other hand, if emotion is primarily organized by discrete emotional states then no systematic relationship between variations along these emotional dimensions and physiological response is expected.

Results from these studies are summarized in Figure 7. The left column illustrates the average response pattern for different physiological measures during the time that participants were viewing a 6-sec picture presentation. In each analysis, data were acquired at a 20-Hz sampling rate, reduced off-line into half-second bins, and deviated from a 1-sec baseline just prior to picture onset in order to assess phasic responses to the picture. The center column illustrates the dimensional covariation between physiological responses and affective judgments obtained from a group of subjects and based on the analysis just described. The right column illustrates the size of the dimensional correlation between relevant affective judgments and physiological response for individual male and female subjects. We next discuss these data more fully.

**Facial EMG Activity.** Facial displays (frowns, grimaces, smiles, etc.) of affective reactions constitute some of the
more obvious overt behaviors associated with emotional processing. Whether facial expressions reliably communicate different types of emotion across cultures intrigued even Darwin (1873), and research supports the view that a small set is recognizable pan-culturally (Ekman & Friesen 1986). A number of coding systems have been designed that allow researchers to code facial movement from videotaped displays, which clearly rely on overt expression (e.g., FACS – Ekman & Friesen 1978; MAX – Izard 1979). As Tassinari and Cacioppo (1992) pointed out, electromyographic recordings made using electrodes placed over the relevant muscles further allow measurement of covert facial responses. A number of studies have indicated that emotional processing is associated with significant changes in EMG activity involving different facial muscles (Cacioppo et al. 1986; Dimberg 1990).

A primary issue in this work concerns the extent to which facial EMG activity reflects spontaneous or voluntarily initiated movement, since the strong voluntary control over facial activity poses obvious interpretive problems in studies of emotion (for discussion of these problems, see Tassinari & Cacioppo 1992; Cacioppo, Bush, & Tassinari 1992b). Tassinari, Cacioppo, and Geen (1989) reported that voluntary but not spontaneous facial expressions are associated with the observance of a cortical readiness potential just prior to movement; Ekman, Davidson, and Friesen (1990) suggested that, whereas a spontaneous (Duchenne) smile involves activity in the zygomatic and orbicularis oculi muscles, a posed smile involves only the zygomatic muscle. The fact that facial expressions such as smiling increase when confederates are present in the experimental context (Fridlund 1991) highlights the important role that voluntary control can play in activity of the facial musculature. Interpretation of facial EMG activity in studies of emotion should carefully consider possible demand interpretations of obtained patterns and include, if possible, methods for assessing whether activity was spontaneous or voluntarily initiated and modified.

**Corrugator EMG Activity.** The corrugator supercilius muscles are responsible for lowering and contraction of the brows. This facial action is held to be an index of distress (see Ekman & Freissen 1986; Fridlund & Izard 1983), and firing of motor units in this muscle region is expected if a stimulus is judged to be unpleasant (even if the degree of unit activity is insufficient to produce visible brow movement). Significant contraction of the corrugator muscle occurs when viewing pictures that are rated as unpleasant (see Figure 7, left panel). The change in corrugator EMG activity is modest (but still above baseline) when viewing neutral materials, and this muscle often shows relaxation below baseline activity for materials rated as highly pleasant (Figure 7, middle panel).

The dimensional correlation between reports of pleasantness and corrugator EMG activity is quite high. When corrugator EMG activity is averaged over pictures ranked from most to least pleasant for each subject, a strong linear relationship is obtained between valence judgments and corrugator activity (Figure 7, middle panel). As ratings become more unpleasant, activity in the corrugator muscle increases steadily. For the most pleasant materials, activity in the corrugator muscle decreases below baseline. A linear relationship obtained in over 80% of participants in the study by Lang et al. (1993), suggesting that subjective reports of pleasure and corrugator EMG activity are strongly associated in a large proportion of the population (Figure 7, right panel). Activity in the corrugator muscle therefore reflects variations in picture valence, increasing in activity for unpleasant stimuli and decreasing for highly pleasant stimuli.

**Zygomatic Major EMG.** Activity in this muscle occurs when the cheek is drawn back or tightened (Tassinari et al. 1989); it is involved in facial expressions of smiling. Consistent with this, activity in the zygomatic muscle region increases with increases in hedonic valence and is greatest when viewing pictures judged to be highest in pleasure (see Figure 7, left panel). As Figure 7 (middle panel) illustrates, there is a significant linear correlation between reports of pleasantness and activity in the zygomatic muscle region.

However, for materials rated as most unpleasant scenes of mutilation and death – there is a tendency for zygomatic EMG activity to again increase. Because of the slight increase in zygomatic EMG activity at the unpleasant end of the valence continuum (and the significant increase at the positive end), there is also usually a reliable quadratic correlation between reports of judged pleasantness and zygomatic EMG activity. Coactivation of zygomatic and corrugator muscles suggests that a facial grimace (involving both lowering of the brow and tightening of the cheek) may accompany perception of some aversive materials.

Roughly two thirds of female subjects show a relationship between zygomatic activity and affective valence, whereas only a quarter of male subjects show this relationship (Figure 7, right panel; Lang et al. 1993). This

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*Figure 7. Left panel. Second-by-second changes in facial EMG activity, heart rate, skin conductance, and electrocortical activity when people view pleasant, neutral, and unpleasant IAPS pictures. Middle panel. Facial EMG activity and heart rate change covaries with judgments of rated pleasantness, whereas skin conductance reactions and cortical potentials covary with rated arousal. Right panel. Correlations of physiological response with reports of pleasure and arousal are plotted for individual male and female participants. Women show stronger relationships between facial EMG activity and pleasure than men; conversely, men show a stronger relationship between skin conductance change and arousal ratings. Based in part on data from Lang et al. (1993) and Cuthbert et al. (1998).*
significant gender difference indicates that women may be more facially expressive than men.

In a recent transfer test, Bradley and Lang (in press b) presented participants with a series of 6-sec sound clips consisting of pleasant, neutral, and unpleasant acoustic events (e.g., rollercoaster, typewriter, bomb), again selected on the basis of normative pleasure and arousal ratings (Bradley and Lang 1999b). Not only were similar patterns of facial EMG changes (i.e., zygomatic and corrugator) obtained when people listened to these affective sounds, the covariation functions and gender distributions were almost identical to those depicted in Figure 7. These data comprise an important next step in emotion research: testing whether patterns obtained with one type of emotional prompt (e.g., pictures) generalize when a specific component of the cue (in this case, sensory modality) is changed.

Patterns of facial EMG activity during mental imagery are also consistent with the notion that activity in the corrugator and zygomatic muscle regions indexes the hedonic valence of the imagined stimulus (Fiorito & Simons 1994; Fridlund, Schwartz, & Fowler 1984; van Oyen Witvliet & Vrana 1995). Schwartz and his colleagues (Schwartz, Ahern, & Brown 1979; Schwartz, Brown, & Ahern 1980) conducted a series of studies which found that corrugator and zygomatic EMG activity primarily differentiated between imagery of negative and positive emotions, whereas EMG activity over the masseter and lateral frontalis muscle regions did not differ. Note also that Schwartz et al. (1980) found women to be more reactive than men, consistent with the gender effects for picture perception. Summarizing the imagery work, Cacioppo et al. (1993) concluded that covert measures of facial EMG activity may reflect “a rudimentary bivalent evaluative disposition or motivational tendency rather than discrete emotions” (p. 136).

Whereas facial EMG activity, particularly corrugator, is quite sensitive to hedonic valence in both perception and imagery, these facial muscles are not as reactive in anticipation – particularly when assessed in aversive conditioning studies. For example, Dimberg (1987) did not find reliable conditioning effects in corrugator or zygomatic muscle activity in a differential conditioning design in which faces served as conditioned stimuli and electric shock as the unconditioned stimulus. In a vicarious conditioning paradigm, Vaughan and Lanzetta (1980) showed that, although the reinforced stimulus tended to elicit higher activity in several facial muscles (e.g., masseter, frontalis), findings were not statistically significant or stable across experiments. Hamm and co-workers (1993) similarly did not find differential corrugator EMG activity when subjects were anticipating an aversive shock stimulus as compared to when a cue signaling "safety" was present. A study in which subjects anticipated the presentation of pleasant, neutral, or unpleasant pictures (cued by a light) found no corrugator EMG differences as a function of valence during a 6-sec anticipatory interval, even when snake phobics anticipated an upcoming snake picture (Sabatinelli et al. 1996). A number of hypotheses might explain the lack of affective facial EMG changes during anticipation, yet overall these findings still highlight the context-specific nature of emotional reactions in psychophysiological studies, which should encourage analyses in which the task context is specified in drawing inferences about emotion and psychophysiology.

Heart Rate. As noted before, the heart is dually innervated by the parasympathetic and sympathetic nervous systems; hence, a measure such as heart rate can be affected by alternation in the level of activation of either system. When viewing pictures, a classic triphasic pattern of heart rate response (see e.g. Lang & Hnatiow 1962) is obtained that includes an initial deceleration and then an acceleratory response followed by a secondary deceleration. In the picture-viewing context, affective valence contributes primarily to the amount of initial deceleration and subsequent acceleratory activity. As found in earlier studies (Winton, Putnam, & Kraus 1984), unpleasant stimuli produce the greatest initial deceleration. Pleasant pictures, on the other hand, prompt the greatest peak acceleration (see Figure 7, right panel). In fact, the cardiac waveform for unpleasant pictures often shows no clear acceleratory peak but instead a deceleration that is sustained across the picture interval (Bradley, Greenwald, & Hamm 1993b), suggesting that the difference in peak acceleration between pleasant and unpleasant pictures is not due to differential initial deceleration.

Although the averaged cardiac waveform clearly discriminates between pleasant and unpleasant pictures, the dimensional covariation between valence and cardiac rate is relatively more modest than found for facial EMG changes (Figure 7, center panel). On the other hand, a large proportion of participants show a positive correlation between ratings of pleasure and heart rate change, and men and women are equally likely to show a positive relationship (Figure 7, center panel). One important difference between facial EMG reactions and cardiac change is that, whereas the face does not have any other obvious tasks during emotional perception, the primary tasks of the heart are homeostatic and metabolic – that is, basic to the survival of the organism. In addition, factors such as posture, respiration, and physical differences (e.g., body weight, fitness) can conspire to obscure affective covariation in cardiac response.

Significant changes in heart rate also occur purely as a function of motor preparation (Graham 1979; Lacey & Lacey 1970; Obrist 1975), which can affect both the shape of the cardiac waveform in a task and the variations due to emotional parameters. For example, in their picture perception study, Winton et al. (1984) required subjects to press a button at picture offset, which somewhat altered
the shape of the heart rate waveform during viewing: both
the initial acceleratory component and secondary decelera-
tion were accentuated relative to a passive viewing context.
Nonetheless, unpleasant pictures led to the greatest ini-
tial deceleration and pleasant (erotic) pictures led to the
greatest acceleration, as in passive viewing. These data
highlight the importance of identifying task variables, such
as somatic requirements, that could have a significant im-
 pact on physiological measures.

Whereas heart rate during perception of unpleasant pictures results in initial cardiac deceleration, heart rate
during unpleasant mental imagery is primarily accelerat-
ory in nature. A number of studies have found that heart
rate increases are greater during text-prompted fearful than
for neutral imagery (Bauer & Craighead 1979; Cook et
al. 1988; Grayson 1982; Grossberg & Wilson 1968; Haney
& Euse 1976; Lang et al. 1983; May 1977a,b; Van Egeren,
Feather, & Hein 1971) and also greater during unpleas-
ant than pleasant imagery (Fiorito & Simons 1994; van
Oyen Witvliet & Vranza 1995). In general, heart rate ac-
celeration during imagery varies most consistently with
stimulus arousal — increasing as arousal (either pleasant
or unpleasant) of the mental image increases (Cook et al.
1991; Fiorito & Simons 1994; van Oyen Witvliet & Vranza
1995).

In an effort to separate cardiac concomitants of mental
imagery from heart rate variance associated with process-
ing text, Schwartz (1971) developed a paradigm in which
subjects first memorized emotionally arousing stimuli and
then imagined these stimuli in a fixed sequence. Simply
imagining arousing stimuli (i.e., without having to process
a text prompt) resulted in greater heart rate acceleration
than when imagining a neutral sequence (e.g., the letters
ABCD). Using tones to cue periods of imagery, May and
Johnson (1973) had subjects memorize neutral or arousing
words, whereas Vranza, Cuthbert, and Lang (1986) em-
ployed sentences describing neutral and unpleasant events.
In all cases, heart rate accelerated when imagining arous-
ing compared to neutral events. A follow-up study by
May (1977b) found that actually imagining a fearful sen-
tence produced more heart rate acceleration than either
thinking the sentence, hearing the sentence, or seeing a
picture depicting the same material as described by the
sentence.

Lang (1987) has interpreted heart rate acceleration dur-
ing emotional imagery as “efferent leakage,” indicating
that — in imagery as in an actual situation — heart rate
changes reflect activation of response information associ-
ated with appropriate actions. Consistent with this, Jones
and Johnson (1978, 1980) obtained faster heart rate during
imagery of high-activity sentences (e.g., “I feel happy, and
I’m jumping for joy”) than during imagery of low-activity,
relaxing sentences (e.g., “I feel happy, and I just want
to relax”). Miller et al. (1987) demonstrated that, like
imagery of fear or anger scenes, imagery of active (neu-
tral) scenes produced greater heart rate acceleration and
electrodermal reactivity than neutral scenes involving low
activity.

Taken together, the heart rate patterns obtained during
emotional perception and imagination are consistent with
Lacey’s (1967) early observation that deceleration is associ-
ated with sensory intake (perception) whereas acceleration
is associated with mentation. However, the interpreta-
tion that heart rate acceleration in imagery reflects sensory
rejection has been refined: rather than focusing on sen-
sory processing (e.g., rejection of perceptual information),
a number of theories (see Cuthbert et al. 1991 for a re-
view) now hypothesize that cardiac activity during imagery
reflects the activation of somatic activity associated with
action in the image (Lang 1979). To the extent that imagi-
ning emotional (i.e., pleasant or unpleasant) events involves
more activity than neutral events, greater heart rate acce-
cleration during this type of mentation is predicted.

Skin Conductance. Whereas the heart is dually innerv-
ated, the electrodermal system is innervated solely by
fibers of the sympathetic nervous system, which could
make this a useful measure of activation of this autonomic
nervous system component. Nonetheless, the mechanism
of its action is cholinergic, in contrast to most sympathetic
fibers, which are adrenergic. Furthermore, Guyton and
Hall (1996) suggested that palmar sweat activity might re-
fect parasympathetic activity (see Figure 2), as these glands
are controlled by the portion of the hypothalamus involved
in parasympathetic control.

Usually measured on the palm of the hand, the amount
of skin conductance activity increases as the rated arousal
of an emotional picture increases, regardless of its emo-
tional valence. Thus, if skin conductance change is plotted
as a function of a priori picture valence, a significant qua-
dratic pattern is obtained in which reactivity is generally
higher when viewing either pleasant or unpleasant (com-
pared with neutral) materials, as illustrated in Figure 7 (left
panel). Winton et al. (1984) also obtained data indicating
larger skin conductance responses to slides that were rated
as highly pleasant and highly unpleasant. Likewise, Man-
nings and Melchiori (1974) observed this skin conductance
pattern when stimuli were words rated as highly pleasant
(e.g. “sex”) or highly unpleasant (e.g. “violence”).

That skin conductance varies consistently with reports
of arousal is evident when assessing the dimensional cor-
relation between arousal ratings and skin conductance. A
significant linear relationship emerges in which a unit in-
crease in rated arousal (regardless of valence) is associated
with an increase in electrodermal reactivity (see Figure 7,
center panel). Over 80% of the subjects in Lang et al.’s
(1993) study showed a positive correlation between arousal
reports and conductance response. A larger proportion
of males than females showed a significant correlation,
suggesting that — whereas females may be more facially
Figure 8. Skin conductance changes when viewing IAPS pictures presented twice in a row indicate a decrease in response magnitude from the first to the second presentation for pleasant but not for unpleasant pictures, suggesting that skin conductance changes for pleasant pictures are mediated in part by novelty.

expressive – males are more reactive in the electrodermal system (Figure 7, right panel).

A similar relationship between skin conductance activity and stimulus arousal is obtained when emotional sounds, rather than pictures, serve as the perceptual stimuli. The covariation functions and gender distributions relating skin conductance response to reports of arousal for sound stimuli were again very similar to those depicted in Figure 7 for pictures (Bradley & Lang in press b).

The magnitude of skin conductance responses has also been found to vary with stimulus arousal in a number of different imagery studies (Cook et al. 1991; Fiorito & Simons 1994; Miller et al. 1987; van Oyen Witvliet & Vrana 1995). Furthermore, a skin conductance increase during anticipation of an aversive electric shock is the prototypical measure of conditioned aversion. That this measure primarily indexes arousal associated with the conditioning procedure – rather than with the aversive stimulus – is supported by findings of significant skin conductance change in appetitive conditioning paradigms (Hamm & Vaitl 1996; Lipp, Sheridan, & Siddle 1994). Significant skin conductance increases were also obtained when subjects anticipated the presentation of either pleasant or unpleasant pictures as compared with anticipating neutral pictures (Sabatinelli et al. 1996).

Therefore, skin conductance responses appear to be reliably modulated by emotional arousal in perception, anticipation, and imagination. One interpretation is that these effects index sympathetic nervous system reactivity, which is greater for emotionally arousing than for neutral materials. Electrodermal reactions are also quite sensitive to the novelty of both the stimulus and the task: with repeated presentations of the same or different pictures, the size of electrodermal changes rapidly decreases (Bradley, Lang, & Cuthbert 1993c). Effects of novelty suggest that differences in the degree of orienting may underlie some effects of stimulus arousal in this response system. In an effort to separate contributions of stimulus arousal due to novelty from those due to emotion, Bradley et al. (1997) presented unpleasant, pleasant, and neutral pictures twice in a row. The logic was that, during the second presentation, the picture was less novel and so effects due to emotional arousal alone should be accentuated. Figure 8 illustrates the electrodermal data from this experiment. Whereas skin conductance magnitude reached the same level when viewing unpleasant pictures on each of the two presentations, electrodermal reactions to pleasant pictures decreased greatly from the first to second presentation. One interpretation is that electrodermal responses to
pleasant pictures may be more related to stimulus novelty than to emotional arousal. More importantly, these data illustrate how one can begin to isolate effects of emotional arousal on physiological response by removing influences due to other factors.

**Cortical ERPs and Slow-Wave Activity.** When electrocortical (EEG) activity is measured during picture viewing (and subsequently corrected for eye movements), specific event-related potentials and sustained slow-wave activity are observed in response to emotionally arousing picture stimuli, irrespective of affective valence (Crites & Cacioppo 1996; Cuthbert et al. in press; Lifshitz 1966; Palomba, Angrilli, & Mini 1997). As Figure 7 (left panel) illustrates, positive cortical evoked potentials starting at about 400 msec after picture presentation are larger for both pleasant and unpleasant than for neutral materials, and a slow sustained positivity is maintained until picture presentation is terminated.

The dimensional correlation between ratings of arousal and cortical positivity (measured at its maximum, 400–700 msec) is also quite high (see Figure 7, middle panel), indicating that activity measured from the cortical surface primarily indicates whether an emotional (pleasant or unpleasant) or neutral stimulus is the focus of processing. There is evidence from cognitive studies that the positive component occurring around 300 msec after stimulus onset might reflect attentional engagement. For example, if attention is directed toward a stimulus then larger positivity is obtained. On the other hand, the same stimulus that generates a large positivity when associated with a task often does not do so when the stimulus is ignored (see Donchin & Coles 1988). Because emotionally evocative pictures are consistently rated as more interesting and more complex than neutral, low-arousal images (Bradley et al. 1993b; Lang et al. 1990), greater cortical positivity may reflect a variation in attentional engagement that covaries with judged affective arousal.

Crites and Cacioppo (1996) further demonstrated that the local context in which a picture is embedded affects the magnitude of the late positive potential. When a series of pictures of the same valence (say, unpleasant) are presented, the late positive potential for a target that is evaluatively distant (here, pleasant) from the context is greater than for similarly valenced targets. This effect also appears to be larger on the right side of the brain when the task requires an evaluative (but not a semantic) judgment. Cacioppo and his colleagues suggested that these effects index an automatic evaluative process that reflects the distance of a stimulus from the current evaluative set.

Differences in lateralized electrical activity of the brain have also been found when people view pleasant or unpleasant films. Davidson and his colleagues (1990; Wheeler, Davidson, & Tomarken 1993) reported that anterior EEG activity (measured as alpha power) is greater on the left than the right when viewing happy films and vice versa for disgusting films. However, these effects were not obtained unless the analysis was constrained to include only epochs containing appropriate facial displays and subjective reports of emotion, suggesting that these cortical effects rely on mobilization of appropriate affective responses in the film-viewing task.

**The Startle Reflex: Emotional Priming.** The autonomic and somatic physiological responses elicited during picture viewing presumably reflect the engagement of neural structures and pathways, many subcortical, in either the appetitive or defensive motivation systems. Lang and his colleagues (1990, 1997) proposed that, during the period that the subcortical circuitry is active, associations and action programs that are linked to the engaged motivational system are primed and ready to respond. Thus, if the defensive motivational system is dominant (i.e., if the affective state is unpleasant), then other defensive responses are primed. Conversely, responses linked to the nondominant system are inhibited. Because the most fundamental motivational priming is at the level of unconditioned reflexes, a concurrent aversive state should prime defensive reflexes whereas an appetitive state should lead to inhibition of defensive responding.

The startle response has proven to be a defensive reflex that demonstrates this type of priming pattern. Startle is a primitive reflex that serves a protective function, helping to avoid organ injury (as in the eyeblink) and acting as a behavioral interrupt (Graham 1979), clearing processors to deal with possible threat. In studies with human beings, rapid eye closure is one of the most reliable components of the behavioral cascade that constitutes the startle reflex. The magnitude of the blink can be measured by electrodes placed over the orbicularis oculi muscle, just beneath the lower eyelid (see Figure 9). Although intense stimuli in most sensory modalities (e.g., acoustic, visual, tactile) elicit a startle response, the most important feature of a startle-eliciting stimulus is its abruptness; thus, its risetime should ideally be instantaneous (see Anthony 1985 for an overview). The most commonly used startle-eliciting stimulus in human research is a brief (50-msec) burst of white noise at around 95 decibels; this prompts a clear blink response but rarely interferes with ongoing foreground tasks.

When startle probes are administered in the context of affective picture perception, results have consistently conformed to the motivational priming hypothesis. As Figure 10 (top panel) illustrates, a significant linear trend is reliably observed over judged picture valence, with the blink response potentiated when viewing unpleasant pictures and inhibited when viewing pleasant pictures (Lang 1995; Vrana, Spence, & Lang 1988). These effects have proven to be highly replicable (Bradley et al. 1990, 1993c, 1995, in press; Cook et al. 1992; Hamm et al. 1997; Patrick,
Figure 9. **Left panel.** Illustration of the placement of electrodes for measuring activity over the orbicularis oculi muscle when assessing startle blink responses. **Right panel.** The resulting raw EMG recorded (top) and the rectified, integrated signal from which the magnitude of the blink is scored (bottom). Reprinted with permission from Lang, Bradley, & Cuthbert, "Emotion, attention, and the startle reflex," Psychological Review, vol. 97, pp. 377–98. Copyright © 1990 by the American Psychological Association.


The neural circuitry underlying potentiation of the startle response during aversive processing has been extensively investigated by Davis (1986, 1989; Davis, Hitchcock, & Rosen 1987) and others (e.g., Koch & Schnitzler 1997). When stimulated by an abrupt noise, the afferent path of the reflex proceeds from the cochlear nucleus to the reticular formation; from there, efferent connections pass through spinal neurons to the reflex effectors. This is the basic obligatory circuit, driven by the parameters of the input stimulus (e.g., stimulus intensity, frequency, steepness of the onset ramp). Startle modulation by emotion implies that a secondary circuit affects this primary reflex pathway. There is now overwhelming evidence that the amygdala is a critical component of the fear-potentiated startle effect. First, there are direct projections from the amygdala to the reticular site that mediates potentiation (i.e., nucleus reticularis pontis caudalis); second, electrical stimulation of the amygdala enhances startle reflex amplitude; finally, and most important, lesions of the amygdala abolish fear-conditioned startle potentiation.

Affective modulation of the startle reflex does not depend on stimulus novelty. Although there is an overall diminution of the blink reflex with repeated presentation of the startle probe, affective potentiation and inhibition to unpleasant and pleasant pictures remains constant, despite repeated presentation of the same pictures (see Figure 10; Bradley et al. 1993c). Similarly, affective modulation persists when the same (or a different) set of pictures is viewed in separate experimental sessions (Bradley, Gianaros, & Lang 1995).

The startle reflex is modulated by affective valence during picture viewing regardless of whether the startle probe is visual, acoustic, or tactile (Bradley, Cuthbert, & Lang 1990; Hawk & Cook 1997), indicating that modality-specific processes are not central in these modulatory effects. Affective modulation of startle is also not confined to static visual percepts: the startle reflex is also modulated by affective valence when dynamic visual stimuli (e.g., affective films) are presented (Jansen & Frijda 1994) or when the sensory modality involves odors (Erlichman et al. 1995). Furthermore, when the emotional stimuli consist of short, 6-sec sound clips of various affective events (e.g., sounds of love-making, babies crying, bombs bursting) and the startle probe is a visual light flash, the same pattern of affective modulation is obtained (Bradley & Lang in press b). This suggests that its mediation is broadly motivational and thus consistent across affective foregrounds of different stimulus modalities.
The startle reflex has also been used to determine the temporal course of emotional processing. Reflex magnitude is reliably affected by picture valence as early as 300 msec after picture presentation and is maintained throughout a 6-sec viewing interval (Bradley et al. 1993a). The same temporal pattern of modulatory effects occurs regardless of whether the subject ignores or attends to the startle probe (for review see Bradley & Lang in press a), suggesting that reflex modulation is not secondary to modality-driven attentional processes. Interestingly, it is not necessary for the actual picture stimulus to be present: when the picture is removed from view at 500 msec, strong effects of affective valence on reflex modulation are obtained for up to 3 sec, suggesting that the startle stimulus probes the “mind’s eye,” indexing cognitive and affective processes associated with picture encoding (Codispoti et al. 1999).

If affective priming of the startle reflex is based on motivational variables, then modulatory effects on the startle reflex should increase with greater activation in each motive system. That is, probe startle potentiation should be largest for unpleasant pictures that are highly arousing; conversely, the most arousing pleasant pictures should prompt the greatest probe startle inhibition. Figure 7 (bottom panel) illustrates reflex modulation for pleasant and unpleasant pictures as they vary in rated arousal (Cuthbert et al. 1996) and supports a motivational priming interpretation: the greatest difference in reflex magnitude is for highly arousing pleasant and unpleasant pictures. For pleasant pictures, startle reflex magnitude decreases progressively with increases in rated arousal. For aversive pictures, an initial reduction in blink magnitude is suggested as arousal begins to increase. Somewhat further along the arousal dimension, however, the direction of reflex modulation is abruptly reversed: startle magnitude begins to increase, peaking for pictures judged unpleasant and highest in arousal.

In many ways, the change in direction of the reflex response that is associated with increasing arousal of unpleasant pictures is reminiscent of Sokolov’s (1963) description of the manner in which orienting changes to defense with increasing intensity of physical stimulation after a period of oscillation between the two responses. It is also consistent with Miller’s (1959) classic conflict theory (for a more recent assessment, see Cacioppo & Berntson 1994), in which behavior is assumed to be driven by activation along gradients of approach and avoidance. Because aversive pictures are consistently judged to be more “interesting” (Bradley et al. 1993b) than neutral pictures, the initial reflex inhibition to unpleasant stimuli of moderate arousal.
TABLE 1. Factor Analysis of Three-System Measures of Emotional Picture Perception

<table>
<thead>
<tr>
<th>Measure</th>
<th>Factor 1 (Valence)</th>
<th>Factor 2 (Arousal)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Valence ratings</td>
<td>0.86</td>
<td>-0.00</td>
</tr>
<tr>
<td>Corrugator muscle</td>
<td>-0.85</td>
<td>0.19</td>
</tr>
<tr>
<td>Heart rate</td>
<td>0.79</td>
<td>-0.14</td>
</tr>
<tr>
<td>Zygomatic muscle</td>
<td>0.58</td>
<td>0.29</td>
</tr>
<tr>
<td>Arousal ratings</td>
<td>0.15</td>
<td>0.83</td>
</tr>
<tr>
<td>Interest ratings</td>
<td>0.43</td>
<td>0.77</td>
</tr>
<tr>
<td>Viewing time</td>
<td>-0.27</td>
<td>0.76</td>
</tr>
<tr>
<td>Skin conductance</td>
<td>-0.37</td>
<td>0.74</td>
</tr>
</tbody>
</table>

may reflect modulation related to orienting, a key feature of appetitive motivation. The abrupt change to increasing startle potentiuation reflects the subsequent dominance of defensive motivation as stimuli become more threatening and therefore more arousing.

Summary: Affective Patterns in Physiological Responses.

Taken together, data obtained in the picture perception paradigm are consistent with the hypothesis that motivational variables of affective valence and arousal predominate in organizing physiological and subjective reports of affective reactions. Supporting this, factor analyses conducted on self-report, physiological, and behavioral measures have consistently produced a strong two-factor solution (Lang et al. 1993). As Table 1 illustrates, the first factor involves high loadings for pleasantness ratings, heart rate change, corrugator EMG activity and zygomatic EMG activity, consistent with the interpretation that this is a primary valence factor of appetite or aversion. A second factor involves high loadings for rated experience of arousal, interest ratings, viewing time, skin conductance, and cortical slow waves, all identifiers of an arousal or intensity factor. The cross-loadings for all measures are very low. Thus, affects appear to be built around motivational determinants.

Attention and Emotion: The Defense Cascade

In the picture paradigm, when startle reflex magnitude is considered together with other measures of affective reactivity (e.g., skin conductance, heart rate, facial EMG), it is clear that different response systems change in different ways as activation within each motivational system increases. For instance, specific phobics (like normal subjects) show potentiated startles when viewing unpleasant pictures. However, startle reflexes are even more enhanced when these subjects view pictures of their own phobic objects (Hamm et al. 1997; Sabatinelli et al. 1996). In addition, the typical bradycardia obtained during unpleasant picture viewing does not characterize the response of phobic subjects to pictures of objects they fear (Cook & Turpin 1997; Hamm et al. 1997; Klorman & Ryan 1980; Klorman et al. 1977). Rather, when high-fear subjects view pictures of the phobic object, the sympathetic system dominates and the heart accelerates, in concordance with predictions regarding defense responses in this context. Also, unlike nonphobic subjects, they quickly terminate “looking” in a free-viewing situation. Thus, whereas reflex potentiation to aversive materials characterizes responses to highly arousing unpleasant pictures for both normal and phobic subjects, cardiac and other behavioral measures of attentive orienting are absent when phobics process highly fearful content.

These data suggest that, rather than a single response indicating activation of the defensive motivation system and reflected in a parallel way by all measures, one instead observes a cascade of different response events that change in different ways and at different levels as activation increases. When activation within the defensive system is moderate, a pattern of responding suggestive of oriented attention is obtained: measurable conductance changes, heart deceleration, and inhibited startle reflexes. Thus, attentive orienting is not a response confined solely to neutral or pleasant stimuli. Rather, “natural selective attention” (Lang et al. 1997) is prompted by stimuli that are motivationally relevant – either appetitive or defensive. Consistent with this, Lacey (1958) recognized that, instead of being automatically “rejected,” unpleasant events can evoke a physiology consistent with sustained attention. On the other hand, strong aversive motivation is clearly a major factor in initiating defense.

The idea that defense involves stages of responding has been advocated by a number of theorists, including Tinbergen (1951), Blanchard and Blanchard (1989), Fanselow and colleagues (1995; Fanselow & Lester 1988), Masterson and Crawford (1982), and others. For instance, Fanselow (1994) proposed a three-stage model of defensive responding, based on predator imminence, in which defensive responses increased as the threatening stimulus became more proximal. Based on data obtained in the picture perception paradigm, Lang and his colleagues proposed a similar defense cascade that is controlled by increases in motivational activation (as measured by judged arousal) and is considered to be an analog to predator imminence. In Figure II, the amplitudes of various physiological measures are shown schematically on the ordinate, with increases in arousal on the abscissa. Consistent with Lacey’s (1967) rejection of a uniformly increasing response as arousal increases, responses in different systems can initially increase or decrease as the level of arousal increases.

At low to moderate stages of arousal for unpleasant stimuli, a pattern of physiological reactivity consistent with oriented attention is obtained that presumably does not differ fundamentally from appetitive orienting at low levels of activation. This pattern involves:
1. a brief, modest, probably parasympathetically driven heart rate deceleration that occurs in reaction to any stimulus change (this bradycardia becomes larger and more sustained as stimuli are perceived to be more arousing);

2. changes in skin conductance that are small when arousal is low but increase in frequency and amplitude with greater activation; and

3. reflex inhibition to a secondary startle stimulus, consistent with the hypothesis of greater resource allocation to a meaningful foreground.

Defensive responding occurs later in the sequence. Clear evidence that the organism has changed to a defensive posture is first seen in the startle reflex: when defensive activation is high – the threat more imminent – the organism is defensively primed. The startle stimulus acts as a trigger that releases a supranormal reflex reaction. The degree of reflex potentiation increases with greater system activation until the prompting stimulus itself invokes a motivationally relevant action (e.g., fight or flight). Startle potentiation occurs primarily in the context of an increasing attentive focus and a parallel, still increasing and dominant bradycardia. At the highest activation level, just prior to action, the vagus releases the heart and so enables a sympathetically driven acceleration that is the classic defense response. Thus, for phobic subjects, cardiac acceleration (rather than deceleration) occurs when processing pictures of their feared material because these subjects are further along in the “defense cascade” than normal subjects processing standard unpleasant pictures.

It is interesting to note that incarcerated psychopaths fail to show startle reflex potentiation for aversive pictures; instead, they show reflex inhibition (relative to neutral pictures) when viewing either arousing pleasant or arousing unpleasant picture stimuli (Patrick et al. 1993). This finding – quite different from what is seen in the normal population or in specific phobics – is consistent with
the hypothesis that unpleasant pictures are relatively less activating for these individuals and that their reflex modulation reflects motivated attention rather than activation of defensive responding. For psychopaths, pictures do not seem to convey the symbolic danger as for normal subjects, nor do they convey an imminent threat that prompts a phobic reaction. These nonempathic individuals remain distanced—and at an early stage in the defense cascade, which might reflect a deficit in defense motivation (Lykken 1957; Patrick 1994).

**Social Context**

Like most psychophysiological investigations, the study of emotion does not occur in a social vacuum. Perhaps more frequently than in studies of affectless cognition, physiological responses in studies of emotions will vary as a function of important social variables (see Chapter 23 of this volume for further discussion). As noted earlier, for instance, appropriate facial expressions increase in the presence of other people—or even when a subject simply believes another person is observing (Fridlund 1991; Fridlund et al. 1990). More generally, Hatfield, Cacioppo, and Rapson (1993a,b) proposed that people automatically and unintentionally mirror the emotional postures, intonations, and moods of those around them. This phenomenon, termed “emotional contagion,” suggests that emotional reactions in the psychophysiology laboratory may depend on variables in the experimental setting that elicit this type of mimicry or modeling.

Individual differences also contribute importantly to the pattern of physiological reactions obtained in studies of emotion, as noted earlier by Duffy (1957). Interpersonal variables particularly relevant to the study of emotion as outlined in this chapter are those relating to (i) individual differences in phasic or tonic activation of appetitive or defensive systems (due e.g. to temperament, gender, cognitive style) and (ii) individual differences in physiological reactivity (e.g., somatic or autonomic).

In terms of differences in motivational activation, current views of personality are converging on the notion that two factors of negative and positive emotionality may underlie temperamental differences in affective reactivity (e.g. Derryberry & Rothbart 1988; Tellegen 1985; Watson, Clark, & Mineka 1994). Empirical evidence that these traits are fundamental in describing personality was provided by Tellegen (1985), who determined (using factor analysis) that a large variety of personality questionnaires share a common variance that is attributable to the existence of two general dimensions of positive and negative affect. Watson et al. (1994) recently conceptualized negative affectivity as a “stable, heritable and a highly general trait dimension” whose affective core comprises “a temperamental sensitivity to negative stimuli” (p. 104). People who are high in negative affect are believed to evidence tonic effects on emotional reactivity (a higher frequency of negative moods such as anxiety, sadness, and depression) as well as phasic effects, such as greater reactivity to aversive stimuli. Consistent with this, a number of studies have found that highly fearful subjects evidence greater startle potentiation when perceiving (Cook et al. 1991) or imagining (Cook et al. 1992) unpleasant stimuli than do subjects who are low in temperamental fearfulness.

Cognitive style differences, such as imagery ability, also appear to affect physiological mobilization during affective processing, presumably owing to differences in motivational activation. Because experimental cues are often symbolic representations (i.e., pictures, films, textual descriptions) of pleasant or unpleasant stimuli, their ability to activate motivational systems may rely, to some extent, on the subject’s ability to elaborate associated information mentally. Differences in retrieval and manipulation of stored information is one facet underlying imagery ability. Lang and his colleagues have consistently found that self-described good imagers respond more during emotional imagery than those reporting poor imagery ability (e.g. Miller et al. 1987; see Cuthbert et al. 1991 for a review). Even more interesting is that imagery ability also affects physiological responsivity when looking at pictures (Lang et al. 1993) or listening to sounds (Bradley & Lang in press b). In both cases, subjects with good imagery ability show a better relationship between their subjective reports of emotion and their physiological responses as well as more reactivity to emotional than to neutral stimulus processing. These data suggest that, when people process degraded stimulus cues (i.e., symbolic representations of objects and events), a cognitive style variable of “good imagery ability” may distinguish those for whom motivational activation and physiological reactivity is more likely to occur.

In addition to individual differences in motivational activation, the notion that people express emotion (especially stress) through different systems (i.e., internal or external) has had a long history in the study of emotion (see Cacioppo et al. 1992c for a review). Early views assumed that some individuals tended to respond in one system (e.g. somatic) rather than in another (e.g. sympathetic), with compensatory effects. Thus, those failing to respond in expressive (somatic) systems were proposed to have greater sympathetic reactivity—a long-term damage that accompanies internal stress.

According to PATTERNs, a model of individual differences in physiological function proposed by Cacioppo and colleagues (1992c), these early views were too simplistic. The PATTERNs model assumes that individual reactions result from the operation of different neurophysiological systems that have such operating characteristics as differential response thresholds, onset delays, time constants (recovery periods), and so on. Differences in system gain—the amount of amplification in responding per unit increase in excitation (arousal)—is proposed to be an important
individual difference variable in affective reactivity. Individuals with high gain in the sympathetic system ("internalizers") tend to show larger skin conductance reactions with increasing arousal, whereas those with high gain in the somatic system ("externalizers") show greater changes in facial expressivity with increasing arousal. Those with equal gain in both systems ("generalizers") show equivalent changes in electrodermal and facial reactions as arousal increases.

Thus, PATTERNS assumes that, for all neurophysiological systems and all individuals, the greater the neural excitation (e.g., emotional arousal), the greater the output. It is the amount of change with increasing arousal that varies with individual differences in system gain. The consistent gender differences obtained in affective perception are consistent with PATTERNS: men tend to be more electrodermally reactive with increasing arousal in emotional perception, whereas women are more facially expressive (Lang et al. 1993); this suggests a higher gain in the sympathetic system for males and a higher gain in expressive reactions for female subjects. It also appears that men and women may differ in ease of activation in different motivational systems. Women tend to be more reactive to unpleasant, arousing perceptual stimuli, whereas men show a bias to respond to pleasant, arousing stimuli (particularly erotic materials). These differences are obtained in subjective reports of pleasure and arousal as well as in autonomic and somatic measures of reactivity. Hence these data suggest differences in the lability of defensive and appetitive reactions as a function of gender.

Epilogue

Emotion and Action

Emotion and motivation have been viewed thus far as processes involving stimuli and events that move an organism toward action. Human emotion, however, differs in some ways from motivated behavior in lower animals. For instance, because of the enormous learning capacity in the human, the range and type of stimuli that come to activate basic subcortical motivational circuits often appear quite distant from those that directly promote or threaten survival. Nonetheless, the mechanisms underlying neural activation can be considered to be similar in both animals and humans. Animal studies have clearly demonstrated that motivational circuits are initially activated by unconditioned stimuli — those that reflexively lead to approach and withdrawal behaviors. New, "conditioned" stimuli come to activate the same circuits, however, through association with these primary appetitive and aversive reinforcers (Halgren 1981). Because humans (as well as animals) learn to respond in adaptive ways to a wide variety of different environmental stimuli and events through this basic learning process, stimuli that activate appetitive and defensive systems through association can be idiosyncratic, not clearly valenced to bystanders, and not obviously related to basic survival mechanisms.

Second, the close link between emotion and overt action has been loosened in humans, presumably because of the evolution of cortical controls on these fundamental behaviors and development of the ability to mentally process, "off-line," events that are not currently perceptually prompted. Nonetheless, if emotion is intense (e.g., an attacker threatens), then action (e.g. fleeing) is evident, even in humans. However, weaker affective cues (e.g., a movie of the same scene) may elicit only small increases in muscle tension, a mere remnant of the original defensive activity. Thus, emotional reactions in humans often involve primarily a disposition toward or preparation for action (Arnold 1970; Frijda 1986; Lang 1987) rather than clear overt expression. Nonetheless, these can still be considered to be mediated by the same neural circuits originally engaged in activating appropriate approach and defensive behaviors. In this view, motivated behavior can be differentiated from other types of human (and animal) activity primarily in the extent to which this subcortical circuitry is involved during processing (Lang 1994a; Lang et al. 1993; LeDoux 1996).

Conscious Experience of Emotion

If emotion is defined in terms of subjective reports, overt behaviors, and bodily responses, then one might wonder which measure (if any) taps conscious feelings. The issue of the conscious experience of emotion — and how to approach it scientifically — has posed a number of problems in emotion research. As LeDoux (1995) noted, "it is understandable why the field of emotion has had so much trouble in solving the problem of emotion — it has set as its goal the task of understanding consciousness" (p. 1039). Animal theorists, in general, balk at using the term "emotion" in describing motivated behavior in their subjects, mainly because of the added assumption of conscious awareness. The study of motivated behavior, however, does not necessitate taking on the Goliath issue of consciousness — which, in the end, may prove to be more amenable to philosophic than to scientific inquiry.

From a measurement perspective, one solution is to operationally define conscious experience on the basis of subjective reports of emotion. Subjects' reports (verbal or nonverbal) about their emotional experience could be used to index the private, internal state that is usually meant when one speaks of "feelings." Some might argue this is unsatisfactory because of the dependence of personal reports on cultural norms and individual differences in disclosure. In addition, feelings are often held to include the bodily reactions involved in emotional response, such as a racing heart or sweaty palms. A second solution has been to include "conscious awareness" as a fourth type of response system in emotion. The difficulty here is that one needs a reliable operational measure of consciousness.
and yet, other than three-system measures discussed in this chapter, there are currently no methods for directly measuring an internal feeling state.

To illustrate the problem that conscious feeling states pose in the study of emotion, consider a friend confronted with a fearful cue. If there were neither reports of fear nor overt behaviors associated with fear (e.g., flight, avoidance) nor measurable physiology associated with aversive reactivity (e.g., cardiovascular, somatic, central, neurohumoral), could the individual still be feeling afraid? For some, the answer is a definite Yes: conscious feelings are different from, or more than, the set of empirical responses the scientist can measure. For others, the answer will be No: emotion is solely defined by what can be measured. The concept of internal state also raises more questions than it answers in the study of emotion. That is, it can be invoked not only as a cause (e.g., he ran because he felt afraid) but also as an effect (he saw the snake and so he felt afraid) as well as a mediator between stimuli and response (he saw the snake and felt afraid, so he ran).

**Revisiting Discrete States: The Tactics of Emotion**

The difference between a biphasic and discrete state view of emotion does not concern whether specific emotional states can be considered appetitive or aversive, since this is clearly possible; rather, it concerns which organization is more fundamental in organizing emotion. Biphasic and discrete state views of emotion are complementary and are not mutually exclusive, as many theorists recognize (see e.g. Mehrabian & Russell 1974). That is, not only can a specific state such as fear be categorized along a dimension of aversiveness, but a particular aversive event can be described as involving fear — assuming a specific definition of this term.

The issue of defining discrete states of emotion is central when distinguishing among specific emotions. Ortony, Clore, and Collins (1988) provided a compelling cognitive analysis detailing the features of situations and stimuli that may differentiate among events that people generally label with different emotional terms. Consistent with a biphasic view, the superordinate division in their scheme is one of hedonic valence, differentiating among desirable and undesirable events. Specific features of environmental events are then proposed to control how different hedonically valenced events are labeled. For instance, "distress" labels the occurrence of an undesirable event and "joy" the occurrence of a desirable event. When there is only a prospect of an event occurring, then the situation is labeled "fear" for undesirable events and "hope" for desirable events. The stimulus feature of actual versus prospective maps well onto the distinctions made between perception and anticipation tasks in this chapter. Ortony et al.'s (1988) semantic analysis is consistent with the notion that emotion is fundamentally built on appetitive and defensive motivations, which become increasingly differentiated based on specific stimulus contexts.

Emotional differentiation is based not only on features of the stimulus input, however. As emphasized throughout, emotional reactions are part and parcel of the basic phenomenon. Specific emotions are inferred on the basis of behavioral actions and physiological reactions, and these behaviors also vary depending upon contextual support. As noted earlier, rats engage in a variety of different behaviors in response to electric shock, depending upon their environment (e.g., escaping if there is an exit and attacking if there is a conspecific). If particular emotions were to be distinguished on the basis of behavior, these two contexts might be described as eliciting fear and anger (respectively), despite the similarities in stimulus and motivational activation. The variability of human emotional behavior in a specific context is likewise complex but certainly more creative. This tactical nature of emotional behavior (see Lang et al. 1990) has thwarted the efforts of psychophysicists to make general inferences regarding the physiology of specific emotional states. Understanding the physiology in situations labeled with discrete emotional states (fear, anger, joy, etc.) will require careful detailing of the elements of behavior elicited (e.g., freezing, fleeing, fighting) as well as the stimulus situation.

Although conscious feeling states are often considered synonymous with a discrete emotion perspective, this is not necessarily the case. Panksepp (1982), for instance, advocates a discrete emotion view in the rat that is based on his hypothesis that four separate neural systems (located mainly in the hypothalamus) of expectancy, rage, fear, and panic underlie motivated behavior. In his view, these emotions stem from systems that have evolved to deal with specific classes of environmental stimuli (i.e., positive incentives, irritation, threat, and loss). The dependence of emotional behavior on specific stimulus contexts is clearly a principal issue in the psychophysiological study of emotion — and one that has been emphasized throughout this chapter. Identifying the critical contextual features in investigations of emotion may help us to understand whether and when there is consistent physiological patterning as a function of contextual similarity.

**Arousal and Emotional Intensity**

The concept of arousal in the psychophysiological study of emotion has not fared well over the past 30 years, owing in part to Lacey's (1967) observation that physiological responses do not show uniform, parallel increases in direction and strength with increasing arousal (defined as sympathetic activation, metabolic load, or verbal report). This was supported by data from the picture perception paradigm, in which the defense cascade model (Lang et al. 1997), for example, described ways that different physiological systems change at different rates and directions, with increases in some measures (such as startle potentiation)
accompanied by decreases in others (e.g., cardiac deceleration). Thus, as Lacey (1967) emphasized, the notion of a parallel increase in all systems as a function of some underlyng arousal dimension is not supported by the data.

Nonetheless, emotional arousal — considered as the intensity parameter of the active motive system — is a critical factor in organizing the pattern of physiological responses in emotion, as evidenced by factor analyses conducted on an array of evaluative and physiological indices of emotional reactivity (see e.g. Lang et al. 1993). Together, these data redefine the construct of arousal as one that relates to the degree of activation in underlying motivational systems of appetite and defense, rather than a global gain parameter. As noted earlier, high motivational (e.g. defensive) activation can lead to low activity, depending upon contextual constraints. Validating this notion of arousal using the evaluative, physiological, and behavioral indices available in the emotion laboratory remains an important task for the psychophysicist.

When defining the degree of motivational activation in animals, theorists have relied on a proximity parameter. As discussed previously, Tinbergen (1951) and Fanselow (1994) based their model of defense behavior on “predator imminence” — the distance of a threatening stimulus from the organism — and Miller (1959, 1966) defined activation in both appetitive and defensive systems in terms of the organism’s distance from a valent goal. In these conceptions, distance is important because the appropriate action (withdrawal) depends upon where the predator is in the environment; distance clearly covaries with measured behavioral and metabolic indices. When humans encounter motivationally relevant objects in the environment, distance is probably as good an index of motivational activation as it is for animals: As threatening objects come closer, defensive action ensues. In the emotion laboratory, however, the common use of symbolic stimuli (films, pictures, stories, etc.) renders a physical distance metric less informative. Instead, determining the variables that control arousal (i.e., degree of motivational activation) will depend upon systematically exploring how cue and task affect the pattern of evaluative and physiological reactions in studies of emotion.

Reacting to the James-Cannon debate, psychophysiology began at the forefront of emotion studies, gathering evidence to determine whether physiological patterns are specific to emotional states. Although these efforts were less substantial in result than was hoped, they nevertheless brought into focus the great methodological issues that currently dominate the field of emotion research. It has become increasingly clear that affective cues need to be explicitly defined and somehow standardized and, for example, that the properties of a stimulus such as modality and medium of presentation may have varying physiological impact that can overwhelm indices of affect. Similarly, the importance of determining the experimental task has become clear. That subjects are doing different things — imagining, watching a movie, playing a video game — can lead to very different psychophysiological patterns, despite the experimenter’s assumption that a common emotion is evoked. A similar concern encourages better description of the measured responses, underlining the importance of a broad assessment and of analyzing the covariation of evaluative reports with the expressive physiology and behavior.

In summary, emotion research in psychophysiology has matured methodologically. It is beginning to incorporate new techniques of brain imaging, rendering investigators more sensitive to the neural foundations of emotion science. The view that motivation determines emotion and that emotions evolved from survival reflexes has found wide agreement. Although theoretical debate will and should continue, there is an increasing coincidence of method. Standardized stimulus sets are being developed and common experimental paradigms are more widely employed. It is hoped that this evolution in methodology will encourage replication, providing an empirical foundation that is more valuable than isolated results. With a firm foundation, the field may be ready to use shared constructs, which encourages a true cumulative science of emotion.

**Conclusion**

This chapter has explored the utility of studying emotion’s psychophysiology from a biphasic view that posits basic neural systems of defensive and appetitive motivation. Motive systems developed with the brain’s evolution, expanding from reflexive approach and withdrawal responses to govern a host of positive incentive and protective behaviors that ensured the survival of our complex species. This motivated visceral and somatic output is parsimoniously described by parameters of hedonic valence and arousal, and both neuroanatomical and cognitive models of emotion have highlighted these organizing dimensions.

**NOTES**

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1. The 1999 International Affective Picture System (IAPS), International Affective Digitized Sounds (IADS), and Affective Norms for English Words (ANEW) are available on CD-ROM; the IAPS is also available as photographic slides. These stimulus sets and technical manuals can be obtained on request from the author at the NIMH Center.
for the Study of Emotion and Attention, Box 100165 HSC, University of Florida, Gainesville, FL 32610-0165, USA.

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