CHAPTER 11

The Psychophysiology of Emotion

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Humans have walked the surface of the earth for about 2 million years, and for all but the last 2,000 or 3,000 years, humans have been hunter–gatherers (Ackerman, 1990). In a strikingly brief span, human civilization has achieved the engineering of the Great Pyramids, the elegance of Beethoven's Ninth Symphony, the refinement of Dom Perignon, the efficiency of mass production, the triumph of modern medicine, the cognizance of heterotic string theory, and the wonder of space exploration. Perhaps we can be excused for tending to see our achievements as the outcome of pure reason and our distant past "through a reverse telescope that compresses it: a short time as hunter–gatherers, a long time as 'civilized' people" (Ackerman, 1990, p. 129).

Despite the constraints of civilization, however, humans are also the source of less rarified achievements: the relentless exploitation of fossil fuels and rainforests, the apocalyptic peril of biological and nuclear warfare, and the savage horror of torture and genocide, to name but a few. We may sing in choirs and bridle our rages behind placid countenances, but we patrol the world under the auspices of an affect system sculpted over millennia of evolutionary forces.

Emotions are shared across species—an observation that has long fueled the concern that emotions are an obstacle to fulfilling human potential (Brazier, 1960). We may sit in quiet repose contemplating the diversity of the linguistic expressions for emotions, but emotions predate language and the human species.

Individuals are revered for cultivated tastes and seemingly dispassionate responses to life's challenges. Yet emotions, however archaic in origin, saturate human existence throughout the lifespan. Emotions guide, enrich, and ennoble life; they provide meaning to everyday existence; they render the valuation placed on life and property. Emotions promote behaviors that protect life, form the basis for the continuity in life, and compel the termination of life. They can be essential ingredients for, as well as overwhelming obstacles to, optimizing human potential, and they often serve as the engines for intellectual development. Given their evolutionary heritage and daily currency, there is little wonder that emotions have preoccupied humankind throughout recorded history, and there is little doubt that emotions are both biologically rooted and culturally molded.

Affect and emotion in human studies have

been treated as the conscious subjective aspect of an emotion considered apart from bodily changes (e.g., Osgood, Suci, & Tannenbaum, 1957; Green, Salovey, & Truax, 1999; cf. Cacioppo, Gardner, & Berntson, 1999; LeDoux, 1996). Like the organization and processes underlying the undeniable percept that the sun circles the earth, however, the organization and processes underlying affective experiences may be far subtler than their apparent manifestations might lead one to suspect (Cacioppo, Gardner, & Berntson, 1997). Although rich in emotional terms (Clore, Ortony, & Foss, 1987; Frijda, Markam, Sato, & Wiers, 1995; Russell, 1978), language sometimes fails to capture affective experiences—especially intense affective experiences—so metaphors become more likely vehicles for rendering these conscious states of mind (Fainsilber & Ortony, 1987; Ortony & Fainsilber, 1989; Hoffman, Waggoner, & Palermo, 1991).

Affective reports have also long been recognized as subject to a host of motivational influences and contextual distortions, as well as being only modestly related to other aspects of affective reactions, such as somatovisceral events and behavior. Dating back to Freud, research from clinical psychology has underscored the dissociation between reportable aspects and affective states (e.g., Bradley, 2000; Davidson, 1998; Lang, 1971); research in neuropsychology and the neurosciences has shown that emotional feelings are neither necessary nor sufficient for the evocation of emotional processes (Gazzaniga & LeDoux, 1978; Tranel & Damasio, 2000); and research from social and cognitive psychology has shown that emotions are capable of being elicited quickly, effortlessly, automatically, or even unconsciously upon exposure to the relevant stimulus (e.g., Bargh, Chaiken, Govender, & Pratto, 1992; Pratto & John, 1991). Zajonc (1980) observed:

When we meet a stranger, we know within a fraction of a second whether we like the person or not. The reaction is instantaneous and automatic. Perhaps the feeling is not always precise, perhaps we are not always aware of it, but the feeling is always there. . . . Perhaps we have not developed an extensive and precise verbal representation of feeling just because in the prelinguistic human this realm of experience had an adequate representation in the nonverbal channel . . . if affect is not always transformed into semantic content but is instead often encoded in, for example, visceral or muscular symbols, we would expect information contained in feelings to be acquired, organized, categorized, represented, and retrieved somewhat differently than information having direct verbal referents. (pp. 157–158).

Zajonc's point that interpersonal judgments and emotional experiences are fundamentally organized in terms of the dimension(s) of positivity and negativity has strong empirical support (see review by Cacioppo & Gardner, 1999). His proposition that emotion is meaningfully associated with, and possibly encoded in, somatovisceral events is more speculative; however, at least when limited to positive and negative processes, it has received preliminary support (Cacioppo, Priester, & Berntson, 1993). The study of the somatovisceral links to emotion, however, has perhaps been fueled most by the common experience that different visceral sensations underlie different emotions. If individuals were to say that they felt butterflies in their stomachs or that they felt they were ready to boil, few observers would fail to understand that the individuals were experiencing fear and anger, respectively. These interoceptive sensations are so distinct and compelling that it is hard to believe that these emotions are *not* differentiated peripherally as well as centrally. In this chapter we examine the psychophysiology of emotions, with a special emphasis on subtle mechanisms by which somatovisceral events may contribute to human emotions. Because of the centrality of hedonic tone in studies of emotion, we examine both the physiological differentiation of discrete emotions and the differentiation of positive and negative states.

HEURISTIC PERSPECTIVES

More than a century ago, William James (1884, 1890/1950) argued that emotional feelings are consequences rather than antecedents of peripheral physiological changes brought about by some stimulus. James (1884) also viewed emotions as being multiply determined. Individuals may recall earlier emotional episodes, including their feelings, and in so doing they may reexperience the emotion. If the remembered emotion was weak originally (e.g., it involved little or no somatovisceral activation), reexperiencing the emotion may occur in the absence of significant peripheral bodily disturbances. James (1884) therefore stated at the

outset that "the only emotions I propose expressly to consider here are those that have a distinct bodily expression" (p. 189). James maintained that within this class of emotional phenomena, discrete emotional experiences can be identified with unique patterns of bodily changes, and that the perception of one of these specific patterns of peripheral physiological changes *is* the emotional experience.

James's (1884) hypothesis that autonomic nervous system (ANS) activity produces the percepts of discrete emotional states implies that emotion-specific somatovisceral patterns generate emotional experiences, and that a somatovisceral pattern begins before the experience of the corresponding emotion. In an early critique of this position, Cannon (1927) provided evidence from animal studies that autonomic events are too slow, too insensitive, and too undifferentiated to contribute to emotions. This critique appeared devastating and led to the notion that emotional experience is the exclusive province of central networks. Consistent with this notion, research on the influence of cognitive appraisals in emotion (e.g., Ellsworth, 1994) and on emotions in the spinal-cord-injured (e.g., Chwalisz, Diener, & Gallagher, 1988) suggests that afferent information from peripheral activity is not a necessary condition for emotional experience. Recently, however, the pendulum appears to have begun to swing in the other direction, as investigations suggest that autonomic processes *can* contribute to the encoding and recall (if not the experience) of emotional information (e.g., see review by Cahill, 1996; see also Demaree & Harrison, 1997).

To the extent that emotional experiences are multiply determined, the experience of a discrete emotion can occur in the absence of the "corresponding" somatovisceral pattern, even if somatovisceral afference can be an antecedent of the emotion. A recent neurobiological model of anxiety emphasizes the reciprocal relations between ascending and descending systems (Berntson, Sarter, & Cacioppo, 1998). This model recognizes not only that affective states may be primed by either top-down (cognition) or bottom-up (visceral reactivity) processes, but that these alternative activational modes may mutually reinforce one another (e.g., as in panic disorder). For this reason, it is more informative to ask under what conditions and for what emotions differential physiological activity is observed than to search for an invariant relationship between emotional experience (or expressions) and physiological response. For instance, Schachter and Singer (1962) shaped thinking about emotions when they suggested that undifferentiated autonomic activity *can* subserve discrete emotions. The mechanism by which this is accomplished, according to Schachter and Singer (1962; see also Mandler, 1975; Reisenzein, 1983), is the perception of neutral, unexplained physiological arousal, which creates an "evaluative need" and motivates the individual to understand and label cognitively the arousal state. The consequent attributional processes were thought to produce discrete feeling states and influence emotional behavior.

Figure 11.1 depicts a general framework summarizing mechanisms by which somatovisceral afference may influence emotional experience (Cacioppo, Berntson, & Klein, 1992). At one end of the continuum (Figure 11.1, top left column), discrete emotional experiences result from the apperception of distinct somatovisceral patterns (e.g., Ekman, Levenson, & Friesen, 1983; James, 1884; Levenson, 1988; Levenson, Ekman, & Friesen, 1990). At the other end of the continuum (Figure 11.1, bottom left column), discrete emotional experiences derive from attributional processes that are initiated by the perception of undifferentiated physiological arousal (e.g., Mandler, 1975; Schachter & Singer, 1962). Falling between these extremes is yet another process by which peripheral bodily reactions may contribute to emotional experience—"somatovisceral illusions," an active perceptual process by which an ambiguous pattern of somatovisceral afference is disambiguated to produce an immediate, spontaneous, and indubitable emotional percept (Figure 11.1, middle left column).

The essential feature of the proposition that discrete emotions can result from somatovisceral illusions can be illustrated by analogy using the ambiguous visual figure depicted in Figure 11.2 (see Cacioppo, Berntson, & Klein, 1992, for a more complete description of the model). Even though there is only one set of visual contours and features in Figure 11.2, top-down processes make it possible for a person looking at this picture to see or experience two very different perceptual images: a young woman facing left or an old woman facing right. Once these images have been identified, the viewer may find that he or she can alternate quickly between seeing these discrete images,
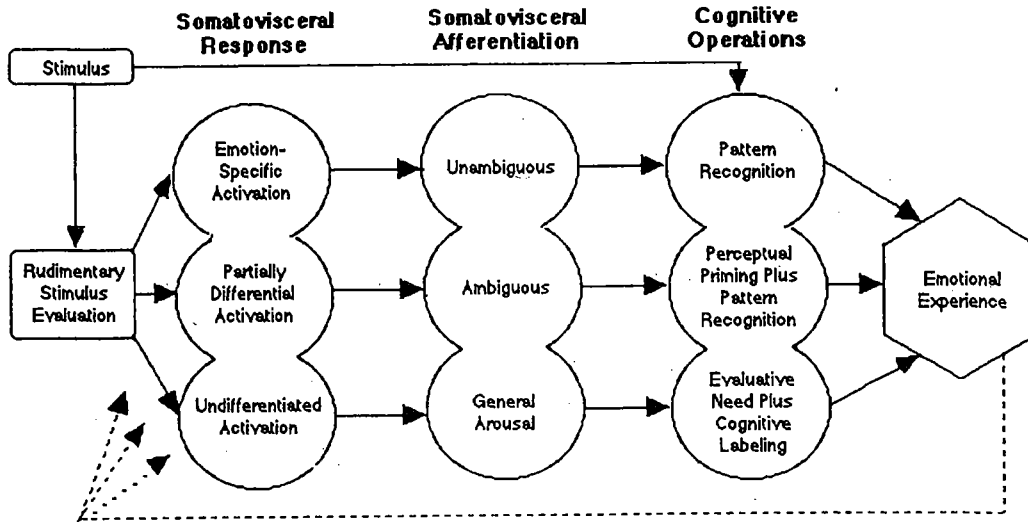
FIGURE 11.1. The somatovisceral afference model of emotion (SAME). The same pattern of somatovisceral activity has been associated with surprisingly different emotions, and the same emotion has been associated with quite different patterns of somatovisceral activity. These results have been viewed as evidence against the importance of somatovisceral afference in emotion. The SAME, depicted above and described in the text, encompasses both of these findings while emphasizing the instrumental role of somatovisceral afference and cognitive/perceptual processes in producing emotion. From Cacioppo, Berntson, and Klein (1992). Copyright 1992 by Sage Publications. Reprinted by permission.

but cannot see both at once. That is, the same visual afference can lead to two different, discrete, and indubitable perceptual experiences, just as the same physiological afference may lead to two different, discrete, and indubitable emotions..

Ambiguous visual figures such as the one depicted in Figure 11.2 are constructed by using elements from two (or more) unambiguous images in such a way that the figure created by overlapping or slightly modifying the elements of the unambiguous images can be interpreted in multiple discrete ways (Sekuler & Blake, 1985). Because the same sensory information in an ambiguous figure can produce such strikingly different, immediately obvious, and unambiguous perceptions, Leeper (1935) referred to ambiguous figures as "reversible illusions." There is little reason to suppose that somatovisceral illusions can not operate similarly. The active perceptual processes underlying reversible visual illusions are not limited to visual information processing, but can also operate on interoceptive (e.g., visceral) and proprioceptive (e.g., postural, facial, vocal) input. Indeed, the architecture of the somatovisceral apparatus may be better suited to produce ambiguous afference than is the visual system (Reed, Harver,

& Katkin, 1990). For instance, in the perception of ambiguous visual figures, the stimulus is a visual array outside the body. However, the central nervous system serves to create and interpret both the stimulus and the response to somatovisceral information. In this regard, visual processes are somewhat more like somatic instrumental processes than like visceral processes. Both of the former differ from visceral perception, for instance, in the distinctiveness of the reafference. In the somatic case, the accuracy of response is readily ascertainable, and correctable, by somatosensory and visual feedback. In the visceral domain, there is no "intended" outcome in the conscious sense (although there are target outcomes in an automatic or homeostatic sense). In the case of all three, feedback can importantly shape subsequent action without conscious awareness. Hence visceral perception differs from somatic and visual perception in that there is no discrete criterion (or "correct" perception) for which an individual is consciously looking. For this reason, visceral afference may be particularly prone to misperceptions and "illusions." Furthermore, it seems likely that events as important and commonplace as the emotions have cognitive representations that include somato-

FIGURE 11.2. This ambiguous figure is called "My wife and mother-in-law" and is constructed from overlapping unambiguous elements. The perceptual system tends to group like or related information together. Rather than presenting some odd mixture of the two alternative pictures, partial identification of a young woman or an old woman in this figure supports a stable perception of a single coherent image. The identification of wholes and of parts is reciprocally supportive, contributing further to the locking-in process. A shift in gaze is not necessary for a perceptual change to occur. In what may be analogous to discrete emotional feelings' being spawned by the same ambiguous pattern of somatovisceral information, ambiguous visual figures demonstrate that discrete images can derive from the same ambiguous pattern of visual information. From Boring (1930).

formation flow (Cacioppo, Berntson, & Klein, 1992). The extent of the cognitive elaboration of the somatovisceral afference required to produce an emotional experience ranges from simple informational analyses such as pattern recognition (e.g., James's theory of emotion as the perception of discrete patterns of somatovisceral afference) to much more complex attributional analyses and hypothesis testing (e.g., Mandler's theory of emotion), with simple cognitive appraisals of the stimulus and perceptual priming of an emotion schema falling between these two endpoints. Note that quite different patterns of somatovisceral afference (see Figure 11.1, left column) can lead to the same emotional experience via three very different psychophysiological mechanisms (see Figure 11.1, right column), whereas the same pattern of somatovisceral afference can lead to discrete emotional experiences by two distinct psychophysiological mechanisms: (1) somatovisceral "illusions" when the afference is ambiguous and an emotion schema has been primed (see Figure 11.2); and (2) cognitive labeling when the perception of the afference is undifferentiated with respect to an emotion and there is an evaluative need. The framework outlined in Figure 11.1 argues against the tendency to view the psychophysiological mechanisms underlying emotion in terms of a simple central–peripheral dichotomy. It also is in accord with robust findings in the literature that discrete emotional percepts can occur even when the autonomic changes do not discriminate fully the emotions that are experienced, and that autonomic activation can alter the intensity if not the nature of emotional experience. In the sections that follow, we examine the nature of the expressive patterns associated with discrete emotions.

visceral attributes. Thus several important features required for the production of somatovisceral illusions are plausibly in place.

The nodes along the continuum in the left column of Figure 11.1 represent important transitions in the constitution of the autonomic response, but the openings between these nodes underscore the continuous nature of this dimension. The pattern of somatovisceral activation produces a parallel continuum of somatovisceral sensory input to the brain. The arrows between nodes denote the major pathways for in-

FACIAL ELECTROMYOGRAPHY

Scientific studies of the link between facial expressions and emotions originated with Darwin's (1872) seminal analysis and were reinvigorated by Tomkins's (1962) proposition that facial movement and feedback play an important role in the experience of emotion. Tomkins suggested that high-speed filming could be used to perform microscopic analyses of facial expressions and emotion. These proposals led to important methodological advances in the coding of facial expressions (e.g., Ekman &

Friesen, 1978; Izard, 1971, 1977). Building on this foundation, investigators have provided provocative evidence that (1) at least some discrete emotions are associated with distinct overt facial expressions; (2) induced states in which individuals report positive and negative emotions are associated with distinctive facial actions; and (3) displays similar to those of adults can be found in neonates and the congenitally blind, suggesting that these displays are inherently linked with basic emotions (e.g., see Ekman, 1973; Ekman & Friesen, 1978; Izard, 1977).

Although facial expressions may seem intuitively to reveal the nature of underlying emotions, many emotional and affect-laden information processes are not accompanied by visually perceptible facial actions. This fact has limited the utility of analyses of facial actions in understanding emotions. Furthermore, although observers across cultures attribute the same emotional meaning to the expressions of happiness, sadness, fear, anger, surprise, and disgust, these attributions are not perfect (Russell, 1994). Complicating research in this area, the specific emotion that is evoked by a stimulus may vary across individuals and cultures. Finally, individuals can invoke display rules to mask or hide the emotion they are feeling, and observers can confuse the meaning of expressions (e.g., fear and surprise; Ekman, 1973; cf. Cacioppo, Bush, & Tassinary, 1992). For these reasons, the coding of overt facial expressions can be a less than perfect measure of affective state. An important complement to visual inspection of facial expression has been the measurement of patterns of activity in facial muscles. This technique—facial electromyography (EMG)—has made it possible to index muscle activity even in the absence of observable facial expressions (Cacioppo & Petty, 1981; Cacioppo, Tassinary, & Fridlund, 1990).

In pioneering research, Schwartz and colleagues demonstrated differences related to emotional imagery in EMG activity over the brow (corrugator supercilii), cheek (zygomaticus major), and perioral (depressor anguli oris) muscle regions. Schwartz, Fair, Salt, Mandel, and Klerman (1976), for instance, asked participants to imagine positive or negative events in their lives. Results revealed that people showed more EMG activity over the brow region and less over the cheek and perioral regions when imagining sad as compared to happy events. Schwartz, Ahern, and Brown (1979) asked subjects to engage in thought and imagery tasks that involved happiness, excitement, sadness, fear, and neutral emotional states. Facial EMG was recorded over two sites, the brow and cheek. The only significant main effects for discrete emotional states indicated higher EMG activity over the cheek and lower EMG activity over the brow during positive than negative emotions.

Although the number of studies is limited, research has consistently shown that EMG activity over the brow (corrugator supercilii, frown muscle) region is lower and EMG activity over the cheek (zygomaticus major, smile muscle) and periocular (orbicularis oculi) muscle regions is higher when emotions that are mildly positive, as opposed to mildly negative, are evoked. These opposing effects are more apparent at the group (nomethetic) level than at the individual (idiographic) level of analysis. In early reports, the facial EMG patterns associated with emotional states were characterized as "miniature representations" of those occurring during overt facial expressions (Schwartz, Fair, Greenberg, Foran, & Klerman, 1975). The evidence for covert emotion-specific facial expressions has been far weaker than the evidence for overt emotion-specific facial expressions, however. In a comprehensive study, for instance, Brown and Schwartz (1980) had participants go through imagery conditions designed to elicit happiness, sadness, fear, and anger at three levels of intensity while EMG activity was recorded over the brow, cheek, forehead, and jaw muscle regions. Results revealed that the imagery of negative emotions (fear, anger, and sadness) was associated with higher EMG activity over the brow muscle regions than was the imagery of the positive emotion (happiness). EMG activity over the cheek region was highest during happy imagery but also was elevated at least somewhat during fear and anger imagery. Whether these latter elevations reflect some participants engaging in miserable or distress smiling (Ekman, Friesen, & Ancoli, 1980), "cross-talk" from other muscles of the middle and lower facial regions, or the putative phylogenetic origin of smiling and laughter in primitive agonistic displays (Andrew, 1963; van Hooff, 1972) is unclear. EMG activity over the jaw and forehead muscle regions did not vary significantly (see also Brown & Schwartz, 1980; Hess, Kappas, McHugo, Lanzetta, & Kleck, 1992; Schwartz et al., 1976). Finally, increasing emotional intensity led to increased

EMG activity, especially over the brow muscle regions during sad, angry, and fearful imagery, and over the cheek muscle region during happy imagery (see, also, Cacioppo, Martzke, Tassinary, & Petty, 1988).

Fridlund, Schwartz, and Fowler (1984), using a unique classification analysis, reported evidence for emotion-specific facial EMG patterns. Subjects were instructed to imagine 48 emotional scenes designed to elicit happiness, fear, sadness, or anger, and EMG activity was recorded over the frontalis, corrugator supercilii, orbicularis oculi, and orbicularis oris muscle regions. A one-way multivariate analysis of variance was performed separately on the data from each subject. The parameter of EMG activity (e.g., mean, peak) that yielded the discriminant function with the clearest separation of emotion categories was selected on a subject-by-subject basis. A linear discriminant analysis differentiated among the emotion categories at better than chance level: Hit rates were 51% for happiness, 49% for sadness and anger, and 38% for fear. Posed expressions were also tested, yielding hit rates ranging from 83% to 89%. The covert facial EMG patterns that best differentiated among the emotions may have varied across subjects, and we have found no subsequent study in which an approach such as this produced evidence for distinctive (and generalizable) incipient facial expressive actions associated with discrete emotional states. Thus the bulk of the evidence to date suggests that the simple differentiation of hedonic tone has a lower threshold for activation than emotion-specific facial displays across individuals. That is, emotions can be characterized as a coalition of normally loosely coupled control mechanisms that are temporally recruited in a hierarchical sequence in order to meet an environmental challenge (imagined or real). The global distinction between hospitable (positive) or hostile (negative) stimuli, which is among the first information extracted from stimuli (Zajonc, 1980), may be one of the first aspects of an emotional response to be reflected in peripheral physiological activation in the form of rudimentary facial efference.

Although facial EMG research has proven to be a sensitive measure of hedonic tone, most psychophysiological research on discrete emotions has focused on the ANS. This emphasis is attributable to several factors. First, and as noted above, different emotions appear to be associated with signature visceral sensations (e.g., feeling steamed when one is angry, feeling butterflies in one's stomach when one is frightened). Second, whether or not visceral responses contribute to emotional experiences, they are clearly involved in emotion—as, for instance, demonstrated by the visceral changes that are observed when central networks associated with emotions are activated (LeDoux, 1996). Third, emotions, like the viscera, are common to all animals and fall largely outside of direct voluntary control. Consequently, the links between emotions and the ANS have been the topic of much research. Much of this research has been influenced by James's (1884) proposal that peripheral physiological changes are antecedents rather than consequences of the perception of emotional experience. Because of the close links between emotions and ANS activity, many researchers have focused their search for emotion-specific patterning on the ANS. We turn to this research next.

AUTONOMIC ACTIVITY

Early research on autonomic activity and affective reactions appeared to be characterized by a lack of replicability or generalizability. Despite the lack of consistency in early findings, the notion that visceral responses differentiate discrete emotions remained popular. In an important development in this area, Ekman, Levenson, and colleagues (Ekman et al., 1983; Levenson, 1988) attributed much of the inconsistency in prior results to various methodological problems. Among the problems they cited are the failure to verify independently that an emotional state has been aroused (e.g., through self-report or behavioral observation); the failure to equate the intensity of the emotions; and the mistiming of physiological recordings, given the likely onset and offset of the emotion. Furthermore, Ekman, Levenson, and colleagues argued that differentiation requires simultaneous examination of a number of indices of ANS activity. They maintained that emotion-specific autonomic differentiation would be obtained if these shortcomings were eliminated.

Ekman's group first presented evidence for the differentiation of discrete emotions in an article in *Science* in 1983 (Ekman et al., 1983). Heart rate, left- and right-hand finger temperature, skin resistance, and forearm flexor muscle tension were recorded during the manipulation of the emotional states of anger, fear, sadness,

happiness, surprise, and disgust. One method for evoking emotions involved a directed facial action task, in which a participant was induced to form a facial expression associated with a discrete emotion through muscle-by-muscle contraction instructions that omitted any reference to the emotional state. For example, a participant might be told to pull the eyebrows down and together, to raise the upper eyelid, to push the lower lip up, and to press the lips together. These instructions corresponded to the facial expression associated with anger.

Emotion was also evoked in this experiment with an imagery task, in which participants were asked to relive a past emotional experience for 30 seconds. Physiological responses during a relived emotion period were compared to a nonimagery resting baseline, revealing higher skin resistance during sadness than during fear, anger, or disgust. Together, the results from the two emotion induction techniques generated considerable enthusiasm for the idea of emotion-specific autonomic patterning, especially because emotions of the same valence (e.g., anger and fear) appeared distinguishable. Similar results were obtained by Levenson et al. (1990), using the directed facial action task, leading these researchers to propose that each discrete emotion is associated with an innate affect program whose role is to coordinate changes in the organism's biological states. They further argued that these changes are directed at supporting the behavioral adaptations and motor programs most likely associated with a particular emotion (e.g., fleeing in the case of fear), and can be recorded as emotion-specific changes in ANS activity (Levenson et al., 1990).

There is now a significant body of research relevant to this hypothesis, and several reviews have been performed (Cacioppo, Klein, Berntson, & Hatfield, 1993, Cacioppo, Berntson, Klein, & Poehlmann, 1997; Zajonc & McIntosh, 1992). These reviews reveal that whereas some reliable autonomic differentiation has been obtained across studies, the results are far from definitive regarding emotion-specific autonomic patterning. Table 11.1 lists in chronological order published research that has contrasted the effects of at least two discrete emotions on two or more autonomic measures in humans.

We (Cacioppo, Berntson, et al., 1997) conducted a meta-analysis providing data relevant to the question of whether emotion-specific au-

tonomic patterning exists. We updated the database (see Table 11.1) and repeated the meta-analyses based on this more complete dataset. Our inclusion criteria yielded numerous effect sizes involving 22 measures across almost two dozen studies. A word of caution is in order before we turn to the results. These meta-analyses allow one to examine statistically the differentiation of discrete emotions by individual measures. It is possible that discrete emotions differ in terms of the patterns of autonomic responses associated with each, even if no single measure is found to differentiate these emotions. Still, the literature is replete with claims of differentiating emotions using individual autonomic measures, and meta-analyses provide a more rigorous test of such assertions. Furthermore, a meta-analytic approach to this literature points to particularly fertile areas of research as well as to barren areas.

Consistent with Ekman et al.'s (1983) finding, greater heart rate acceleration was obtained to anger, fear, and sadness as compared to disgust. There was also a tendency for happiness to be associated with greater heart rate acceleration than disgust. However, disgust was associated with the same heart rate response as control conditions; indeed, disgust did not differ from control conditions on any autonomic measure. The meta-analysis also revealed heart rate responses to be larger in (1) anger than happiness, (2) fear than happiness (which also differed on finger pulse volume), and (3) fear than sadness (which also differed on respiration rate). Emotion-specific differentiation for cardiorespiratory measures other than heart rate was less reliable (e.g., measures of bodily tension, facial temperature, respiration amplitude, inspiration volume, or cardiac stroke volume; (Cacioppo, Berntson, et al., 1997). The only other replicable autonomic differentiation noted by Levenson et al. (1990; Levenson, Carstensen, Friesen, & Ekman, 1991) was that finger temperature decreased less in anger than in fear. Meta-analyses revealed that this effect did not achieve statistical significance when the results of all studies were considered. A study by Boiten (1996) also raises the possibility that at least some of the cardiac differentiation of emotions that has been observed may be secondary to effort and respiratory changes.

Several other reliable results emerged from our meta-analyses. Consistent with prior claims, diastolic blood pressure was higher in anger than in fear, but meta-analyses also re-

TABLE 11.1. Studies Comparing Two or More Physiological Measures as a Function of Two or More Discrete Emotions

Study	Age range (mean or mode)	Emotions [Induction]	Dependent variables
Ax (1953)	21–55 (27) $n = 43*$	Anger, fear [Real life]	SBP, DBP, SV, HR, FCT, FT, NNSCR, NMTP, SCL, EMG, RR
Funkenstein, King, & Drollette (1954)	19–24 $n = 52*$	Anger in (21 Ss), anger out (22 Ss), fear (anxiety; 9 Ss) [Psychological stressor]	HR, SBP, DBP, SV, CO
Schachter (1957)	(Normotensives, 38; potential hypertensives, 41; hypertensives, 42) $n = 48^a$	Anger, fear, pain [Real life]	HR, SBP, DBP, FCT, HT, SCL, EMG, II, RR, SV, CO, TPR
Sternbach (1962)[b]	All 8 years old $n = 10$	Fear, happiness, humor, sadness [Film]	SRL, gastric motility, RR, HR, EOG, FPV
Averill (1969)	17–24 (18) $n = 54$	Happiness, sadness, control [Film]	HR, SBP, DBP, FCT, FT, SCL, FPV, NNSCR, RR, RI
Tourangeau & Ellsworth (1979)	Undergrads $n = 123$	Fear, sadness, neutral [Film[c]] crossed with fear, sadness, neutral expression, undirected as to expression [DFA]	HR, SRL, NNSCR
Schwartz, Weinberger, & Singer (1981)	Undergrads $n = 32$	Anger, fear, happiness, sadness, relaxation, control [Imagery[d]]	HR, SBP, DBP
Roberts & Weerts (1982)	Undergrads $n = 16*$	Anger, fear, neutral [Imagery]	HR, SBP, DBP
Ekman, Levenson, & Friesen (1983)[e]	Nonundergrads $n = 16$ Only "best faces" and "best imagery" trials were reported	Anger, disgust, fear, happiness, sadness, surprise [DFA, relived emotion]	HR, FT, SRL, EMG
Stemmler (1989)	(23) $n = 42$	Anger, fear, happiness, control [Real life, imagery]	HR, FT, SCL, EMG, MVT (finger and head acceleration), RR, PTT, FPV, BV, NNSCR, FCT
Tassinary, Cacioppo, & Geen (1989)	Undergrads and grads $n = 15$	Anger, happiness, control [DFA]	SCL, HR
Levenson, Ekman, & Friesen (1990)	18–30 $n = 62^f$	Anger, disgust, fear, happiness, sadness, surprise [DFA]	HR, FT, SCL, EMG, MVT
Levenson, Carstensen, Friesen, & Ekman (1991)	71–83 (77) $n = 20*$ Only "best faces" and "best imagery" were reported	Anger, disgust, fear, happiness, sadness, surprise [DFA, relived emotion]	HR, FT, SCL, MVT
Hess, Kappas, McHugo, Lanzetta, & Kleck (1992)	Undergrads $n = 27$	Anger, happiness, peacefulness, sadness [Feel, express, feel-and-express]	Facial EMG, SCL, HR

TABLE 11.1 *(continued)*

Study	Age range (mean or mode)	Emotions [Induction]	Dependent variables
Levenson, Ekman, Heider, & Friesen (1992)	16–27 $n = 46^g$ Only "best faces" were reported.	Anger, disgust, fear, happiness, sadness [DFA]	HR, FT, SCL, PTT, FPV, RD, RR
Sinha, Lovallo, & Parsons (1992)	21–35 $n = 26*$	Anger, fear, joy, sadness, neutral state [Imagery]	HR, SBP, DBP, SV, CO, TPR, PEP, LVET
Vrana (1993)	Undergrads $n = 50$	Anger, disgust, pleasure (happiness), joy [Imagery]	HR, SCL, facial EMG
Boiten (1996)	Undergrads $n = 15*$ Data also broken down into emotional and nonemotional responders	Anger, disgust, fear, happiness, sadness, surprise, nonemotion, standard control [DFA]	RSP (T_i, T_e, P_i, T_{tot}, V_t, FRC), HR
Sinha & Parsons (1996)	21–35 $n = 27^h$	Anger, fear, neutral [Imagery]	FT, HR, SBD, DBP, SCL, facial EMG
Collet, Vernet-Maury, Delhomme, Dittmar (1997)	19–26 (22) $n = 30$	Happiness, surprise, sadness, fear, disgust, anger [Imagery]	EDR-Dur, HT, RR, SBF-Nod, SCL
Alaoui-Ismaili, Robin, Rada, Dittmar, & Vernet-Maury (1997)	20–28 (25) $n = 44$	Happiness, surprise, sadness, ear, disgust, anger [Odorants ^{i}]	EDR-Dur, HR, HT, RR, SBF-Nod
Miller & Wood, 1997	8–17 $n = 24^j$	Happiness, sadness, sadness/happiness, neutral [Film ^{k}]	HR, HRV, OS

Note. BV, blood volume; CO, cardiac output; DBP, diastolic blood pressure; DFA, directed facial action; EMG, muscle activity; EOG, eyeblink rate; EDR-Dur, electrodermal response duration; FCT, face temperature; FPV, finger pulse volume; FRC, functional residual capacity; FT, finger temperature; HR, heart rate; HRV, heart rate variability; HT, hand temperature; II, inspiratory index; LVET, left ventricular ejection time; MVT, movement; NMTP, number of muscle tension peaks; NNSCR, number of nonspecific skin conductance responses; OS, oxygen saturation of the blood; PEP, preejection period; Pi, postinspiratory pause; PTT, pulse transit time; RD, respiration depth; RSP, respiration; RI, respiration irregularity; RR, respiration rate; SBF-Nod, nonoscillatory duration of the skin blood flow response; SBP, systolic blood pressure; SCL, skin conductance level; SRL, skin resistance level; SV, stroke volume; T_i, inspiratory time; T_e, expiratory time; TPR, total peripheral resistance; T_{tot}, total cycle duration; V_t, tidal volume. An asterisk that indicates that participants were selected based on ability to control facial muscles, on ability to produce appropriate imagery, or on whether they experimented the emotions of interest.

[a] 18 hypertensives, 8 potential hypertensives, and the same 15 normotensives as in Ax (1953).

[b] Although this study is included in this descriptive table, it is not included in the meta-analyses because no interemotion comparisons were reported.

[c] No significant effects were found for differences in facial expressions during the film.

[d] Participants imagined a scene in which they felt the appropriate emotion as they were (in their imaginations) exercising on a one-step exercise machine.

[e] The DFA results of this study were subsequently incorporated into Levenson et al. (1990).

[f] Article combined results from three experiments: Ekman et al. (1983); a group of 16 Ss selected from 103 screened; and a group of 30 Ss selected from 109 screened.

[g] Participants were from the Minangkabau community in West Sumatra.

[h] Only males with Minnesota Multiphasic Personality Inventory *T*-scores between 30 and 70 were selected.

[i] Ss inhaled vanillin, menthol, eugenol, propionic acid, and dental resin. Vanillin and propionic acid evoked happiness and disgust, respectively; the other odorants did not reliably evoke the intended emotions and were not included in the meta-analyses.

[j] All Ss were asthmatics; no comparison sample was reported.

[k] Ss viewed clips from the film *E.T.: The Extra-Terrestrial.* The sadness/happiness clip was a farewell scene; the data from this condition were not included in the meta-analyses.

vealed that anger was associated with more nonspecific skin conductance responses, smaller increases in heart rate, smaller increases in stroke volume and cardiac output, larger increases in total peripheral resistance, larger increases in facial temperature, and larger increases in finger pulse volume than fear. Thus anger appears to act more on the vasculature and less on the heart than fear. Whether these differences generalize to other conditions of evocation requires further research.

The diastolic blood pressure response was also higher in anger than in sadness or happiness, and in sadness than in happiness (which also differed on the measure of systolic blood pressure). No other differences were reliable. Most of these meta-analytic results were characterized by high heterogeneity, however; this suggests that anger, fear, sadness, and happiness may have differential effects on peripheral vascular function, but that one or more unspecified variables are also likely to be moderating these relationships.

Meta-analyses showed that skin conductance level increased less in happiness than in disgust, but as noted above, disgust did not differ from control conditions in terms of any autonomic response. Fear was associated with greater increases in nonspecific skin conductance responses and smaller increases in skin conductance level than sadness. Too few data exist on several other measures (e.g., systolic time intervals, finger pulse volume, pulse transit time, body movement) to permit us to draw strong conclusions (see also Cacioppo, Berntson, et al., 1997, Tables 2.2 and 2.3).

Several reviews have also noted the failure of imagery to produce differentiation reliably or to produce the same pattern of differentiation as other operationalizations; this is problematic for the notion of *emotion*-specific patterning (e.g., Cacioppo, Berntson, et al., 1997; Zajonc & McIntosh, 1992). Skin resistance level, for instance, has been observed to decrease more during sadness than during fear, anger, or disgust, but these comparisons were not significant when requested facial actions were used to manipulate discrete emotions (Ekman et al., 1983).

The notion that ANS activity is mobilized in response to perceived or expected metabolic demands is consistent with a distinction made by Lang and colleagues (Lang, Bradley, & Cuthbert, 1990; Bradley, 2000) between "strategic" and "tactical" aspects of emotions.

Tactics are specific, context-bound patterns of action. Although affective reactions can be organized into a finite set of discrete emotions, tactical demands may vary among situations, making it possible for the same emotion to be associated with a range of behavior and varying patterns of somatovisceral activation. For example, Lang et al. (1990) note that the behaviors associated with fear can range from freezing to vigilance to flight. This tactical variability may account in part for the poor reliability of emotion-specific autonomic patterning unless one considers the modulation of ANS substrates by these factors.

In contrast to tactics, strategies are viewed as underlying organizations that direct actions in the pursuit of broad end goals. The dimensions of valence (appetitive or aversive) and intensity are viewed by Lang and colleagues as strategic aspects of emotion. The ability of the ANS to mobilize metabolic resources in response to hostile and hospitable stimuli is crucial to survival. Despite unreliable emotion-specific autonomic patterning, valence-specific patterning may exist. A variety of theoretical and empirical work suggests that, all else being equal, negative emotions may be characterized by greater autonomic activation than that found in positive emotions (Cacioppo, Berntson, et al., 1997; Taylor, 1991). Among the ways in which negative and positive affective processes appear to differ, for instance, is the tendency for the change in negative motivational output to be larger than the change in positive motivational output per unit of activation. This effect, which has been observed in animal learning (Miller, 1961), human affective judgments (Ito, Cacioppo, & Lang, 1998), attitudes and impression formation (Cacioppo & Berntson, 1994; Skowronski & Carlson, 1989), and late positive brain potentials to affectively discrepant stimuli (Ito, Larsen, Smith, & Cacioppo, 1998), is termed the "negativity bias" (Cacioppo & Berntson, 1994; Cacioppo et al., 1999).

To examine whether autonomic responses differed for positive and negative discrete emotions, we conducted moderated meta-analyses of the data from the studies in Table 11.1. The results are depicted in Table 11.2. Diastolic blood pressure, blood volume, cardiac output, left ventricular ejection time, preejection period, pulse transit time, and heart rate all showed significantly greater activation during negative than during positive discrete emotions. The effect size for systolic blood pressure was compa-

rable to that found for heart rate, but the effect size was not significant given the relatively small number of comparisons that went into this meta-analysis. Inspection of Table 11.2 further reveals that electrodermal measures did not differentiate positive from negative states, with the exception that negative emotions were associated with shorter-duration electrodermal responses than was happiness. A similar effect was found for cutaneous blood flow responses (see Table 11.2). The tests for heterogeneity suggest caution in interpreting the effects for the measures of diastolic blood pressure, blood volume, nonoscillary duration of the skin blood flow response, and electrodermal response duration. Thus, of the 22 measures that were meta-analyzed, 5 showed clearly greater activation to negative than to positive emotions, and none showed the reverse.

In sum, the meta-analyses indicated that even a limited set of discrete emotions such as happy, sad, fear, anger, and disgust cannot be fully differentiated by visceral activity alone, but follow-up meta-analyses did suggest that the negative emotions in this literature are associated with stronger ANS responses than are the positive emotions. Thus the evidence for the visceral differentiation of emotion, like that for incipient facial differentiation, is clearer when positive and negative emotions are contrasted than when discrete emotions are contrasted. To return to the heuristic portrayed in Figure 11.1, a stimulus is depicted as initially undergoing a rudimentary evaluation. Although not sufficient to produce emotion-specific somatovisceral activation, the rudimentary evaluation of the stimulus may at least identify it as one that is to be approached or avoided, producing a cascade of central and peripheral responses. We have thus far covered somatovisceral processes. We turn in the final section to central processes, where it has been found that anterior hemispheric asymmetries differentiate motivational dispositions and responses.

TABLE 11.2. Number of Comparisons, Combined Effect Size, and _p_ Value for Comparisons of Negative (Anger, Fear, Disgust, Sadness) and Positive (Happiness[a]) Emotions by Physiological Measure

Measure	k	$d+$	$p(d+)$	$p(Q)$
DBP	7	0.54	.01	.01
BV	2	0.50	.01	.01
CO	3	0.47	.01	.14
LVET[b]	3	0.32	.05	.48
PEP[b]	3	0.32	.05	.42
PTT[b]	6	0.22	.01	.18
SBP	5	0.18	.15	.39
HR	32	0.17	.01	.10
RSP-Dur[b]	11	0.11	.14	.03
FPV[b]	7	0.09	.27	.82
FT[b]	15	0.07	.22	.82
RSP-Amp	7	0.04	.65	.75
SCL	26	0.03	.49	.04
NNSCR	3	0.02	.87	.95
MVT	2	0.01	.97	.58
SV	3	−0.03	.85	.89
FCT[b]	3	−0.11	.44	.01
EMG	10	−0.12	.08	.52
HT[b]	4	−0.12	.34	.60
TPR	3	−0.14	.04	.13
SBF-Nod	5	−0.25	.02	.02
EDR-Dur	5	−0.29	.01	.01

Note. k, = number of comparisons; $d+$, the average d weighted by the inverse of the variance of the measure ($d+ > 0$ indicates greater activation by negative emotion relative to positive emotion); $p(d+)$, the probability of obtaining the $d+$ by chance; $p(Q)$, the probability that heterogeneity of the k effect sizes is due to chance (a significant test of heterogenity indicates heterogeneity among the effect sizes). Variables representing the same construct were all given the same abbreviation, regardless of the name used in the original article. Abbreviations are as follows: DBP, diastolic blood pressure; BV, blood volume (includes head blood volume); CO, cardiac output (includes average height of IJ wave × pulse rate); LVET, left ventricular ejection time; PEP, preejection period; PTT, pulse transit time; SBP, systolic blood pressure; HR, heart rate; RSP-Dur, respiration duration (includes respiration rate, respiratory period, postinspiratory pause, expiratory time, inspiratory time, total cycle duration, respiratory intercycle interval); FPV, finger pulse volume (includes finger pulse volume amplitude, finger blood volume); FT, finger temperature; RSP-Amp, respiratory amplitude (includes respiratory depth, tidal volume, increase in functional capacity); SCL, skin conductance level (includes log conductance change, log palmar conductance); NNSCR, number of nonspecific skin conductance responses (includes number of galvanic skin responses, rate of galvanic skin responses); MVT, movement; SV, stroke volume (includes ballistocardiogram); FCT, face temperature; EMG, muscle activity (includes number of muscle tension peaks, maximum muscle tension increase); HT, hand temperature; TPR, total peripheral resistance (includes peripheral vascular resistance); SBF-Nod, nonoscillatory duration of the skin blood flow response; EDR-Dur, electrodermal response duration.

[a]Includes four comparisons involving Vrana's (1993) joy condition.

[b]Indicates measures coded such that lower values represent greater activation.

ELECTROENCEPHALOGRAPHIC ASYMMETRY

The left anterior region of the brain appears to be involved in the expression and experience of approach-related emotions, and the right anterior region appears to be involved in the expression and experience of avoidance-related emotions (see reviews by Davidson, 1992, 1993). Speculation relating hemispheric asymmetry to affective reactions was originally spurred by clinical observations linking depressive symptomology to hemispheric damage. Left anterior brain lesions, for instance, are more likely to produce major depression, whereas right anterior brain lesions are more likely to produce mania (Robinson & Downhill, 1995). Particularly compelling evidence was provided by Robinson and colleagues (Robinson, Kubos, Starr, Rao, & Price, 1984; Robinson & Downhill, 1995), who used computerized tomography to link stroke-related lesion location with the severity and valence of affective symptomatology. Severity of poststroke depression was positively related to lesion proximity to the left frontal pole, but negatively related to lesion proximity to the right frontal pole. Moreover, patients with right lateralized infarctions were more likely than their left-hemisphere-lesioned counterparts to display inappropriate cheerfulness.

These clinical observations are supported by experimental research suggesting that stable individual differences in activation of left and right anterior cortical areas result in a predisposition to experience approach-related positive affective states and withdrawal-related negative affective states, respectively. Davidson (1993, 1998) and colleagues have integrated these findings into a diathesis–stress model linking individual differences in anterior cortical asymmetry to dispositional affective tendencies. An important feature of this model is the requirement of an affective elicitor (e.g., Davidson, 1992; Davidson & Tomarken, 1989). That is, differences as a function of cerebral asymmetry are expected only when a stressor or affective challenge is experienced.

In studies illustrative of this body of research, emotionally evocative film clips served as the affective challenge, and self-reported reactions to the films were related to anterior cortical activity that was measured prior to film exposure (e.g., Wheeler, Davidson, & Tomarken, 1993; Tomarken, Davidson, & Hen-

riques, 1990). In these studies, as in much of the research in this area, cortical asymmetry was quantified via scalp electroencephalographic (EEG) recordings. The dependent measure of interest in this and other studies was power in the alpha band (8–13 Hz), which is inversely related to hemispheric activation (Lindsley & Wicke, 1974). Consistent with the diathesis stress model, relative left anterior cortical asymmetry in the resting EEG was positively correlated with intensity of positive reactions reported to positive film clips, but negatively correlated with intensity of negative reactions in response to negative film clips. Importantly, this relationship between asymmetry and affective responses was valence-dependent, and not simply a function of greater affective reactivity associated with one or the other hemispheres. That is, global reactivity, computed as the sum of the positive reactions to the positive films and the negative reactions to the negative films, was uncorrelated with cerebral asymmetry.

Differences in temperament as a function of cortical asymmetry are also apparent in children. For example, behaviorally inhibited toddlers tend to show relative right midfrontal activation, whereas their uninhibited counterparts display relative left midfrontal activation (Davidson, 1993). A similar relation between anterior cortical asymmetry and childhood temperament was observed in infants as young as 10 months (Davidson & Fox, 1989), with maternal separation serving as the affective challenge. Those children who cried during the 60-second separation had greater relative right-hemisphere activation in a resting EEG period that preceded the separation, whereas infants who did not cry showed relative left-hemisphere activation.

The studies reviewed thus far have sought to relate cortical asymmetry to phasic differences in the tendency to activate either approach- or withdrawal-related motivation. It is also possible to classify affective states as resulting from a hypoactivation of one of these systems. Depression, in particular, may result from a hypoactivation of approach-related motivation. This characterization of depression is supported by differences in resting EEG asymmetry recorded from clinically depressed and control participants (Henriques & Davidson, 1991). Whereas the two groups did not differ in right midfrontal activation, the clinically depressed participants showed decreased left midfrontal

activation relative to controls. Similar results have been obtained with currently normothymic participants with a history of depression (Henriques & Davidson, 1990). It is important to note that in this latter study, previously depressed and control participants did not differ in their current self-reported mood—a result that has been interpreted to mean that left-hemisphere hypoactivation renders individuals vulnerable to depressive episodes. Similarly, the studies comparing resting EEG asymmetry to reactions elicited by emotionally evocative films in nondepressed populations reveal relations between left-hemisphere activation and positive affective states and between right-hemisphere activation and negative affective states, even when the effects of baseline mood are statistically removed (Tomarken et al., 1990; Wheeler et al., 1993).

Phasic shifts in cortical asymmetry have also been observed during the actual experience of affective reactions. Davidson, Ekman, Saron, Senulis, & Friesen (1990) recorded EEG during the presentation of film clips chosen to elicit the approach-related positive states of amusement and happiness and the withdrawal-related state of disgust. Surreptitious video recording of the participants as they watched the films allowed for offline coding of facial expressions. EEG epochs corresponding to the facial expressions of either happiness or disgust were retained for analysis. Disgusted as compared to happy expressions were associated with greater activation over right midfrontal and anterior temporal regions, similar activation over left midfrontal regions, and less activation over left anterior temporal regions. Analyses conducted across all artifact-free EEG data (i.e., including those times in which a facial expression was not present) failed to reveal any relation between positive or negative film clips and cerebral asymmetry. Thus it may be that only emotional experiences strong enough to produce overt facial expressions are associated with measurable concomitant cortical asymmetry.

Cerebral asymmetry was measured as the difference between log alpha power in the right and left hemisphere (for an exception, see Wheeler et al., 1993)—a computation that implies a single continuum of activation. As evidence suggesting separable motivational systems has grown within cerebral asymmetry research (e.g., Sutton & Davidson, 1997) and other areas of neurophysiology, theoretical accounts of cerebral asymmetry have similarly evolved, and now explicitly incorporate separable systems (c.f. Sutton & Davidson, 1997). Anterior EEG asymmetries have not differentiated discrete emotions, however; instead, they appear more generally to differentiate approach-related emotions (e.g., happiness, anger) from withdrawal-related emotions (e.g., sadness, fear; Harmon-Jones & Allen, 1998).

EPILOGUE

As the varied perspectives represented in this volume suggest, the study of emotion can be informed from a wide range of viewpoints. One of the more interesting questions concerning the psychophysiology of emotions is the role of somatovisceral afference in emotional experience. The research on the somatovisceral differentiation of emotions is provocative, but the cumulative evidence for emotion-specific patterns remains inconclusive (Wagner, 1989). The psychophysiological research reviewed in this chapter suggests the following conclusions. Facial EMG activity over the cheek (zygomaticus major) and periocular (orbicularis oculi) muscle regions varies as a function of positivity, whereas EMG activity over the brow (corrugator supercilii) muscle region varies as a function of negativity, and research on EEG asymmetries similarly suggests that anterior brain regions are differentially involved in approach-related versus avoidance-related behavioral processes. Although autonomic activation differs as a function of the energetic (e.g., metabolic action) components of affective states, meta-analyses have revealed that negative emotions are additionally associated with larger changes than positive states on several autonomic indices.

Emotions—particularly *negative* emotions—have also been linked to increases in health problems, including an enhanced susceptibility to infection (see review by Herbert & Cohen, 1993), poorer response to an influenza vaccine (Kiecolt-Glaser, Glaser, Gravenstein, Malarkey, & Sheridan, 1996), and impaired wound healing (Kiecolt-Glaser, Marucha, Malarkey, Mercado, & Glaser, 1995). The mechanisms underlying the relationship between emotion and health are complex and are not yet fully understood, but several different mechanisms are likely to be involved, some of which imply autonomic differentiation of positive from negative affective states. Health problems increase with aging as well, with negative emotions augmenting age-related declines in health and

well-being (e.g., Kiecolt-Glaser, Dura, Speicher, Trask, & Glaser, 1991) and positive emotions having less impact (Ewart, Taylor, Kraemer, & Agras, 1991). Given this backdrop, it is understandable why investigators have been receptive to the idea that the emotions have distinct somatovisceral effects.

The psychophysiology of emotion might benefit from an expansion to include neuroendocrine systems, as these may serve as a gateway by which different emotions influence health. In addition, the potential elements and patterns of autonomic activity have not been exhaustively examined. Potential patterns may not be describable in terms of gross measures of end-organ response (e.g., heart rate), for instance. Among the possible obstacles to identifying autonomic patterning as a function of emotion, particularly for dually and antagonistically innervated organs such as the heart, are the many-to-one mappings between neural changes and organ response. Emotional stimuli do not invariably evoke reciprocal activation of the sympathetic and parasympathetic branches of the ANS. For instance, the presentation of an aversive conditioned stimulus can produce coactivation of the sympathetic and parasympathetic nervous systems, with the consequent heart rate response being acceleratory, deceleratory, or unchanged from prestimulus levels, depending upon which activational input is greater (see Berntson, Cacioppo, & Quigley, 1991). Berntson et al. (1991) have proposed a theory of autonomic control and modes of autonomic activation that resolves the loss of fidelity in the translation between changes in sympathetic and parasympathetic activation and organ responses. It is possible that emotions (e.g., disgust) or components of emotions (e.g., attention) could be differentiated if the focus were on indices of the sympathetic and the parasympathetic innervation of the viscera, rather than on visceral responses per se.

Whether or not the conditions for and the elements of emotion-specific peripheral patterns of activity can be identified, what does seem clear from this research is that discrete emotional percepts can occur even when the autonomic changes do not discriminate fully the emotions that are experienced. If discrete emotional percepts can occur even when the autonomic changes do not discriminate fully the emotions that are experienced, does it necessarily follow that somatovisceral afference plays no role in defining these discrete emotional percepts? Whereas Cannon's (1927) answer to

this question was "yes," we have outlined three routes by which somatovisceral afferentiation may influence emotional experience—emotion-specific ANS patterns, somatovisceral illusions, or cognitive labeling of unexplained feelings of arousal. Perhaps the most important implications of the model, however, are twofold: First, undifferentiated (or incompletely differentiated) physiological activation can still be an essential determinant of discrete emotional experiences. This can occur through any route except the first. Second, the traditional tendency to view the mechanisms underlying emotion in terms of a simple central–peripheral dichotomy appears no longer to be tenable.

Finally, studies of the "psychophysiology" of emotion have tended to focus on autonomic and, to some extent, somatic responses, as reflected by the content of the current chapter. Given recent advances on the interactions among the autonomic, neuroendocrine, and immune systems and the role of neuropeptides in integrating these systems, this focus is unnecessarily restrictive. Similarly significant advances in human brain imaging have now placed measures of central processes squarely within the psychophysiologist's armamentarium as well. Although experimental studies of discrete emotion are still new to these areas, it is our hope that by the next edition of the *Handbook* the chapter on the psychophysiology of emotions will be able to broaden the coverage from single somatovisceral measures to patterns of reactions across central and multiple peripheral (e.g., somatic, autonomic, endocrinological, and immunological) systems. Such an approach should provide a more complete picture of the central and peripheral processes associated with discrete emotions, and should enrich our understanding of the interactions among these central and peripheral processes.

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