

The psychophysiology of emotion

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You see me here, you gods, a poor old man,
As full of grief as age; wretched in both!
If it be you that stir these daughters' hearts
Against their father, fool me not so much
To bear it tamely; touch me with noble anger.

Shakespeare, *King Lear*, II.5

Just as Shakespeare used words to give voice to King Lear's outrage at his daughters' betrayal, psychology has often used the words that people use to describe their emotions to understand those emotions (e.g., Green, Salovey, & Truax, 1999; Osgood, Suci, & Tannenbaum, 1957; cf. Cacioppo, Gardner, & Berntson, 1999; LeDoux, 1995). Psychology's reliance on self-reports has been remarkably successful in terms of uncovering functional relationships between different variables. The words people use to describe their current emotions typically show consistent patterns (e.g., Russell, 1980). Those who report feeling happy, for instance, are unlikely to report feeling sad (Russell & Carroll, 1999; but see, Larsen, McGraw, & Cacioppo, 2001). In addition, situational manipulations reliably elicit different patterns of self-reported emotional states. People generally report feeling happy when hearing fast music in the major key and sad when hearing slow music in the minor key (Gagnon & Peretz, 2003). Moreover, children as young as 6 years of age can find words not only that describe their emotions but the putative causes of their emotions (e.g., Stein & Levine, 1987).

One factor that allows people to use words to convey their emotion is the fact that the world's languages are rich in emotional terms (e.g., Clore, Ortony, & Foss, 1987; Russell, 1978), which are supplemented with even richer metaphors (Fainsilber & Ortony, 1987; Hoffman, Waggoner, & Palermo, 1991). Yet words have their limitations. They are sometimes used to deceive rather than inform (e.g., DePaulo et al., 2003). Even when used in earnest, they are subject to contextual distortions that operate outside of awareness (e.g., Schwarz & Clore, 1983).

One implication is that emotions are not merely cerebral; they are embodied. Indeed, Lear's emotions are most powerfully conveyed not when his lines are read but when they are enacted by an actor on the stage. It is perhaps not surprising, then, that many of the metaphors people use to express emotion involve bodily sensations. People express anxiety by remarking that they have butterflies in their stomach or anger by remarking that their blood is boiling. Of course, such metaphors are just that. They are not emotions; they merely symbolize emotions—albeit imperfectly.

Dating back to Freud, research from clinical psychology has revealed that some aspects of emotional states can be reported and that others cannot (e.g., Bradley, 2000; Lang, 1971). In addition, research from the neurosciences (e.g., Gazzaniga & LeDoux, 1978; Tranel & Damasio, 2000) and social psychology (e.g., Winkielman, Berridge, & Wilbarger, 2005) has shown that emotional processes can occur in the absence of emotional experience, which is a prerequisite for the verbal expression of emotion. Thus, self-reports of emotion tend to be only modestly related to somatovisceral and behavioral aspects of emotion (e.g., Bradley & Lang, 2000a; but see, Mauss, Levenson, McCarter, Wilhelm, & Gross, 2005). One goal of the psychophysiology of emotion, then, is to investigate the physiological processes by which emotion is embodied and to thereby complement and clarify insights gleaned from ratings of emotions that people are willing and able to report. A second goal is to use psychophysiological methods to decompose the component processes that result in an emotional experience or response (Cacioppo & Petty, 1986).

Most contemporary definitions of emotion share several features. Most important is the notion that emotions consist of affective, valenced (i.e., positive and/or negative) reactions to meaningful stimuli (Frijda, 1994). Yet not all valenced reactions constitute emotions. Emotions typically are directed at particular objects, unlike moods, which tend to be more diffuse (Frijda,

1994). Emotions also tend to be short-lived, lasting on the order of seconds to minutes (Ekman, 1994). Other affective reactions, such as moods (Ekman, 1994; Frijda, 1994) and especially attitudes (cf. sentiments; Frijda, 1994) tend to be more enduring (Eagly & Chaiken, 1993). Thus, individuals who fear dogs do not live in a constant state of fear, but the appearance of a dog is likely to elicit fear (Frijda, 2000).

Fear can be conceptualized as a discrete emotion, along with anger, sadness, happiness, relief and other states that putatively differ in terms of a variety of factors including antecedent appraisals (e.g., Scherer, Schorr, & Johnstone, 2001), facial expressions (Ekman, 1992), and action tendencies (Frijda, 1986). Alternatively, emotions can be conceptualized in terms of a small number of dimensions, such as valence and arousal (Russell & Feldman Barrett, 1999), positive and negative activation (Tellegen et al., 1999), or positivity and negativity (Cacioppo et al., 1999). Though a review of the relative merits of each approach is beyond the scope of this chapter, we have argued that discrete and dimensional approaches are not incommensurable and that both approaches can be useful (Cacioppo et al., 1999). Indeed, many of the findings reviewed in this chapter indicate that the psychophysiological substrates of emotion are organized in terms of dimensions (e.g., valence), but other findings highlight the utility of postulating the existence of discrete emotions.

Overview

The nervous system is divided into two broad components. The central nervous system comprises the brain and spinal cord, which send and receive inputs from the peripheral nervous system. In turn, the peripheral nervous system comprises the autonomic and somatic nervous systems. The autonomic nervous system innervates smooth muscles (e.g., the heart) and glands and is divided into the sympathetic and parasympathetic branches. Whereas the sympathetic branch generally prepares the body for action (e.g., by stimulating heart rate), the

parasympathetic branch aids restorative functions (e.g., by stimulating digestion). Finally, the somatic nervous system innervates skeletal muscles, including those of the face.

Common to all definitions of psychophysiology is that it involves the use of physiological signals to understand psychological processes (e.g., Cacioppo, Tassinary, & Berntson, 2007; Coles, Donchin, & Porges, 1986; Stern, Ray, & Quigley, 2001). Cognitive psychophysiology, for instance, is largely concerned with mental processes and has therefore relied heavily on the electroencephalogram (EEG), which reflects the electrical activity underlying central nervous system processes (e.g., Coles et al., 1986). So extensive is the embodiment of emotion, however, that surface recordings of central, autonomic and somatic nervous system activity have all shed light on the physiological substrates of emotion. Early theory and research on the psychophysiology of emotion focused on the peripheral nervous system, so we begin there. We then turn to the somatic nervous system, where research has investigated relationships between emotional states and activation of the facial musculature. Finally, we turn to the central nervous system, where electroencephalographic research has helped delineate the neural mechanisms underlying emotion.

The peripheral nervous system

As mentioned above, many metaphors used to describe emotions involve bodily states. Most of those metaphors make reference to peripheral physiological processes in particular. Though most individuals in Western cultures presumably recognize that the heart is in reality a mere pump, it is often described as the seat of emotion, in general, and love, in particular. Thus, our hearts go aflutter when we are in love but break when our beloved departs. Though intuition about psychological phenomena is often imprecise at best and inaccurate at worst, psychophysiology has demonstrated that peripheral processes in the form of autonomic (i.e.,

visceral) and somatic (e.g., motor, expressive) events are indeed associated with emotional processes.

Autonomic Nervous System

The rich connections between the central and peripheral nervous systems have long fueled debates over the precise role of peripheral activity in emotion. These connections are reciprocal, such that the central nervous system both sends and receives input from the viscera. The fact that the brain sends efferents to the periphery raises the possibility that the experience of emotions (i.e., “feelings”) cause peripheral changes. On the other hand, the fact that the central nervous receives afferents from the periphery raises the perhaps more counterintuitive possibility that the peripheral changes contribute to the experience of emotion. The former possibility was set forth by William James (1884, 1890/1950) more than a century ago. By this account, specific somatovisceral patterns can not only precede but also generate the experience of emotion. In an early critique of James’ position, however, Cannon (1927) argued that different autonomic patterns did not produce different emotions; rather, different emotions produced different autonomic patterns.

Schachter and Singer (1962) proposed an alternative to both James (1884, 1890) and Cannon (1927). Like James, Schachter and Singer contended that autonomic activity could generate different emotions. Unlike James, however, they also suggested that the same pattern of autonomic activity could result in the experience of different emotions (see also, Mandler, 1975). By this account, the perception of neutral, unexplained physiological arousal creates an “evaluative need” that motivates the individual to come up with a cognitive label for the arousal state. Depending on situational cues, the individual may come to experience different emotional states (e.g., anger, euphoria; Schachter & Singer, 1962; cf. Reisenzein, 1983).

Thus, theories have proposed three distinct relationships between somatovisceral activity and emotional state. Whereas Cannon (1927) contended that different emotions produce different patterns of somatovisceral activity, James (1884) contended that different patterns of somatovisceral activity can produce different emotions. Finally, Schachter and Singer (1962) contended that even undifferentiated somatovisceral activity can produce distinct and different emotions depending on the situational context. Several subsequent theories of emotion can be seen as falling within each of these camps. Damasio's (1994) somatic marker hypothesis and Barrett's (2006) somatic marker hypothesis and conceptual act model of emotion, for instance, bear resemblance to the conceptualizations of James (1884) and Schachter and Singer (1962), respectively. Researchers have marshaled empirical evidence both for and against each position. Vianna, Weinstock, Elliott, Summers, and Tranel (2006) studied individuals with Crohn's disease, which is associated with excessive visceral outflow from the gut. As both James and Schachter and Singer would expect, individuals with Crohn's disease showed greater gastric myoelectrical activity during emotionally evocative films than did comparison participants, which may help explain why they also experienced more subjective arousal. (For a review of work on interoception and emotion, see Craig, this volume). Indirect evidence for James' position comes from Barrett, Quigley, Bliss-Moreau, and Aronson's (2004) recent finding that individuals who are more sensitive to their heartbeats also tend to emphasize the arousal-related meanings of emotion words (see also Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004).

On the other hand, Cannon (1927) provided evidence from animal studies that autonomic events were too slow, insensitive, and undifferentiated to influence emotions. More recently, neuropsychological research with humans suggests that spinal cord injuries have little impact on individuals' experience of emotion (Chwalisz, Diener, and Gallagher, 1988; see also, Cobos, Sánchez, Garcia, Vera, & Vila, 2002). Perhaps most problematic for James' hypothesis was that

early research failed to demonstrate replicable and generalizable emotion-specific autonomic patterns. Ekman, Levenson, and Friesen (1983; Levenson, 1988) attributed such inconsistency to a variety of methodological limitations. For instance, previous investigators made no attempt to equate the intensity of different emotions and failed to synchronize physiological recordings with the likely onset and offset of the emotion or even collect self-reports or behavioral observations to confirm that the expected emotions had been elicited. Furthermore, Ekman et al. argued that differentiation requires simultaneous examination of a number of indices of autonomic nervous system activity.

Ekman, Levenson, and Friesen (1983) overcame these limitations in a groundbreaking article published in *Science* that provided evidence for emotion-specific autonomic patterns. Ekman et al. measured heart rate, finger temperature, skin resistance, and forearm flexor muscle tension as participants completed two sets of tasks designed to elicit anger, fear, sadness, happiness, surprise, and disgust. In one task, participants were asked to remember and relive past emotional episodes. Participants also completed a directed facial action task in which they were asked to contract sets of muscles to produce facial expressions associated with each emotion. During the anger condition, for instance, participants were asked to pull their eyebrows down and together, raise their upper eyelids, push the lower lips up, and press their lips together.

Ekman et al. (1983) found that, in addition to differentiating positive from negative emotions, combinations of autonomic measures could differentiate some negative emotions (e.g., fear) from others (e.g., anger). During the facial action task, for instance, happiness was characterized by decreased heart rate, anger by increased heart rate and increased skin temperature, and fear by increased heart rate and decreased skin temperature. Based on such findings, Levenson, Ekman, and Friesen (1990) proposed that each discrete emotion is associated with an innate affect program that coordinates changes in the organism's biological states. They

further argued that such changes support the behavioral reactions most often associated with particular emotions (e.g., fleeing in the case of fear).

Levenson and colleagues' work sparked a flurry of research on emotion-specific autonomic patterning, which has been reviewed by numerous researchers (e.g., Wagner, 1989). Different reviewers, however, have come to strikingly different conclusions (e.g., Levenson, 1992; Zajonc & McIntosh, 1992). Levenson contended that the literature provided compelling evidence for emotion-specific autonomic responding. For instance, he reviewed evidence that sadness is associated with greater heart rate acceleration than anger and fear, which are both associated with greater acceleration than happiness. Disgust, on the other hand, is associated with heart rate decelerations. Zajonc and McIntosh, however, contended that the evidence for emotion-specific autonomic responding was inconsistent at best.

In an attempt to resolve the debate, Cacioppo, Berntson, Klein, & Poehlmann (1997) and Cacioppo, Berntson, Larsen, Poehlmann, and Ito (2000) conducted meta-analyses of all published studies comparing the effects of at least two discrete emotions on at least two autonomic measures. Though 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 even if they do not differ in terms of each isolated autonomic response. Nonetheless, the literature contains claims that emotions can be differentiated with individual autonomic measures and such hypotheses can be rigorously tested with meta-analysis.

Results of Cacioppo et al.'s (2000) meta-analysis were consistent with some of Levenson's (1992) claims. For instance, anger, fear, and sadness were associated with greater heart rate acceleration than disgust. Anger was also associated with higher diastolic blood pressure than fear and disgust was associated with larger increases in skin conductance level than happiness. Other claims were not supported. For instance, fear was not associated with larger

decreases in finger temperature than control conditions, nor was fear associated with larger increases in skin conductance level. Several other reliable results emerged from Cacioppo et al.'s (2000) meta-analyses. In addition to being associated with higher diastolic blood pressure than fear, anger was associated with more nonspecific skin conductance responses, smaller heart rate acceleration, smaller increases in stroke volume and cardiac output, and larger increases in total peripheral resistance, facial temperature, and finger pulse volume than fear. Thus, anger appears to be more strongly associated with vascular activity than is fear, but less strongly associated with cardiac activity.

Only a handful of studies were available for many of Cacioppo et al.'s (2000) comparisons, so these results should only be accepted tentatively and may need to be revisited pending more recent and future research. For instance, Cacioppo et al. found that anger was associated with greater total peripheral resistance and more nonspecific skin conductance responses than fear, but only a few previous studies had examined these relationships. Thus, it is not especially surprising that whereas Pauls and Stemmler (2003) recently found that anger was associated with greater total peripheral resistance, they also found that anger was associated with *fewer* skin conductance responses than fear. By way of comparison, Pauls and Stemmler's results corroborated Cacioppo et al.'s finding that fear was associated with larger increases in heart rate, which was based on 15 studies. Recent and future research will also allow meta-analytic comparisons that Cacioppo et al. (2000) were unable to complete because the necessary data were simply unavailable. Britton, Taylor, Berridge, Mikels, and Iberzon (2006), for instance, measured participants' heart rate and skin conductance as they watched films that elicited happiness, sadness, and disgust. They found that disgust was associated with greater skin conductance than sadness—a comparison that no studies in Cacioppo et al.'s database had reported.

As a research literature develops, meta-analysis becomes especially useful for identifying moderator variables. Several narrative reviews (e.g., Zajonc & McIntosh, 1992) have noted that different emotion inductions appear to elicit different autonomic patterns. Skin resistance level, for instance, declines more during sadness than during other negative emotions (e.g., anger) when emotions are induced with imagery tasks; these patterns are not obtained, however, when emotions are induced with facial action tasks (Ekman et al., 1983). Similarly, whereas Cacioppo et al. found that fear is associated with greater heart rate increases than anger, Labouvie-Vief, Lumley, Jain, and Heinze (2003) found that imagery-induced fear and anger elicited comparably large increases in heart rate. As it turns out, Labouvie-Vief's null effect is consistent with the results of a recent meta-analysis by Stemmler (2004) that focused exclusively on the autonomic differentiation of fear and anger. Stemmler's meta-analysis revealed that whereas "real life" fear inductions (e.g., unanticipated sudden darkness after hearing a frightening short story; Stemmler, 1989) elicited larger heart rate increases than real life anger inductions (e.g., an experimenter's aggressive demands; Pauls & Stemmler, 2003), fear imagery elicited no larger heart rate increases than anger imagery. Stemmler's meta-analysis revealed the opposite pattern for diastolic blood pressure: fear imagery elicited larger increases than anger imagery, but real life fear elicited no larger increases than real life anger. Moreover, whereas sadness is typically associated with increased heart rate, sad music seems to decrease heart rate (Etzel, Johnsen, Dickerson, Tranel, & Adolphs, 2006; Krumhansl, 1997). Such intriguing findings are problematic for the notion of *emotion*-specific patterning (e.g., Cacioppo et al., 1997, Zajonc & McIntosh, 1992).

Lang, Bradley, and Cuthbert's (1990; Bradley, 2000) distinction between strategic and tactical aspects of emotions may help explain the limited evidence for emotion-specific patterning. Tactics refer to the specific, context-bound patterns of action aimed at achieving

narrow goals. The same discrete emotion may call for different tactics in different situations. Lang et al. (1990), for instance, note that the behaviors associated with fear can range from freezing to vigilance to flight, all of which pose different metabolic demands. Such tactical variability may account in part for the limited evidence of emotion-specific autonomic patterning (Zajonc & McIntosh, 1992).

In contrast to tactics, strategies direct actions aimed at achieving broad end goals. Securing appetitive stimuli (e.g., food) and avoiding aversive stimuli (e.g., predators), for instance, represent strategic aspects of emotion (Lang et al., 1990). The ability of the autonomic nervous system to mobilize metabolic resources in response to hostile and hospitable stimuli is crucial to survival, so valence-specific patterning may be more pronounced than emotion-specific patterning. 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. Though subject to contextual factors (e.g., Smith et al., 2006), this *negativity bias* (Cacioppo & Berntson, 1994; Cacioppo, Larsen, Smith, & Berntson, 2004) has been observed in animal learning (Miller, 1961), risky decision making (Kahneman & Tversky, 1979), human affective judgments (Ito, Cacioppo, & Lang, 1998), and event-related brain potentials to affective stimuli (Ito, Larsen, Smith, & Cacioppo, 1998; Smith, Cacioppo, Larsen, & Chartrand, 2003).

A variety of theoretical and empirical work suggests that, *ceteris paribus*, negative emotions may also elicit greater autonomic activity than positive emotions (e.g., Taylor, 1991). To further examine this hypothesis, Cacioppo et al. (2000) conducted additional meta-analyses of autonomic activity in response to all negative emotions combined compared with all positive emotions combined. 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 positive emotions and none showed the opposite pattern. Thus, whereas Cacioppo et al.'s (2000) meta-analyses indicated that even a limited set of discrete emotions such as happiness, sadness, fear, anger, and disgust could not be fully differentiated by visceral activity alone, they also indicated that negative emotions are associated with stronger autonomic responses than are positive emotions.

Of course, Cacioppo et al.'s (1997; 2000) meta-analyses are mute with respect to the enduring theoretical question of whether autonomic activity contributes to or follows from emotional experience. At first glance, the debate between James (1884) and Cannon (1927) presupposes the existence of a single invariant relationship between emotional experience and peripheral physiological activity. Overlooked is the fact that James actually viewed emotions as being multiply determined. At the outset, James (1884) stated that "the only emotions I propose expressly to consider here are those that have a distinct bodily expression" (p. 189). Thus, in addition to contending that peripheral patterns can produce emotions in a bottom-up fashion, he acknowledged that emotional experiences are sometimes governed by top-down processes that fail to produce somatovisceral activity (Ellsworth, 1994). Along these lines, a recent neurobiological model delineates the reciprocal relations between ascending and descending systems that may contribute to anxiety (Berntson, Sarter, & Cacioppo, 1998). This model contends that affective states may be primed by top-down processes (e.g., appraisals) or bottom-up processes (e.g., visceral reactivity) and that the top-down and bottom-up mechanisms may mutually reinforce one another (e.g., as in panic disorder).

Cacioppo, Berntson, and Klein (1992) provided a general framework for conceptualizing the multiple pathways by which peripheral activity may shape emotional experience. At one end of the continuum, 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, attributional processes instigated by the perception of undifferentiated physiological arousal generate discrete emotional experiences (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. By this account, “somatovisceral illusions” represent the result of an active perceptual process by which ambiguous patterns of somatovisceral afference are immediately and spontaneously disambiguated to produce distinct emotional experiences.

The essential feature of the proposition that discrete emotions may result from somatovisceral illusions can be illustrated by analogy using the ambiguous visual figure depicted in Figure 1 (see Cacioppo et al., 1992, for a more complete description of the model). Even though the figure itself is unchanging, top-down processes allow viewers to perceive two very different images: a young woman facing left or an elderly woman facing right (Leeper, 1935). Thus, the same visual afference can lead to two different, discrete, and indubitable perceptual experiences just as Schachter and Singer (1962) argued that the same physiological afference may lead to two different, discrete, and indubitable emotional experiences. Indeed, the architecture of the somatovisceral apparatus may be better suited to produce ambiguous afference than that of 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. In contrast, the central nervous system serves to both create and interpret the stimulus and the response to somatovisceral information.

Cacioppo et al.’s (1992) model argues against the tendency to view the psychophysiological mechanisms underlying emotion in terms of a simple central-peripheral dichotomy. It is also in accord with robust findings in the literature that discrete emotional percepts can occur even when the autonomic changes do not fully discriminate the emotions that

are experienced, and that autonomic activation can alter the intensity, if not the nature, of emotional experience. From this perspective, the question is not whether emotion-specific autonomic patterns occur, but under what conditions do emotion-specific autonomic patterns occur. We have emphasized visceral contributions to emotional experience to this point, but, like Tomkins (1962), Cacioppo et al. (1992) also suggested that somatic processes can also affect emotional experience. In an ingenious test of this hypothesis, Strack, Martin, and Stepper (1988) reported that participants who had unknowingly been induced to smile found comic strips funnier than participants in a control condition. In the next section we examine the relationships between emotion and somatic activity, particularly facial expressions.

The somatic nervous system

Scientific studies of the link between facial expressions and emotions originated with Darwin (1890/1989), who noted, for instance, that among grief-stricken individuals, “the eyelids droop;...the lips, cheeks, and lower jaw all sink downwards from their own weight. Hence all the features are lengthened; and the face of a person who hears bad news is said to fall” (p. 134). Investigators have since provided provocative evidence that each of at least a subset of discrete emotions is associated with distinct overt facial expressions (Ekman, 1973). Additional evidence suggest that congenitally blind individuals, members of non-Western cultures, and infants make emotional facial expressions similar to those of sighted Western adults, thereby raising the possibility that emotion-specific facial expressions are not merely the product of social learning (e.g., see Ekman, 1973; Ekman & Friesen, 1978; Izard, 1977).

Although facial expressions may often reveal the nature of underlying emotions, many emotional reactions are not accompanied by visible facial actions (Cacioppo & Petty, 1981). Furthermore, although there is evidence that observers across cultures recognize the facial expressions of happiness, sadness, fear, anger, surprise, and disgust (Ekman, 1973), the data are

open to alternative interpretations (Russell, 1994). In addition, 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 & surprise; Ekman, 1973; but see Cacioppo, Bush, & Tassinari, 1992). As a result, the coding of overt facial expressions can be a less than perfect measure of emotion. An important complement to visual inspection of facial expression has been the use of measurement of patterns of electrical activity associated with contraction of the facial muscles. This technique—facial electromyography (EMG)—has made it possible to index muscle activity even in the absence of visible facial expressions (Cacioppo & Petty, 1981; Cacioppo, Tassinari, & Fridlund, 1990).

In pioneering research, Schwartz and colleagues demonstrated that different types of emotional imagery can elicit different patterns of EMG activity over the brow (*corrugator superciliaris*), 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 sad imagery elicited more EMG activity over the brow and less activity over the cheek than happy imagery. Thus, facial EMG patterns associated with emotional states appeared to represent “miniature representations” of those occurring during overt facial expressions (Schwartz, Fair, Greenberg, Foran, & Klerman, 1975). Subsequent research has examined whether the facial EMG patterns observed by Schwartz et al. (1975, 1976) with emotional imagery tasks generalize to other types of emotion inductions. Hess, Banse, and Kappas (1995), for instance, found that humorous films elicit greater activity over *zygomaticus major* and *orbicularis oculi*, particularly when participants are accompanied by friends. Patterns similar to those obtained with emotional imagery and films have also been obtained with emotional pictures (Cacioppo, Petty, Losch, & Kim, 1986; Lang,

Greenwald, Bradley, & Hamm, 1993; Larsen, Norris, & Cacioppo, 2003) and sounds (Bradley & Lang, 2000b; Larsen et al., 2003).

Recent research also indicates that affective stimuli can automatically elicit facial electromyographic reactions. Neumann, Hess, Schulz, and Alpers (2005) instructed participants to smile or frown whenever a word appeared on the screen. Facial EMG recordings indicated that participants smiled more quickly when pleasant words appeared and frowned more quickly when unpleasant words appeared. Dimberg, Thunberg, and Elmehed (2000) exposed participants to backwardly masked pictures of angry and happy faces for a mere 30 ms. Results indicated that subliminal happy faces elicited more activity over *zygomaticus major* and less activity over *corrugator supercilii* than did angry faces. Taken together, these results indicate that facial reactions to affective stimuli occur spontaneously (Neumann et al., 2005), even when the eliciting stimulus is presented outside of awareness (Dimberg et al., 2000). An unresolved issue is whether the facial EMG patterns observed by Dimberg et al. (2000) reflect emotional reactions or mere mimicry (cf., Hess, Philippot, & Blairy, 1998). In any event, such mimicry may reflect the operation of circuitry involving mirror neurons in the prefrontal cortex, which fire not only when the individual performs some action (e.g., smiling; Leslie, Johnson-Frey, & Grafton, 2004) but also when the individual observes someone else performing that action.

Though most research has investigated the effects of valence on EMG activity, some research has focused on discrete emotions. Schwartz, Ahern, and Brown (1979) asked subjects to engage in thought and imagery tasks that involved happiness, excitement, sadness, fear, and neutral emotional states. 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. In a similar study by Brown and Schwartz (1980), fear, anger, and sadness imagery elicited greater activity over the brow than did happiness imagery. Happiness imagery

elicited the most activity over the cheek, but fear and anger also elicited elevations over the cheek. Whether these latter elevations reflect “miserable smiles” (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. More recently, Vrana (1993) found that disgust and anger imagery elicited similar levels of activity over the brow and that disgust imagery also elicited greater activity over the *levator labii*, which elevates the upper lip and wrinkles the nose. Thus, the literature provides some evidence for distinct covert facial expressions associated with some emotions, but a great deal more evidence for distinct covert facial expressions associated with broad positive and negative affective states (Cacioppo et al., 2000).

The central nervous system

EMG activity reflects the end result of central nervous system (CNS) activity and can therefore shed some light on CNS processes involved in emotion. Early research by Schwartz et al. (1979) suggested that negative and positive emotional imagery elicited greater activity over the right and left sides of the face, respectively. The facial musculature is to some extent contralaterally innervated, so Schwartz et al.’s findings are consistent with neuropsychological evidence suggesting the left and right hemispheres are differentially involved in negative and positive emotional processing, respectively (Robinson & Downhill, 1995). Whereas left anterior brain lesions are more likely to produce major depression, for instance, right anterior brain lesions are more likely to produce mania. Subsequent research, however, has provided limited evidence for asymmetries in EMG responses (Hager & Ekman, 1985).

Unlike EMG activity, electroencephalographic (EEG) activity directly reflects CNS activity and has therefore been more useful in exploring the hemispheric specialization of emotion. Much of this work has focused on measurement of EEG power in the alpha band (8-13

Hz), which is inversely related to hemispheric activity (Lindsley & Wicke, 1974). A variety of evidence EEG evidence has corroborated the neuropsychological evidence that the right hemisphere is more strongly associated with negative affect and the left hemisphere with positive affect. For instance, those with greater relative left frontal activity tend to report higher levels of subjective well-being (Urry et al., 2004) and dispositional behavioral activation (Coan & Allen, 2003; Sutton & Davidson, 1997). Earlier in life, toddlers with greater relative left frontal activity tend to be less behaviorally inhibited (Davidson, 1993).

Davidson (1993, 2003) has integrated these and other findings into a diathesis-stress model linking individual differences in anterior cortical asymmetry to dispositional affective tendencies. According to this model, differences in cerebral asymmetry have greater impact on affective reactions to stressors and other challenges than on baseline affect (e.g., Davidson, 1993; Davidson & Tomarken, 1989). Consistent with the diathesis-stress model, participants with greater relative left frontal asymmetry reported stronger positive affective reactions to pleasant film clips and weaker negative affective reactions to unpleasant film clips, but did not differ from those with greater relative right frontal asymmetry in terms of baseline mood (Tomarken, Davidson, & Henriques, 1990; see also, Wheeler, Davidson, & Tomarken, 1993). Similarly, infants who cried when their mother left the room had greater relative right hemisphere activity prior to the separation (Davidson & Fox, 1989). Some evidence also suggests that those with greater relative left frontal activity experience shorter bouts of negative affect in response to unpleasant pictures (Jackson et al., 2003).

To this point, EEG asymmetry has been related to differences in affective traits, but there is also substantial state-dependent variance in EEG asymmetry (Hagemann, Naumann, Thayer, & Bartussek, 2002), and some of that variance may be due to differences in affective states. Davidson, Ekman, Saron, Senulis, & Friesen (1990) recorded EEG during a variety of evocative

film clips. Participants showed greater relative left frontal activation during those moments when they displayed facial expressions of happiness than when they displayed facial expressions of disgust. Analyses conducted across all artifact-free EEG data (i.e., including those times in which a facial expression was not present), failed to reveal an effect of film valence on EEG asymmetry. Thus, it may be that only emotional experiences strong enough to produce overt facial expressions are associated with measurable hemispheric asymmetry.

Recent research has clarified whether frontal activity better reflects approach- and avoidance-related behavioral motivation or positive and negative affective valence. Motivation and valence tend to be correlated, such that positive emotions are associated with approach and negative emotions with avoidance. An interesting exception is anger, which is a negative emotion that is associated with approach motivation. Harmon-Jones and Allen (1998) found that those who tend to experience anger show greater relative left frontal, as opposed to right frontal, activity. Similarly, anger induced with facial action tasks is associated with greater relative left frontal activation (Coan, Allen, & Harmon-Jones, 2001). Such findings indicate that frontal activity reflects approach/withdrawal motivation more so than positive/negative valence (Harmon-Jones, 2003).

Early conceptualizations of EEG asymmetry focused on the relative difference between activity in the left and right hemispheres. In light of neurophysiological and psychological evidence for separable approach- and avoidance-related motivational systems (e.g., Cacioppo & Berntson, 1994; Larsen, McGraw, & Cacioppo, 2001), current conceptualizations explicitly relate activity in the left hemisphere with approach motivation and activity in the right hemisphere with avoidance motivation. Individuals with depression or a history of depression show less left anterior activity than comparison participants, but do not differ in right anterior activity (Henriques & Davidson, 1990, 1991). These findings suggest that depression reflects

hypoactive approach motivation rather than hyperactive avoidance motivation (Henriques & Davidson, 1990, 1991). More recently, Schmidt (1999) extended prior evidence that shyness and sociability are separable by demonstrating that women who report high levels of shyness and sociability show greater right and left frontal activity. Schmidt's findings, in particular, highlight the utility of considering left and right frontal activity separately. Indeed, difference scores would have failed to disambiguate individuals who are both shy and sociable from those who are neither shy nor sociable.

Epilogue

As the varied perspectives represented in this volume suggest, a comprehensive understanding of emotions must encompass a wide range of viewpoints. One of the more interesting questions concerning the psychophysiology of emotions in particular is the role of somatovisceral afference in emotional experience. Though it appears that negative emotions are associated with greater autonomic reactivity than positive emotions, the cumulative evidence for emotion-specific patterns remains inconclusive. In addition, facial EMG activity over the cheek (*zygomaticus major*) and periocular (*orbicularis oculi*) muscle regions increase with positivity whereas EMG activity over the brow (*corrugator supercilii*) muscle region increases with negativity and decreases with positivity, and research on EEG asymmetries similarly suggests that anterior brain regions are differentially involved in approach-related versus avoidance-related behavioral processes. Thus, EEG activity can differentiate approach- and avoidance-related negative emotions such as anger and fear, respectively.

As detailed above, the patterns of autonomic activity associated with emotion have not been thoroughly delineated. One obstacle to identifying emotion-specific autonomic patterns, particularly for dually and antagonistically innervated organs such as the heart, is the multiple causal pathways connecting neural changes and end-organ response (e.g., heart rate). Emotional

stimuli do not invariably evoke reciprocal activation of the sympathetic and parasympathetic branches of the autonomic nervous system. For instance, aversive conditioned stimuli can produce coactivation of the sympathetic and parasympathetic nervous system, yielding accelerated, decelerated, or even unchanged heart rate, depending on the relative strength of sympathetic and parasympathetic activation (see Berntson, Cacioppo, & Quigley, 1991).

Rainville, Bechara, Naqvi, and Damasio (2006) recently provided initial evidence that measures of sympathetic and parasympathetic activity can differentiate discrete emotions even when end-organ responses cannot. Heart rate increased during both anger and fear imagery in their study, but spectral analyses of heart rate variability indicated that the effect of anger imagery was mediated by sympathetic activation and the effect of fear imagery by parasympathetic deactivation. Whether Rainville et al.'s findings will be replicated with larger samples, different types of emotion inductions (cf. Stemmler, 2004), and different discrete emotions remains to be seen.

Whether or not the conditions for and elements of emotion-specific peripheral patterns of activity can be identified, what does seem clear from the extant research is that discrete emotions can be experienced even in the absence of completely differentiated autonomic patterns. Though Cannon (1927) took this as evidence that somatovisceral afference has no influence on the experience of emotion, Cacioppo et al. (1992) outlined three routes by which somatovisceral afferentiation may influence emotional experience—emotion-specific autonomic patterns, somatovisceral illusions, or cognitive labeling of unexplained physiological arousal. From this perspective, the traditional tendency to view the mechanisms underlying emotion in terms of a simple central-peripheral dichotomy is untenable.

Emotions, particularly negative emotions, have also been linked to increases in health problems including an enhanced susceptibility to infection (e.g., Cohen, Doyle, Turner, Alper, &

Skoner, 2003; see review by Herbert & Cohen, 1993), poorer response to an influenza vaccine (Kiecolt-Glaser, Glaser, Gravenstein, Malarkey, & Sheridan, 1996), impaired wound healing (Kiecolt-Glaser, Marucha, Malarkey, Mercado, & Glaser, 1995). Mediators of the relationship between emotion and health have not yet been fully delineated but several mechanisms are likely 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).

Studies of the psychophysiology of emotion have tended to treat autonomic, somatic, and central nervous system activity in isolation (cf. Davidson et al., 1990; Mauss et al., 2005). Recent work highlights the utility of studying the relationships among these systems and related systems (e.g., the immune system). In a recent study investigating autonomic and immune responses to stress, for instance, individuals who responded to an experimenter's demands with fear, as assessed by facial action coding, showed greater cardiovascular and cortisol reactivity than did those who responded with a combination of anger and disgust (Lerner, Gonzalez, Dahl, Hariri, & Taylor, 2005). In another study, Waldstein et al. (2000) found that those who showed greater left frontal EEG activation during anger inductions also showed greater cardiovascular activation. Hagemann, Waldstein, and Thayer (2003) have incorporated such findings into a model that integrates the roles of the central and autonomic nervous systems in emotion.

Hagemann et al.'s (2003) model relied in part on evidence from positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), which now allow psychophysiolgists to visualize the human brain during emotional episodes with tremendous spatial resolution (Wager, this volume). One must bear in mind, however, that PET and fMRI have limited temporal resolution because they rely on relatively gradual changes in blood flow through the brain. Emotional reactions

tend to be fleeting (Ekman, 1994), so a useful approach may be to conduct studies combining fMRI data with traditional psychophysiological recordings, many of which offer superior temporal resolution (e.g., Critchley et al., 2003). In the years to come, such integrative approaches promise to yield ever clearer insights into the physiological substrates of emotion.

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Figure 1