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25 Emotion and Motivation

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PROLOGUE

Part of the complexity in studying emotion is defining it: There are almost as many definitions as there are investigators (see Panksepp, 1982, for a representative list). An aspect of emotion upon which most agree, however, is that in emotional situations, the body acts. The heart pounds, flutters, stops and drops; palms sweat; muscles tense and relax; blood boils; faces blush, flush, frown, and smile. We note these reactions in ourselves, and make inferences about the emotional life of others based on visible bodily responses. These changes are clear and strong in what William James (1890) called the "coarser emotions: fear, rage, grief, love, in which everyone recognizes a strong organic reverberation." James, however, also thought that body was involved in subtle emotions, even though the "organic reverberation is less obvious and strong." Lange (1882), joined with James in their eponymous theory, was even more grounded in biology, defining emotion explicitly as a cardiovascular response: "We owe . . . the emotional side of our mental life, our joys and sorrows, our happy and unhappy hours, to our vasomotor system." (p. 80)

In the late 19th and early 20th centuries when James and Lange were speculating about the basis of affective life, emotion's "organic reverberation" was not easy to assess in a precise, quantitative way. With the advent of electronic amplifiers, however, it has become possible to measure a broad ranged of physiological reactions to emotional challenges in the laboratory. In 1958, John Lacey could confidently state: "Such measures as skin resistance, heart rate, blood pressure, blood flow, skin temperature, blood-oxygen saturation, gastric motility, pupillary diameter, muscle tension, and other variables have been shown to be remarkably sensitive and responsive measures in a variety of "emotional" states. Conflict, threat and frustration; anxiety, anger, and fear; startle and pain; embarrassment; pleasant and unpleasant stimuli; – all these produce autonomic changes." (p. 160).

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Despite this clear relation to bodily physiology, emotion is often considered synonymous with mental "feelings" in the popular culture, but its etymological roots are consistent with the biological imperative: the word emotion stems from the Latin *movere*, meaning to move. When emotions are intense, people move: they act, they react, sometimes dramatically, as in crimes of passion. It is instructive that the word 'motivation' stems from the same verb; a motive is, literally, 'something that moves one'. Whereas the term 'emotion' is usually reserved for describing stimuli that are felt to be moving, prompting an affective experience in humans, 'motivation' is the word more often used in interpreting the actions of animals.

[1] The International Affective Picture System (IAPS, Lang, Bradley, & Cuthbert, 2004), International Affective Digitized Sounds (IADS, Bradley & Lang, 1999a) and Affective Norms for English Words (ANEW, Bradley & Lang, 1999b) are available on CD-ROM. These stimulus sets and technical manuals can be obtained on request from the authors at the NIMH Center for the Study of Emotion and Attention, Box 100165 HSC, University of Florida, Gainesville, FL 32610–0165, USA.

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Not surprisingly, William James noted the conjunction of these two descriptors, and, influenced by Darwin, emphasized a close relationship between emotion and motivation. In James's view, the basic motives (which he called "instincts") of both humans and animals are obligatory actions that are elicited by specific stimuli in the environment. The organism automatically freezes, flees, or fights at the sight of a predator, depending on the environmental context. Instincts, for James, were very like what we would now call motivational systems, defined by limbic circuits, and now a major focus of neuroscience research. James further noted that any object that elicited an instinct elicited an emotion as well, and that instincts and emotions "*shade imperceptibly into each other*". Even so, instinctive (motivated) behavior differs from the emotions: "Emotions . . . fall short of instincts, in that [whereas] the emotional reaction usually terminates in the subject's own body, the instinctive reaction is apt to go farther and enter into practical relations with the exciting object." That is, emotions are action dispositions, mobilizing the body for behavior, but in which the overt action itself is often delayed or totally inhibited.

CONCEPTUALIZING MOTIVATIONAL ORGANIZATION

Those studying motivated behavior in animal subjects have consistently agreed that two basic parameters of *direction* and *intensity* control action (e.g., Schneirla, 1959; Hebb, 1949). That is, in the simplest organism, stimuli that promote survival (e.g., food, nurturance) elicit behaviors towards the eliciting stimulus, whereas those that threaten the organism prompt withdrawal, escape, or avoidance. Both approach and avoidance behaviors can occur with varying strength, speed and vigor. In humans, although the specific direction of behavior (i.e., approach, avoid) is no longer completely dictated by the eliciting stimulus, the basic motivational parameters of direction (towards, away) and intensity can still be considered fundamental in organizing emotional behavior.

Biphasic motivation

For instance, most theorists agree that the primary distinction among emotional events is whether they are good or bad (Arnold, 1960), appetitive or aversive (Dickinson & Dearing, 1979) agreeable or disagreeable (MacLean, 1993), positive or negative (Cacioppo & Berntson, 1994), pleasant or unpleasant (Lang, Bradley, & Cuthbert, 1990), hospitable or inhospitable (Cacioppo, Berntson, & Crites, 1996) which clearly relates to the motivational parameter of direction in animal behavior. Moreover, all agree that hedonically valenced events differ in the degree of to which they arouse or engage action – a link to motivation's intensity parameter. Based on these observations, a number of theorists have advocated a biphasic approach to emotion, which posits that emotion fundamentally stems from varying activation in centrally organized appetitive and defensive motivational systems that have evolved to mediate the wide range of adaptive behaviors necessary for an organism struggling to survive in the physical world (Konorski, 1967; Davidson et al., 1990; Lang, Bradley, & Cuthbert, 1990; Cacioppo & Berntson, 1994).

Dickinson and Dearing (1979) further proposed that these two motivational systems, (*aversive* and *attractive*) were activated by a wide range of different unconditioned stimuli, and additionally that they had *reciprocal inhibitory connections* (p. 5) which modulated learned behavior and responses to new unconditioned input. However, Miller (1959) proposed that motivation to approach and avoid could be simultaneously engaged (e.g., a stimulus could be both aversive and attractive) resulting in an inhibition of action with an intermediate state of arousal. More recently, Cacioppo and Berntson (1994) suggested a flexible conceptualization of biphasic activation, in which appetitive and defensive activation varies from being mutually reciprocal (Dickinson & Dearing, 1979), to being simultaneously active, to being separably active. Different points in bivariate space, defined by the intensity of biphasic motivational activation, identify instances when defensive and appetitive activation are highly co-active to when they reciprocally related, with the entire space representing all possible scenarios.

Discrete states

Another way to conceptualize emotion is in terms of a set of diverse, discrete emotions, such as fear, anger, sadness, happiness, and so on. Lists of basic emotions have typically varied from theorist to theorist. Descartes (discussed in Panksepp, 1982) listed wonder, love, joy, desire, hate, and sadness as fundamental; this is the last time that positive emotions outrepresented negative, and that love was included on the list. Watson (1924), observing allegiance to definitions based on observable behavior, had a short list of fear, rage, and sexual activity. More contemporary lists include surprise, enjoyment, interest, disgust, shame, distress, fear, contempt, and anger (Izard, 1972); surprise, acceptance, desire, fear, rage, panic, and disgust (Plutchik, 1980), and others.

Lists of discrete states have traditionally been the products of introspective analyses. James famously conjectured that our feelings, consciously apprehended, were in fact percepts of the bodily changes induced directly by a compelling stimulus; and furthermore, that (at least for the stronger, *coarse* emotions of anger, fear, etc.), specific emotions would have a specific physiology. This hypothesis prompted intense psychophysiological research over the last century. However, as John Lacey noted already in 1958: "The search for differential patterns of bodily response in differently named affective states was abandoned early in the history of psychophysiology, with results generally conceded to be disappointing." That is, while there were some provocative findings (e.g., Ax, 1953; Ekman, 1971; see Cacioppo et al., 1993, for a review), the stimulus contexts were generally idiosyncratic to the laboratory, participant response variability was high, and results failed to replicate. More recently, Cacioppo et al. (1993) noted additional problems including inadequate experimental designs, inappropriate comparisons, use of different dependent measures, and, importantly, comparisons across very different induction contexts. Nonetheless, Cacioppo et al. (1993) selected studies that met a number of important criteria for determining emotional specificity, and still, the data were quite disappointing, with "... little evidence for replicable autonomic differences ..." (p. 125).

Physiology and action

In addition to a lack of empirical confirmation, the question of whether specific emotional states are related to specific physiological patterns neglects the important facts that physiology will vary with action, and that actions associated with the same emotional state will also often vary. That is, most, if not all, peripheral (and to some degree, central) indices of physiological activity will vary as a function of the amount and type of somatic involvement and the accompanying demand for metabolic support. Put bluntly, running (or preparing to run) will produce a very different configuration of physiological activity than sitting and observing, with activity in one system (e.g., cardiovascular) dependent, to some degree, on activity in another system (e.g., somatic). Moreover, both animal and human research indicate that a cue signaling threat, for example, can lead to fight, flight, or freezing, as well as a variety of specific idiosyncratic behaviors ("displacement" behaviors as described by Tinbergen, 1969, and other ethologists; also see Mackintosh, 1983), depending upon available contextual support and the organism's learning history. The physiology of fear in the context of headlong flight will necessarily be different from the physiology of fear in the context of freezing. From a psychophysiological standpoint, it will at least be necessary to specify whether a commonly proposed discrete emotion (e.g., "fear") occurs in a context which prompts fleeing fear or freezing fear or fighting fear.

STUDYING EMOTION IN THE PSYCHOPHYSIOLOGICAL LABORATORY: INDUCTION CONTEXT, AFFECT VARIATION & THREE SYSTEMS MEASUREMENT

Lacey (1958) noted the great variety of contexts in which emotion can be induced in the laboratory: "The threat to the organism can be real or imagined, present or recalled or anticipated, social or physical, verbalizable or totally inaccessible to verbalization at the time. In all these situations many physiological changes occur. ... Indeed, in predisposed individuals, painful and even dangerous somatic changes – such as headache, backache ... production of blood, bile and excessive hydrochloric acid in the stomach ... can be precipitated by the [mere] discussion of conflictful and psychologically threatening material." (p. 160). Lacey was also cognizant of what he called "situational stereotypy" – the idea that the nature and direction of physiological change is dependent, to a great extent, on the experimental context.

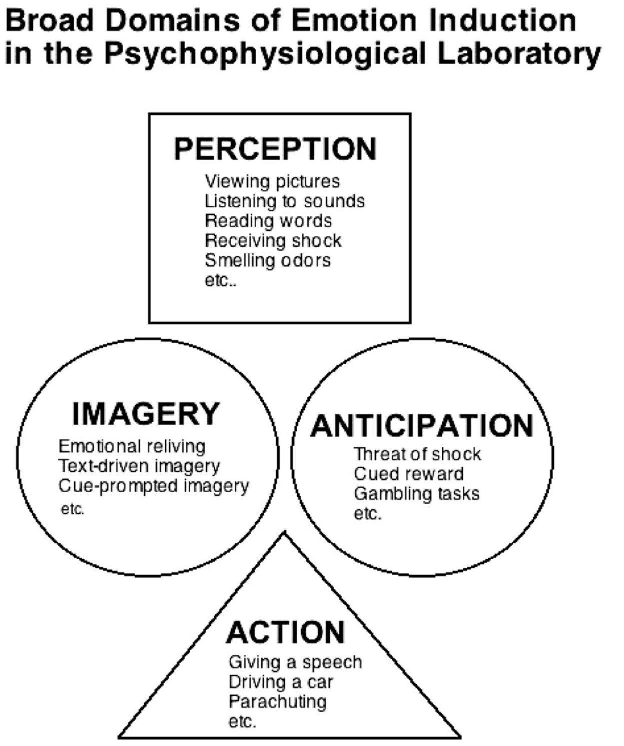


Figure 25.1. The most common induction paradigms in the psychophysiological study of emotion can be roughly classified as involving perception, imagination, anticipation, or action.

In the emotion literature, on the other hand, inferences regarding the physiology of fear, for example, are often made by comparing data from contexts as diverse as hearing loud noises, anticipating shock, imagining an intruder in the house, looking at a picture of an amputated leg, viewing a scary film, giving a speech, putting one's hand in cold water, or hearing an anguished scream. Conversely, responses to stimuli such as receiving money, listening to joyful music, looking at a picture of puppies, viewing an erotic film, imagining a day on the beach, receiving a good grade, thinking about winning the lottery, or anticipating a vacation are compared on the basis that they prompt a happy emotional state. The diverse sensory, cognitive, and motor processes elicited by these induction procedures may prompt quite different physiological profiles, irrespective of modulation by emotion. Moreover, the nature and direction of affect's modulatory influence can also depend on the specific induction context. Taken together, understanding the psychophysiology of emotion will depend on clearly specifying the context of the emotional induction in the laboratory.

Induction context

In the laboratory, contexts routinely used to induce affective reactions can be roughly organized into those that primarily target perception, anticipation, imagination, or action (see Figure 25.1). While clearly not mutually exclusive (e.g., most anticipatory or imagery tasks include some perceptual input), these induction domains represent broadly similar contexts with respect to psychophysiological responses that may be task, but not emotion, related. For instance, physiological reactions in perception differ both quantitatively and qualitatively from those in imagination, due to the requisite physiology of these different tasks. Moreover, both within and between broad induction contexts, specific parameters can have strong effects on the degree and nature of emotional engagement – i.e., the ease with which neural systems mediating emotional responses are activated – and the resulting pattern of physiological change that can be associated with affective engagement.

Perception. Tasks that primarily target ***emotional perception*** focus on measuring affective responses to sensory information that is presented in visual (e.g., pictures, words, films, etc.), acoustic (e.g., sounds, music, etc.), tactile (e.g., shock, cold pressor, etc.), olfactory, or gustatory modalities. Perceptual cues can vary in a number of ways that may influence the magnitude and likelihood of emotional engagement, including their modality (e.g., visual, acoustic, tactile, etc.) and duration, the degree to which they are unconditioned (e.g., an electric shock) or conditioned stimuli (e.g., picture of bomb exploding) and the extent to which they involve static (e.g., picture) or dynamic cues (e.g., film). For instance, it is likely that cues in different modalities have differential access to motivational circuits. In non-human primates, visual input to the amygdaloid complex, a neural structure implicated in affective reactivity, is more extensive than auditory input (Amaral et al., 1992), suggesting that modality may be important in engaging affective responses. Similarly, whereas intense physical stimuli (e.g., painful shocks, loud noises) reflexively (and unconditionally) prompt defensive reactions, symbolic (conditioned) stimuli such as the pictures, films, and language cues often used in emotion research rely on learning and association formation for motivational activation, with ramifications for the strength of emotional response.

Imagery. Many psychophysiological studies of emotion measure responses in the context of mentally created or "relived" emotional events. In the *emotional imagery* context, participants are prompted to mentally engage in imagining events that represent a wide range of emotional experiences in the world. Parameters potentially affecting the extent and strength of emotional and physiological engagement in this context include the information in the eliciting cue, and whether the events imagined are non-fictional (i.e., personally experienced) or fictional (i.e., non-experienced). For instance, Jones and Johnson (1978) demonstrated that imagery cues describing action produced more cardiac reactivity during imagery than cues describing passive scenes, and Lang and his colleagues (Miller et al., 1987; Lang et al., 1980) further demonstrated that when information describing appropriate responses (e.g., your palms are sweaty) is included, emotional responding during imagery is enhanced. Moreover, when subjects imagine emotional events that have been personally experienced, larger skin conductance and heart rate changes occur than when events are imagined that are not personally relevant (Miller et al., 1987), suggesting that motivational and physiological activation is more successful when a specific event is episodically represented in memory. Importantly, in the experiments described above, specific texts were used to prompt imaginal experience. Because the degree of psychophysiological responding during imagery relies intimately on information in the prompting cue, those which specify *only* the image's affective quality (e.g., "imagine a happy event in your life") may fail to clearly define or control important features of the imagined event.

Anticipation. In this affective context, emotional reactions are assessed during a period in which a subject awaits the presentation of an affective stimulus. Threat of shock studies (e.g., Grillon et al., 1991), and classical conditioning paradigms (see Ohman, this volume) fall into this class. Anticipating rewards or payoffs in gambling tasks represent an appetitive anticipatory context (Skolnick & Davidson, 2002). Numerous temporal and associative parameters have been noted as critical in modulating conditioning effects (e.g., MacIntosh, 1983; Stern, 1972), and are potentially relevant when assessing emotional reactions during anticipation (see Putnam, 1990). Among these are the duration of the cuing stimulus, and the nature of the cue (i.e., a light or a picture, for example), both of which can affect the amount of orienting activity (e.g., perceptual intake) that is occurring during the anticipatory interval. The specificity of the warning cue can also affect anticipatory reactions, in terms of whether the cue provides specific (e.g., snake) or non-specific (e.g., something bad) information regarding the upcoming affective event.

Action. Emotional actions, such as giving a speech, driving a car (for a phobic), or parachuting from an airplane represent active induction contexts in which psychophysiological reactions can be measured. Contexts involving overt action are employed less often in psychophysiological investigations of emotion, and for good reason. Gross motor activity can saturate amplifiers, produce artifact in cardiovascular and electrodermal records, and generally interfere with recording the often smaller physiological effects related to emotional parameters. The main variable in an action context is the required activity: Giving a speech will obviously be more physiologically demanding than a simple button press. Ambulatory monitoring studies, which attempt to study emotional reactions (e.g., panic) as they occur in the natural environment, fall within this class, and these investigators are coping with the issues involved in trying to separate the physiology of emotion

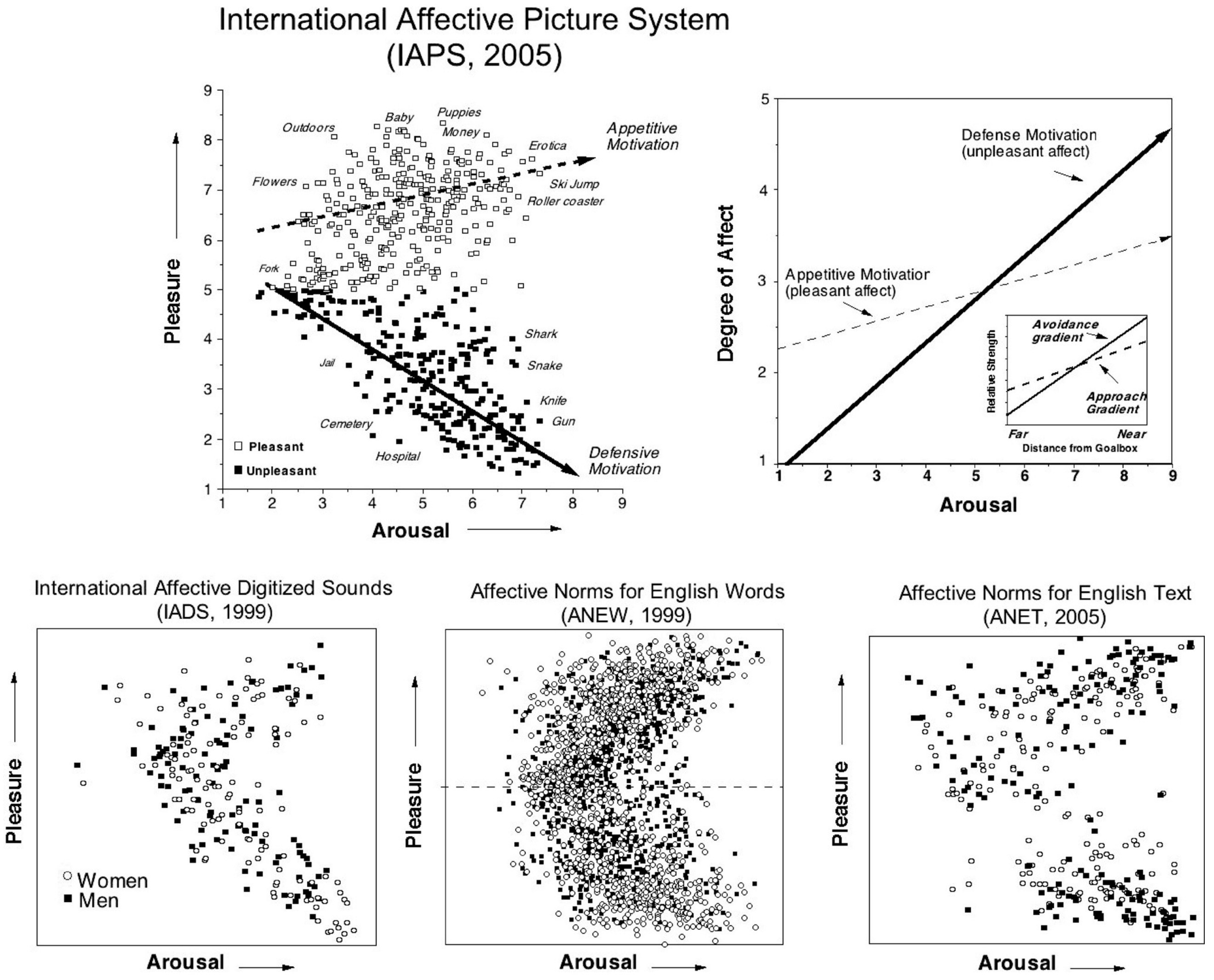


Figure 25.2. Emotional stimuli (pictures, sounds, words, text) are each plotted in the 2-dimensional space defined by the mean ratings of judged pleasure and arousal for each stimulus by a large group of participants. Regression lines drawn through the pleasant and unpleasant stimuli for affective picture ratings are similar to the approach and avoidance gradients first found by Miller (1959) when studying motivated behavior in rats. From Lang et al. (2005), Bradley & Lang (1999a), and Bradley and Lang (1999b).

from the physiology of ongoing action (e.g., see Wilhelm & Roth, 1996; Turpin, 1990; Alpers, Wilhelm, & Roth, 2005).

Affect variation

Following selection of a specific induction procedure, the emotion researcher will need to systematically vary affective features of the stimulus or task, and investigators working from a biphasic motivational perspective will be concerned with varying the degree to which the stimulus activates the defensive and/or appetitive systems. Beginning with Wundt's (1896) early studies of feeling states, it has been recognized that emotional differences among stimuli – words, objects, events – can succinctly be described by a few affective dimensions. In more current factor analyses of evaluative reports (e.g., Osgood, Suci, & Tannenbaum, 1957; see also Mehrabian & Russell, 1974; Russell, 1980), two dimensions of *pleasure* and *arousal* control the majority of the variance. In the biphasic view, evaluative reports of *pleasure* roughly index which motivational system is activated by the stimulus or task (i.e., appetitive "pleasant," or defensive "unpleasant"), whereas judgments of *arousal* index (again, roughly) the degree of activation in each motivation system.

Using ratings of *pleasure* and *arousal* gathered from large standardization samples, Lang, Bradley, and their colleagues have developed several sets of affective stimuli defined by these evaluative reports for use in emotion research. The stimulus sets include extensive samples of pictures (Lang, Bradley, & Cuthbert, 2004), sounds (Bradley & Lang, 1999a), words (Bradley & Lang, 1999b) and texts. The distribution of these stimuli in Cartesian space defined by their mean pleasure and arousal rating are quite similar across stimulus sets (see Figure 25.2).

Furthermore, it is noteworthy that the separate regression lines for pleasant and unpleasant pictures (Figure 25.2, top right) are consistent with the hypothesis of varying activation in two underlying appetitive or defensive motivational systems. When activation in both systems is minimal (neither pleasant nor unpleasant), emotional arousal is low and events are usually labelled Unemotional or Neutral. From a motivational perspective, this suggests only a weak tendency to approach or withdraw from the stimulus, and little energy mobilization required for what is, essentially, an absence of response. As defensive or appetitive motivation increases, arousal increases as well, presumably indexing the metabolic requirements of increased attention and anticipated actual action (e.g., approach or avoidance; appetitive incentive or defense).

The slopes and intercepts of the separate regression lines for pleasant and unpleasant pictures (Figure 25.2, top right) also recall the motivational gradients of approach and avoidance that Neal Miller described (1959) based on the strength of behavior in rodents, moving in a runway either towards a food reward or away from a punishing shock (Figure 25.2, top right, inset). Like Miller's data, the slope of the regression line for appetitive motivation is less steeply inclined than the slope for defense-activating, unpleasant stimuli, and the intercept for appetitive materials has a larger offset than does aversive material. Miller noted that the activation of approach behavior (towards food) began when the animal was relatively distant from the goal (hence the larger offset); in contrast, avoidance behavior (i.e., away from shock) began at a point more proximal to the site of the shock and showed a more rapid increase in intensity.

Broadening Miller's analysis, Cacioppo and his colleagues (Berntson, Boysen, & Cacioppo, 1993; Cacioppo, Gardner, & Berntson, 1997) suggest that weak appetitive activation is the base motivational disposition of organisms. They propose, furthermore, that this *positivity offset* of the appetitive gradient – the tendency to approach at low levels of motivation – is the foundation of orienting and exploratory reactions that mediate necessary, quotidian interactions with environmental stimuli. On the other hand, when unpleasant stimuli are proximal, the defense system is abruptly engaged, and rapidly dominates the organism's behavior. The point at which defensive motivation overcomes appetitive motivation is a function of the strength of aversive stimulation and individual differences in temperament and learning history. Survival, however, is always the bottom line and *negativity bias* and the ascendancy of defense when aversive stimuli are near is a fundamental disposition in a world full of diverse threats and dangers.

Discrete emotional states. Researchers proceeding from a discrete emotion view, on the other hand, will seek stimuli or tasks that are held to induce specific emotional states such as fear, anger, sadness, etc. Many recent efforts to study discrete emotions have used facial expressions to define discrete emotions in experimental stimuli, and Ekman and colleagues (Ekman & Friesen, 1979) have developed a coding system (Facial Action Coding System: FACS; Ekman, Friesen, & Hager, 2002) that has been widely used in the observational analysis of the human face, reacting to emotional stimuli. Based on the facial data, Ekman defined a set of primary affects (fear, anger, disgust, joy, sad, surprise), proposing that they were programmed centrally and accompanied by specific patterns of bodily reactions.

A number of facial stimulus sets that reliably vary in the discrete emotion labels people apply to them are now available to researchers that consist of photographs of models posing the basic affective expressions (Pictures of Facial Affect, Ekman & Friesen, 1979; the Karolinska Directed Emotional Face System (KDEF), Lundqvist, Flykt, & Öhman, 1998). The latter collection includes color photographs of several different male and female actors posing facial expressions in a naturalistic manner. In general, posed facial expressions communicate the intended specific emotions, as evidenced by the reliability of emotion labeling by naive observers. Furthermore, research (Ekman, 1971) suggests that at least a subset of facial expressions communicates similar emotions that are reliably labelled across different races and cultures (an issue that intrigued even Darwin, 1873).

3-system measurement

The indices that can be measured and quantified across emotional induction contexts include three systems of (1) evaluative reports, (2) physiological responses, and (3) overt actions (e.g., Lang, 1968). In much of psychological research, emotion measurement relies mainly on evaluative reports, including verbal descriptions (e.g., "I'm afraid"), ratings (e.g., ratings of fear on a scale of 1 to 10), reports of associated responses (e.g., circling or listing bodily reactions), and a variety of other methods that elicit judgments from subjects regarding their affective reactions. On the other hand, overt actions, such as running, jumping, fighting, freezing, and so on, which are used extensively in studies of motivated behavior in laboratory animals, are somewhat less commonly measured in human studies, but have included observable behaviors such as overt facial expressions. Physiological responses are those bodily events that can be assessed using psychophysiological instrumentation and methods, and are not necessarily observable. In emotion research to date, these have included responses in cardiovascular, electrodermal, somatic, reflex, gastric, respiratory, central, and neuroendocrine systems.

There are a number of possible relationships between three-system measures of emotion. Affective reactions can be assessed by measuring only overt behavior (e.g., freezing) or physiology (e.g., cardiovascular), in the absence of verbal reports, as studies of motivated behavior in animals demonstrates. Motivational systems operate independently of a link to a developed language system. In addition, when behavior is observable, changes in associated physiological measures will also tend to occur. Most obviously, if a person is overtly smiling, changes will be detected in EMG measured over the appropriate muscles. Because of their inter-dependence, behavioral and physiological measures will not be 'discordant' in the same sense that reports of affective experience and physiology may be.

THE PSYCHOPHYSIOLOGY OF EMOTION: AUTONOMIC AND SOMATIC MEASURES

The autonomic and somatic responses – heart, skin, and muscles – that are hallmarks of affective response are proximally controlled by the peripheral nervous system (see Guyton & Hall, 1996, for an overview), and the anatomical and functional distinctions between its parasympathetic ("homeostatic") and sympathetic ("fight or flight") branches have been important in the study of emotion. The sympathetic nervous system is characterized by post-ganglionic fibers that are quite lengthy, and which branch and divide as they make their way to specific target organs. Functionally, this means that a single sympathetic fiber activates a number of different effectors, providing an anatomical substrate for Cannon's emergency reaction, which proposed a volley of responses – heart rate and blood pressure increases, electrodermal reactions, increase in respiration rate and depth – on the basis of sympathetic activation. Conversely, the post-ganglionic fibers in the parasympathetic branch are short, and therefore more likely to quickly target a specific effector.

Most organs are innervated by nerves from both the parasympathetic and sympathetic divisions, which tend to exert opposite effects. The reciprocal effects of these two systems on different organs are mediated by the release of different neurotransmitters at the neuro-effector junction, with acetycholine released by parasympathetic fibers (cholinergic) and noradrenaline released by sympathetic fibers (adrenergic). Their subsequent action (e.g., increase or decrease in heart rate) is also temporally differentiated by the fact that noradrenaline dissipates slowly, whereas acetycholine dissipates more rapidly. Thus, parasympathetic control will tend to activate specific organs with rapid, phasic effects, whereas sympathetic control is not only more diffuse, but also somewhat longer lasting.

Cardiovascular reactions and emotion

Early investigations exploring emotion in perception assessed cardiovascular activity such as vascular changes and heart rate (e.g., Roessler, Burch, & Childers, 1966; Epstein, 1971; Turpin & Siddle, 1983) as a function of differences in stimulus intensity, as this variable was considered critical in eliciting orienting or defense responses. Low-intensity sensory stimuli were held to prompt orienting activity, mediated by parasympathetic dominance and associated with a pattern of peripheral and cephalic vasoconstriction and heart rate deceleration, whereas intense stimuli were hypothesized to prompt defense responses, mediated by sympathetic reactivity, and associated with peripheral vasoconstriction, cephalic vasodilation, and heart rate acceleration (see Sokolov, 1963; Graham 1979; Turpin, 1986).

In this conception, sympathetic activity was associated with mobilization to respond to aversive events, whereas pleasant affect was associated with parasympathetic dominance (Arnold, 1960; Gellhorn & Loofbourrow, 1963; Schneirla, 1959). This notion suggests a mode of consistent reciprocal activation between the sympathetic and parasympathetic branches that is no longer tenable. Rather, Berntson, Cacioppo and Quigley (1991; see also Berntson et al., 1994) have proposed a theory of autonomic control in which physiological measures of a dually-innervated end-organ (e.g., the heart) may differ as a function of the weighting of activation in the parasympathetic and sympathetic systems: systems can be independently active, reciprocally controlled, or co-active.

For instance, Quigley and Berntson (1990) demonstrated that heart rate acceleration to an aversive stimulus (in the rat) is larger than to a low-intensity stimulus not because of differential sympathetic activity, but because parasympathetic activity decreases with high-intensity stimulation. Similarly, in humans, an aversive loud noise prompts a cardiac defense response that consists of an initial acceleration (4–6 s), followed by a decelerative component (17–23 s), and a later secondary accelerative component (31–76 s). Similar to Quigley and Berntson (1990), Reyes del Paso, Godoy and Vila (1993) concluded that the initial acceleratory component is mediated by the parasympathetic system (vagal release), as this component was not blocked by the administration of a sympathetic beta-adrenergic blockade. On the other hand, the delayed secondary acceleration *was* blocked by the drug (as was stroke volume), suggesting that the slower cardiac component was at least in part sympathetically mediated.

In a picture perception context, stimulus "intensity" has generally been implemented by varying hedonic valence, and work by the Laceys (e.g., Libby, Lacey, & Lacey, 1973), Klorman (e.g., Klorman, Weissberg, & Austin, 1975; Klorman, Weissbert, & Wiessenfeld, 1977), and Hare (e.g., Hare, 1973; Hare, Wood, Britain, & Shadman, 1971; Hare, Wood, Britain, & Frazelle, 1971) consistently found that the heart decelerated, rather than accelerated, when people viewed pictures of unpleasant emotional events, contrary to the notion that these aversive stimuli might prompt defensive heart rate acceleration. Based on these kinds of data, Lacey (1967) originally proposed the notion of *stimulus specificity* (i.e., that specific stimuli or tasks are associated with specific patterns of physiological response). Based on these data, Lacey hypothesized that cardiac deceleration was an index of perceptual processing, reflecting sensory intake, whereas cardiac acceleration was an index of mental processing, reflecting sensory rejection.

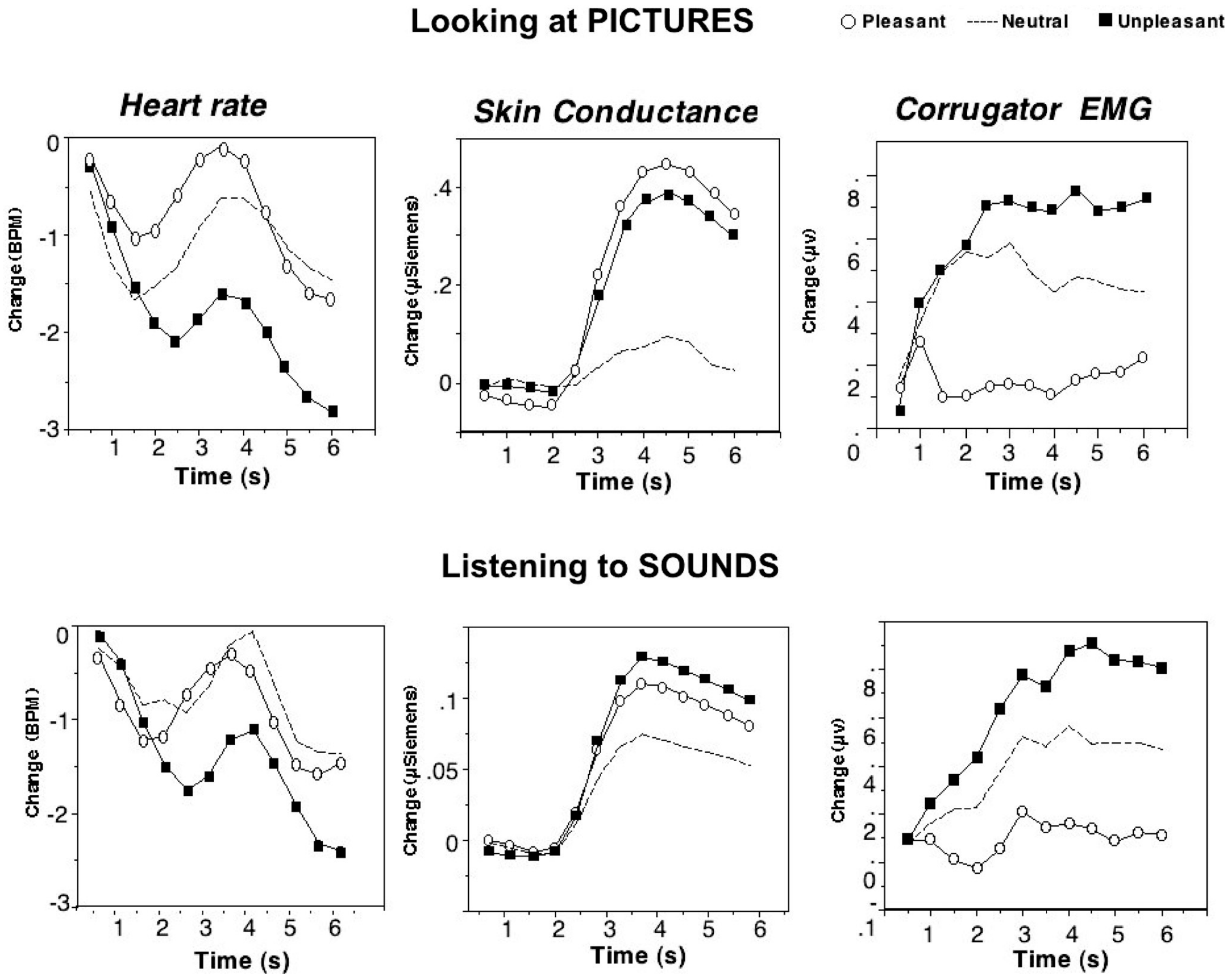


Figure 25.3. Cardiac, electrodermal, and facial EMG (corrugator supercilii) activity during perception of 6 s presentations of pleasant, neutral, or unpleasant pictures (top) and sounds (bottom) show similar affective modulation. Based on data reported in Bradley et al. (2005) and Bradley and Lang (2001).

In the aversive picture perception context, Lacey assumed people were perceptually rejecting the aversive content and turning inward, or away from the sensory display.

Many recent studies have confirmed that the cardiac response during aversive picture viewing involves significant initial deceleration. When viewing pictures, those that are rated as unpleasant typically prompt more initial deceleration than do pleasant or neutral pictures (Lang et al., 1993; see Figure 25.3, top left). When specific picture contents are explored, significant cardiac deceleration is obtained for all unpleasant contents, including both highly arousing pictures of threat and mutilation, as well as relatively low arousal contents such as pollution and loss (Bradley et al., 2001a). An initial deceleratory response when viewing unpleasant pictures is reminiscent of the fear bradycardia elicited in animals to threatening stimuli. In animals, this decelerative response is vagally mediated, as atropine (a parasympathetic blockade) completely eliminates it, indicating release of parasympathetic control, and has been interpreted as reflecting heightened sensory intake and orienting (see Campbell, Wood, & McBride, 1996). Consistent with a hypothesis of increased sensory intake, highly arousing appetitive pictures, particularly those involving erotica, prompt significantly more initial cardiac deceleration than pleasant pictures rated as lower in arousal (Bradley et al., 2001a), suggesting that pleasant, arousing contents can also attract increased perceptual processing and sensory intake.

If cardiac deceleration during picture perception reflects sensory processing, cardiac responses in other perceptual contexts should also show decelerative differences that reflect hedonic valence. Consistent with this, heart rate also reliably decelerates when viewing films (rather than pictures) that depict bloody surgical interventions (Palomba et al., 2000), suggesting a stance of heightened attention and intake. Moreover, listening to highly arousing unpleasant sounds (e.g., bombs exploding, etc.) also prompts greater initial deceleration than listening to neutral sounds (Bradley & Lang, 2000; Figure 25.3, bottom left). On the other hand, reading sentences that describe emotional or neutral events prompts significant cardiac deceleration, but does not vary with emotion: In this perceptual context, the sensory cues (words) require equivalent processing and the cardiac response reflects sensory intake that does not differ in terms of the affective meaning of the words. However, associative processes stimulated by affective texts (after encoding) do reflect differences in emotional arousal, but are not decelerative.

Imagery. Lacey originally proposed that heart rate acceleration indicated "sensory rejection," and was an index of internal processing on the basis of data indicating clear accelerative responses during tasks involving mentation, such as silent arithmetic calculations. Consistent with these findings, the general heart rate response during mental imagery is an acceleratory response that is often enhanced by affective features of the imagined stimulus, with a number of studies finding greater heart rate increases during text-prompted fearful, compared to neutral imagery (Bauer & Craighead, 1979; Cook et al., 1988; Grayson, 1982; Grossberg & Wilson, 1968; Haney & Euse, 1976; Lang et al., 1983; May, 1977b; Van Egeren, Feather, & Hein, 1971).

Heart rate similarly accelerates when imagining pleasant, compared to neutral, scenes (Vrana & Rollock, 2002), and the increase is even more pronounced when participants imagine emotional scenes based on their actual life experiences (Miller, Patrick, & Levenston, 2002). In general, heart rate acceleration during imagery varies most consistently with stimulus arousal – increasing for emotionally arousing (either pleasant or unpleasant) images (Cook et al., 1991; van Oyen Witvliet & Vrana, 1995; Fiorito & Simons, 1994), and these effects are more pronounced when the imagined scenes are personally relevant (Miller, Patrick, & Levenston, 2002).

In an effort to separate cardiac concomitants of mental imagery from heart rate variance associated with simply processing text, Schwartz (1971) developed a paradigm in which subjects first memorized emotionally arousing texts, then imagined the events described by these texts in a fixed sequence. Simply imagining arousing stimuli (i.e., without prior processing of the text prompt) resulted in greater heart rate acceleration than when imagining a neutral sequence (e.g., the letters ABCD). May and Johnson (1973) required subjects to memorize neutral or arousing words, and Vrana, Cuthbert, and Lang (1986) had subjects memorize sentences describing neutral and unpleasant events and then used tones to cue imagery. In all cases, heart rate acceleration was increased when imagining emotional, compared to neutral, events. A second study by May (1977b) found that actively imagining a fearful sentence produced more heart rate acceleration than either hearing the sentence, or seeing a slide depicting the same material as the sentence.

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

Taken together, the heart rate patterns obtained during picture perception and imagination are consistent with Lacey's (1967) early observation that deceleration is associated with sensory intake (perception), whereas acceleration is associated with mentation. On the other hand, Lacey's interpretation of heart rate acceleration during imagery as reflecting sensory rejection, has been refined: Rather than focusing on sensory processing (e.g., rejection of perceptual information), a number of theories (see Cuthbert, Vrana, & Bradley, 1991, for a review) hypothesize that cardiac acceleration during imagery reflects action engagement prompted by the imagery scene.

According to Lang's (1979) bioinformational theory of emotional imagery, affective events are represented in memory by an associative network that includes coded sensory, conceptual, and action information. Stimulus units in the associative network code information regarding specific sensory and perceptual features of the event (e.g., visual, acoustic, and tactile features of a snake and the current context), whereas meaning units code conceptual information previously learned about the stimulus (i.e., snakes are dangerous). An important feature of bio-informational theory are units that code appropriate actions in the representation of emotional events. Although many cognitive models primarily focus on stimulus and semantic information, bio-informational theory emphasizes the importance of action units, which code associated behaviors (e.g., running) and relevant autonomic support (e.g., heart rate acceleration) that are part of the associative structure of an emotional event. During mental imagery, activation of relevant action units in affective networks prompts heightened physiological engagement during emotional, compared to neutral, events, because emotion is, inherently, a disposition to act.

Electrodermal reactivity and emotion

Whereas the heart is dually innervated, and subject to modulation by either parasympathetic or sympathetic activity (or both), the electrodermal system is innervated solely by the sympathetic system, although the mechanism of its action is cholinergic, rather than adrenergic. In a variety of induction contexts, electrodermal reactivity consistently varies with emotional intensity, with larger responses elicited in either unpleasant and pleasant contexts and that are most pronounced in those that rated highly arousing.

During picture perception, for example, many studies have found increased skin conductance when people view pictures rated as emotional, compared to neutral, regardless of whether they are rated pleasant or unpleasant in hedonic valence (e.g., Lang et al., 1993; Winton, Putnam, & Krause, 1984; see Figure 25.3, top middle). Moreover, electrodermal reactions increase with increases in defensive or appetitive activation, with the most arousing pleasant and unpleasant contents (e.g., erotica, threat, and mutilation) prompting the largest responses (Bradley et al., 2001a). Similarly, when listening to affective sounds (Bradley & Lang, 2000; Verona et al., 2004) or music (Gomez & Danuser, 2004), skin conductance activity increases as the acoustic stimuli are rated higher in emotional arousal, regardless of hedonic valence (see Figure 25.3, bottom middle). Demonstrating consistent modulation by affective intensity across perceptual contexts, elevated electrodermal reactions are also clearly found when people view film clips that are either unpleasant (Kunzmann, Kupperbusch, & Levenson, 2005; Palomba et al., 2000) or pleasant (Christie & Friedman, 2004). When hedonic valence and emotional arousal of film stimuli were co-varied, skin conductance responses were largest for highly arousing films, irrespective of hedonic valence (Gomez et al., 2004), consistent with the notion that these reactions primarily reflect differences in emotional arousal, rather than hedonic valence.

Whereas the cardiac patterns seen in perception and imagery are quite different, skin conductance responses during imagery often show the same modulation by emotional arousal as perceptual contexts. For instance, Miller, Patrick, and Levenston (2002) found increased skin conductance responses when people imagined pleasant or unpleasant, compared to neutral, events, and these responses were accentuated when personally relevant scenes were imagined. Similarly, as Figure 25.4 (left panel) illustrates, anticipating the presentation of a threatening stimulus (e.g., shock; Bradley, Moulder, & Lang, 2005) or a pleasant stimulus (e.g., a picture of erotica; Sabatinelli, Bradley, & Lang, 2001) also prompts large skin conductance changes that reflect increased arousal during anticipation.

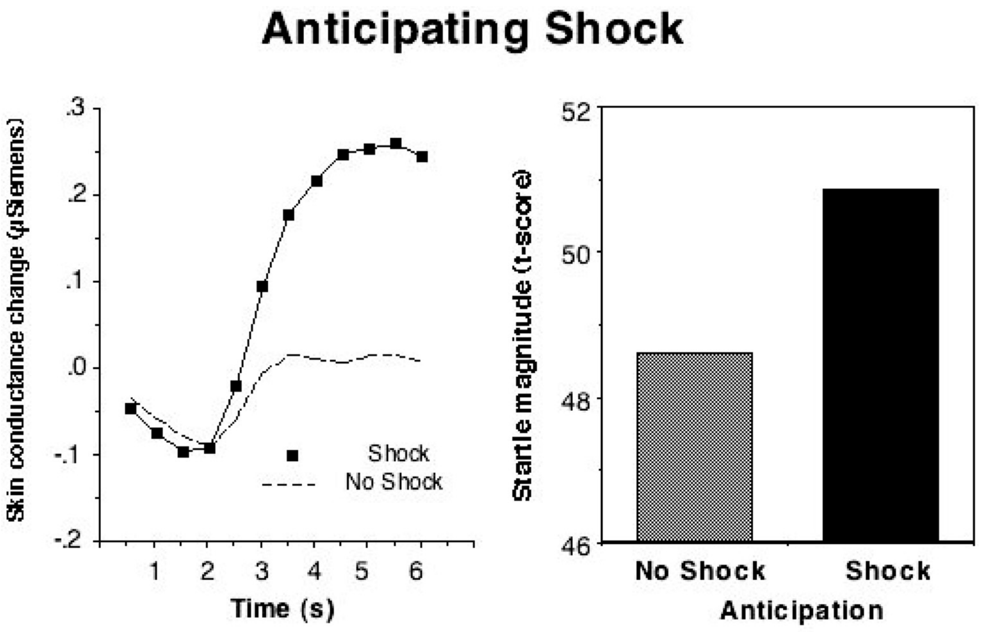
Taken together, rather than simply responding to aversive stimulation, the sympathetic nervous system, as indexed by the electrodermal reaction, is also engaged by appetitive activation, and, moreover, appears to be similarly activated in perception, imagery, and anticipation contexts. One interpretation is that this physiological measure reflects the primary nature of emotions as action dispositions that are mediated by sympathetic activity preparing the organism for fight, flight, and other appropriate appetitive and defensive behaviors. Regardless of whether the affect cue involves perceptual, imaginal, or anticipatory processing, those that activate the fundamental appetitive or defensive motivation systems engage measurable sympathetic activity, as measured by the palmar skin conductance response. Thus, whereas the cardiac response differs in emotional perception and emotional imagery, presumably reflecting differences in sensory intake in the different induction contexts, the electrodermal response in both perception and imagination indexes the preparation for action that is the hallmark of both motivation and emotion.

Facial EMG and emotion

Facial expressions of emotion, such as frowns, grimaces, smiles, and so on are often the most overt signs of emotional response, and are mediated by muscles that are attached to the skin of the face, all of which are innervated by the facial nerve (cranial nerve VII) via the facial motor nucleus located in the pons. The facial motor nucleus is organized into subdivisions (medial, lateral, dorsal, intermediate) that contain the motor neurons controlling different facial muscles, with the upper half of the nucleus containing neurons that generally control the lower part of the face, and neurons in the lower half innervating the upper facial muscles. Different branches of the facial nerve (temporal, zygomatic, buccal, cervical, and marginal mandibular) innervate different facial muscles, with combinations of activity in different muscles related to various facial expressions that are common in emotion.

In the Facial Action Coding System (FACS; Ekman & Friesen, 1986; Ekman, Friesen, & Hager, 2002), “action units” that correspond to observable activity in specific muscles and facial regions can be scored by an observer. In a recent study, Kohler et al. (2004) used FACS to code expressions in a set of 128 photographs that included posed and evoked faces displaying happy, sad, fearful, and angry expressions. Their primary goals were to identify the characteristic action units present in different expressions and to determine whether unique action units are related to correct recognition performance (in a sample of naive participants). For happy expressions, an action unit associated with a lip corner pull was present in all expressions, and appeared to be critical in both defining and recognizing a smile. On the other hand, expressions of sadness elicited characteristic features (e.g., furrowed eyebrows, opened mouth with raised upper lip) but no clear unique features, seeming instead to rely on a combination of features for successful recognition.

Identification of more subtle changes in facial muscle activity can be achieved by monitoring electromyographic (EMG) activity using electrodes placed over appropriate facial muscles. In fact, appropriate facial EMG activity accompanies changes in appetitive and defensive activation in a number of different induction contexts (e.g., Fridlund, Schwartz, & Fowler, 1984; Tassinary, Cacioppo, & Geen, 1989). Most commonly, measurement of activity



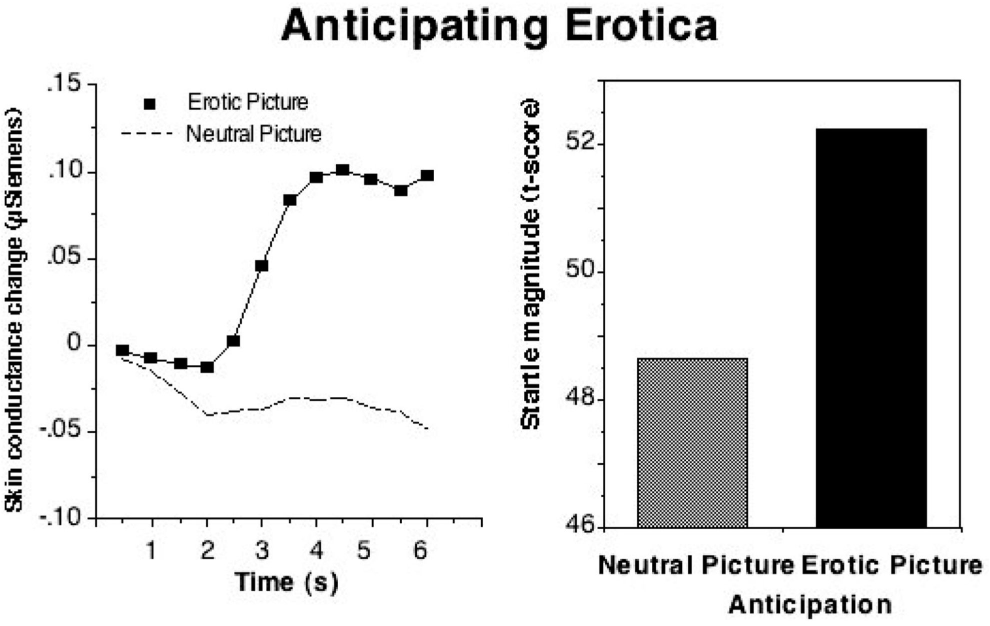


Figure 25.4. Electodermal and startle reflex magnitude when anticipating an electric shock or anticipating the presentation of an erotic picture show similar modulation. Based on data reported by Bradley et al. (2005) and Sabatinelli et al. (2001).

over the muscles associated with frowning and smiling have been used as indices of affective engagement in perception, imagery, and anticipation.

The corrugator supercilii muscles, located above and between the eyes, are responsible for lowering and contraction of the brows. This facial action is held to be an index of distress (see Ekman, Levenson, & Freissen, 1983; Fridlund & Izard, 1983, for a review) and firing of motor units in this muscle region is obtained if a stimulus is judged to be unpleasant (even if the degree of unit activity is insufficient to produce visible brow movement). Significant contraction of the corrugator muscle occurs when viewing pictures that are rated as unpleasant, compared to neutral pictures (Cacioppo et al., 1986; Lang et al., 1993), and shows similar modulation when people listen to unpleasant, compared to neutral, sounds, as Figure 25.3 (left panel) illustrates. Moreover, activity measured over this muscle often shows relaxation below baseline activity for materials rated high in pleasure.

Larsen, Norris, and Cacioppo (2003) measured facial EMG activity in a variety of different perceptual contexts, including viewing affective pictures, listening to affective

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sounds, and reading affective words. In all contexts, a highly significant linear relationship was found relating corrugator supercilii EMG activity to hedonic valence, with greater corrugator supercilii activity elicited when viewing the most unpleasant stimuli. Moreover, the most highly pleasant materials prompted significant inhibition, consistent with the hypothesis that appetitive and defensive activation show reciprocal effects on this facial muscle. When exploring specific picture contents, Bradley et al. (2001a) found that all unpleasant picture contents prompted significant increases (over neutral) in corrugator EMG activity, with pictures of mutilations and contamination (i.e., disgust) prompting slightly larger changes than other unpleasant stimuli. Although women responded with greater overall facial EMG activity than men, both men and women showed significant increases in corrugator EMG reactivity when viewing unpleasant pictures (Bradley et al., 2001b), indicating that both men and women facially respond to aversive stimuli. The least corrugator EMG activity was obtained for pleasant pictures depicting babies and families, which are rated quite high in pleasure, but relatively low in arousal. The most arousing pleasant contents, such as erotica and sports, however, did not prompt significant relaxation from baseline.

Activity measured over the *zygomaticus major* muscle occurs when the cheek is drawn back or tightened (Tassinary, Cacioppo, & Geen, 1989), and this muscle is involved in facial expressions of smiling. Because emotional expressions such as smiling have communicative function in human culture and can be initiated for instrumental effect, their connection to a reflexive psychophysiology of emotion cannot be automatically assumed. That is, a person may choose to look “happy,” engaging in deceptive behavior to achieve some goal, in much the same way that individuals may, for similar reasons of social use, *say* that they are “happy”(or angry) in the absence of any confirming physiology. Ekman, Davidson, and Friesen (1980) have considered this issue, and noted an interesting observational difference between true and false smiles. Whereas an authentic “Duchenne” smile includes both action of the zygomaticus major and orbicularis oculi muscles, false “social” smiles involve only the zygomaticus major muscle.

Consistent with the hypothesis that facial EMG activity in picture perception reflects an authentic emotional reaction, Cacioppo et al. (1986) found co-activation of the zygomaticus major and orbicularis oculi muscles when participants viewed pleasant, compared to neutral, pictures. When specific picture contents were assessed (Bradley et al., 2001a), co-activation in these facial muscles was again apparent, and was most pronounced for pictures judged to be high in pleasure, but not highly arousing, including pictures of babies, families, and food. Facial EMG activity consistent with smiling at babies and families was only apparent for women (Bradley et al., 2001b), however, and neither men nor women showed any evidence that pictures of highly arousing erotica evoked facial expressions related to smiling.

Unpleasant materials that are highly arousing also prompt slight increases in activity measured over the zygomaticus major muscle. Lang et al. (1993) noted a significant quadratic trend for this zygomatic muscle in which highly unpleasant pictures prompted significant activity (although less than for highly pleasant stimuli). Larsen, Norris, and Cacioppo (2003) replicated this finding, and further found that this pattern was more representative of reactions to pictures and sounds; simply reading unpleasant words did not engage strong activity over this facial muscle. When exploring specific picture contents, Bradley et al. (2001a) found that increased zygomatic activity during unpleasant picture viewing tended to co-occur with significant changes in both the corrugator supercilii and the orbicularis oculi muscles. Co-activation in these three muscles was associated with a pattern of facial activity that was most pronounced for pictures rated as disgusting, including mutilated bodies and contamination (e.g., spoiled food, etc.) scenes. Thus, this muscle also appears to be active in a facial expression of disgust that involves both lowering of the brow and tightening of the cheek and eyes.

Studies investigating facial EMG activity during mental imagery have also consistently found that activity measured over the corrugator supercilii and zygomaticus major muscle regions index the hedonic valence of the imagined stimulus (e.g., van Oyen Witvliet & Vrana, 1995; Fiorito and Simons, 1994; Fridlund, Schwartz, & Fowler, 1984). Schwartz and his colleagues (e.g., Schwartz, Ahern, & Brown, 1979; Schwartz, Brown, & Ahern, 1980) conducted a series of studies which indicated that corrugator and zygomatic EMG activity primarily differentiated between imagery of negative (e.g., fear, sadness, anger) and positive (e.g., happy) emotions, whereas EMG activity over the masseter and lateral frontalis muscle regions did not differ. Importantly, Schwartz, Brown, and Ahern (1980) also found that women were more reactive than men, consistent with the effects of sex obtained in picture perception.

Summarizing the imagery work, Cacioppo et al. (1993) conclude that covert measures of facial EMG activity in imagery may reflect “ . . . a rudimentary bivalent evaluative disposition or *motivational tendency* rather than discrete emotions” (p. 136). Facial expressions of disgust may be an exception, however. In a recent study in our laboratory, imagining unpleasant events was, as usual, associated with increased corrugator EMG activity for scenes that people label as evoking fear, anger, and disgust. On the other hand, similar to picture perception, scenes involving disgust uniquely involved co-activation of corrugator supercillii and orbicularis oculi EMG activity, consistent with the idea that EMG reliably discriminates facial expressions of disgust in both perception and imagery.

Startle reflex modulation

In most mammals, an abrupt sensory event will prompt a startle response, a chained series of rapid extensor-flexor movements that cascade throughout the body (Landis &

Hunt, 1939). This reaction is a defensive reflex, facilitating escape in simpler organisms, and perhaps still serving a protective function in more complex animals (i.e., avoiding organ injury as in the eyeblink, or in retraction of the head to avoid attack from above, Yeomans, Steidl, & Li, 2000). When under threat (of pain or predation) animals show an exaggerated startle reflex. As first described by Brown, Kalish, and Farber (1951), the amplitude of the acoustically elicited startle reflex in rats is increased when elicited in the presence of a light previously paired with footshock. Humans similarly show larger startle blink reflexes when processing cues previously paired with exposure to aversive shock (Hamm et al., 1993).

Davis (1989; Davis, Hitchcock, & Rosen, 1987) and others (e.g., Koch & Schnitzler, 1997) have systematically investigated the neural circuitry underlying potentiation of the startle response during aversive learning in animals. When stimulated by an abrupt noise, the afferent path of the reflex proceeds from the cochlear nucleus to the pontine reticular formation; from there efferent connections pass through spinal neurons to the reflex effectors. This is the basic obligatory circuit, driven by the parameters of the input stimulus (e.g., stimulus intensity, frequency, steepness of the onset ramp). A secondary circuit, intersecting this primary reflex pathway, determines startle potentiation after fear conditioning. There is now overwhelming evidence that the amygdala is the critical structure mediating this effect: First, there are direct projections from the central nucleus of the amygdala to the reticular site which mediates potentiation (i.e., nucleus reticularis pontis caudalis); second, electrical stimulation of the amygdala's central nucleus enhances startle reflex amplitude; finally, and most important, lesions of the amygdala abolish fear conditioned startle potentiation (Davis, 1989).

In studies with human beings, rapid eye closure is one of the most reliable components of the behavioral sequence that constitutes the startle response, and the associated blink reflex can be measured electromyographically by placing sensors over the orbicularis oculi muscle beneath the eye (see Figure 25.5). When startle probes are administered in the context of picture perception, blink responses are reliably potentiated when viewing unpleasant pictures, and inhibited when viewing pleasant pictures, compared to neutral picture processing (see Figure 25.5; Vrana, Spence, & Lang, 1988; see Bradley, Cuthbert, & Lang, 1999 for an overview). These effects have proven highly replicable in the picture perception context (e.g., Bradley et al., 2001a; Buchanan, Tranel, & Adolphs, 2004; Cook et al., 1992; Dichter et al., 2004; Hamm et al., 1997; Vanman et al., 1996). Startle potentiation is largest for unpleasant pictures that are rated highly arousing (e.g., threat and mutilation), while the most arousing pleasant pictures evidence the largest startle inhibition (e.g., erotica and romance; Bradley et al., 2001a, Schupp et al., 2004).

The startle reflex is modulated by affective valence during picture viewing regardless of whether the startle probe is visual, acoustic, or tactile (e.g., Bradley, Cuthbert, & Lang, 1991; Hawk & Cook, 1997), indicating that modality-specific processes are not central in these modulatory effects. Affective modulation of startle is also not confined to static visual percepts: The startle reflex is modulated by affective valence when dynamic visual stimuli (i.e., affective films) are presented (Jansen and Frijda, 1994; Koukounas & McCabe, 2001), or when the sensory modality involves odors (Erlichman et al., 1995). Furthermore, when the emotional stimuli consist of short, 6 s sound clips of various affective events (e.g., sounds of love-making; babies crying; bombs bursting), and the startle probe is a visual light flash, the same pattern of affective modulation is obtained, suggesting that its mediation in perception is broadly motivational and thus consistent across affective foregrounds of different stimulus modalities (Bradley & Lang, 1998).

In the picture viewing context, a search for differences in startle potentiation when viewing different categories of unpleasant pictures have produced mixed results. Balaban and Taussig (1994) first found evidence for greater reflex potentiation when viewing pictures depicting fearful scenes than other unpleasant contents, and more recently Stanley and Knight (2004) reported greater potentiation when viewing threat, compared to mutilation, pictures. On the other hand, Yartz and Hawk (2002) found that startle reflexes elicited when viewing disgusting pictures that either involved blood or other disgusting contents (e.g., bugs, toilets, etc.) showed potentiation similar to that elicited when viewing pictures of threat. Bradley et al. (2001a), in a similar design, also found equivalent potentiation for threatening scenes involving animals (presumably eliciting fear) and disgusting contents (e.g., mutilations or others), although fearful pictures of human attack (particularly toward the viewer) prompted slightly (and significantly) larger reflexes than pictures of mutilated humans. Taken together, although there is some evidence of slightly larger reflex potentiation when viewing scenes involving threat or imminent danger (fear?), the effect is somewhat variable, possible reflecting differences in material or participant samples.

The defense cascade in picture perception. Like normal subjects, specific phobics show potentiated startles when viewing unpleasant pictures. However, startle reflexes are even more enhanced when these subjects view pictures of the objects they fear (Hamm et al., 1997). On the other hand, the typical bradycardia obtained during unpleasant picture viewing does not characterize the response of phobic subjects to pictures of objects they fear (e.g., Hamm et al., 1997; Klorman, Weissbert, & Wissenfeld, 1977): rather, when high fear subjects view pictures of the phobic object, the heart accelerates. Also unlike non-phobic subjects, they quickly terminate "looking" in a free-viewing situation. Thus, whereas reflex potentiation to aversive materials characterizes responses for highly arousing unpleasant pictures for both normal and phobic subjects, cardiac and other behavioral measures of attentive

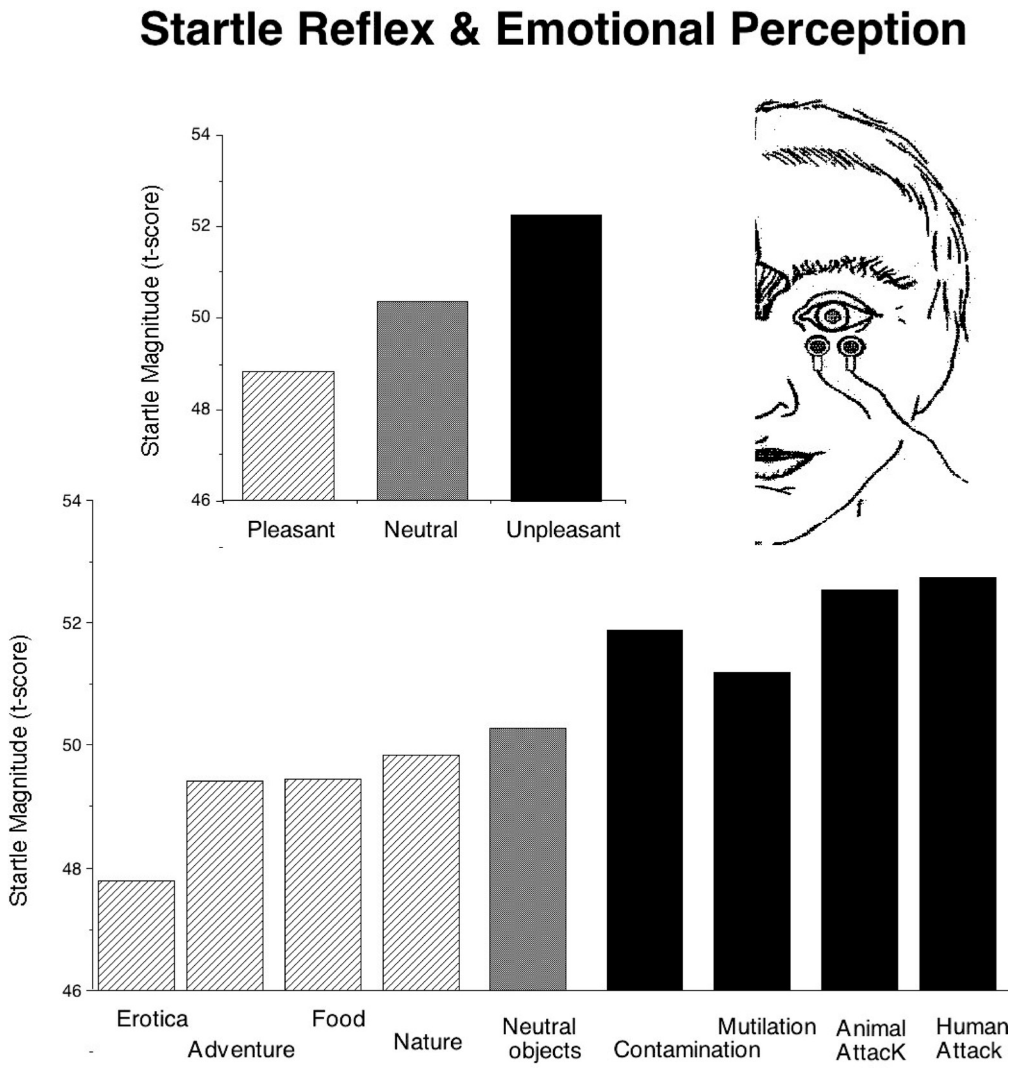

Figure 25.5. During picture perception, the startle blink reflex is modulated by hedonic valence, with potentiation during unpleasant picture viewing, and attenuation during appetitive picture viewing. Startle reflex modulation is greatest for pictures that are rated as highly arousing, including erotica, threat, and mutilation. Based on data from Bradley et al. (2001a).

orienting are absent when phobics process very highly fearful content.

These data suggest that, instead of a single response indicating activation of the defensive motivation system, one observes instead a cascade of physiological responses, changing in different ways as activation increases. The idea that defense involves stages of responding has been advocated by a number of theorists, including Tinbergen (1969), Blanchard and Blanchard (1989), and Fanselow (1994). Based on data obtained during picture perception, we have proposed a similar cascade of changing defensive reflexes, determined by increasing metabolic and neuromuscular mobilization that is paralleled by greater judged emotional arousal. Figure 25.6 illustrates the defense cascade model in picture perception.

Stimuli that moderately activate the defensive system prompt a pattern of responding that is suggestive of oriented attention, in which measurable conductance changes are obtained, the heart decelerates under vagal control, and startle reflexes are not potentiated. In fact, at lower levels of rated arousal, the startle reflex is inhibited when viewing unpleasant, compared to neutral, pictures (Bradley et al., 2001a; Cuthbert, Bradley, & Lang, 1996). Thus, at this first stage of defensive activation, heightened attention and orienting are apparent, signaled by cardiac deceleration and dampened startle reflexes, both of which are consistent with the hypothesis of greater sensory intake and resource allocation to a meaningful foreground. (As Lacey [1958] recognized, unpleasant events are not automatically "rejected," but instead evoke a physiology consistent with sustained attention.) This reflex pattern changes dramatically, however, when danger becomes more imminent, with mobilization and active defense reflexes occurring later in the sequence. Evidence of a change in defensive posture is first seen in the startle reflex: As the stimulus becomes more threatening/arousing

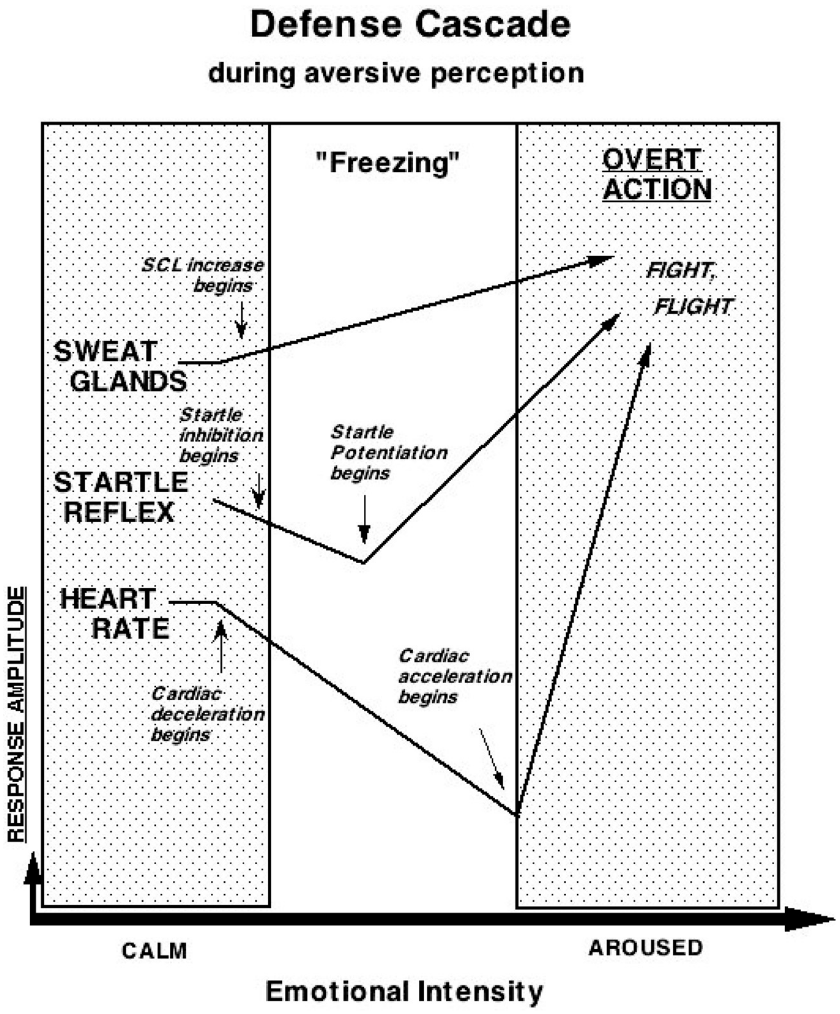

Figure 25.6. Stages of defensive responding are depicted, in which different physiological systems change at different rates, based on the intensity of activation in defensive motivation (see Lang, Bradley, & Cuthbert, 1997).

(a negative outcome is more imminent), startle amplitude increases and the reflex is potentiated rather than inhibited. As defensive activation increases, just prior to action, the heart rate response is also modulated: Vagal release is followed by a sympathetically driven acceleration that is the classic cardiac defense response. Thus, when processing pictures of their feared objects, phobic subjects do not show the initial decelerative stage of defense, but instead show an immediate cardiac acceleration, accompanied by dramatically large startle reflex potentiation. In effect, phobics are more aroused by these stimuli, and thus further along in the 'defense cascade' than normal subjects processing standard unpleasant pictures.

Reflex modulation in anticipation. The defense cascade model describes defensive reactions that occur specifically concurrent with *perception* of external stimuli, i.e., when sensory stimuli are processed that vary symbolically in degree of threat (probability of harm), and thus weakly or strongly activate the defense motivational system. In the picture-viewing context, of course, pleasant stimuli (varying in arousal) do not prompt a similar change in startle probe modulation. Rather, there is a progressive augmentation of the cardiac decelerative/inhibitory startle attentive set that is maximal at the highest levels of picture arousal (most dramatically, for pleasant erotic images). Interestingly, however, and highlighting the importance of understanding the local effects of the emotion inducing context, these two physiological measures (heart rate and startle blink reflexes) show parallel responses to pleasant and unpleasant stimuli in the context of *anticipation* and *imagery*.

For instance, when men reporting high fear of snakes anticipated (during a 6 s interval) presentation of an erotic, snake or neutral picture, startle reflexes were significantly and similarly potentiated during anticipation of either type of arousing content – snakes or erotica – compared to neutral household objects (Sabatinelli, Bradley & Lang, 2001). The same pattern of reflex potentiation was found when non-fearful participants anticipated viewing a selection of pleasant or unpleasant images, relative to anticipation of neutral pictures (Nitschke et al., 2002). Furthermore, numerous studies have demonstrated that the startle reflex is reliably enhanced during an interval when participants anticipate the possibility of receiving electric shock, compared to a "safe" period (e.g., Grillon et al., 1991; Bradley, Moulder, & Lang, 2005). Recently, reflex potentiation was consistently observed in our laboratory during an interval in which participants anticipated the possibility of winning a substantial sum of money. Similarly, Skolnick and Davidson (2002) found reliable reflex potentation when participants anticipated winning in a gambling game, as well during a period in which they anticipated the presentation of aversive noise.

Reflex modulation in imagery. Several studies (Witlviet & Vrana, 1995; Robinson & Vrana 2000) have examined startle modulation during text-driven imagery, varying both the hedonic valence (pleasant, unpleasant) and judged arousal (low, high) of the imagery scripts. Although startle blinks were consistently larger when imagining unpleasant, compared to pleasant scenes; nevertheless, reflexes elicited when imaging pleasant, arousing scenes were potentiated relative to pleasant scenes rated lower in arousal. Bradley, Cuthbert, and Lang (1995) obtained similar results: Compared to imagining neutral scenes, the startle reflex was significantly potentiated when imagining either unpleasant or pleasant events.

In a series of imagery studies conducted in our laboratory, the pattern of startle modulation that we obtained replicated Vrana and colleagues, with low arousal scenes again prompting significantly smaller blink reflexes than high arousal scenes during both pleasant and unpleasant imagery. No differences were found among unpleasant scenes rated as highly arousing (regardless of different emotion reports of eliciting fear, anger, and disgust). However, when the participants imagined pleasant, highly arousing scenes (e.g., winning the lottery), startle reflex magnitude was substantially greater than for less arousing pleasant contents, and equivalent to blinks elicited when imagining highly arousing unpleasant scenes. Miller et al. (2000) also found that blinks elicited during pleasant (arousing) imagery were equivalent to those elicited during unpleasant (arousing) imagery, noting this particularly for imagined scenes that were personally relevant.

Thus, different from the modulatory pattern found during *perception* and attentive intake (i.e., the reflex inhibition seen during picture perception), reflex modulation during mental *imagery* is more similar to that observed in *anticipation*, that is, the startle reflex is potentiated when imagining highly arousing events, regardless of their affective valence. Overall, the startle data suggest that reflex inhibition – both during appetitive perception and early defensive vigilance – accompanies sensory processing and heightened attention to external stimulation, with a resulting inhibition of reactions to other sensory input (as is also found for non-startling reaction time probes, Bradley, Cuthbert, & Lang, 1996). However, when the perceptual stimulus is sufficiently arousing (proximal, threatening, imminently aversive), active defense mobilization ensues, priming related defensive reflexes, such as the startle blink.

During the anticipation of a future event (or during mental imagery), however, there is generally no concurrent sensory intake that competes with startle probe processing. Moreover, during mental imagery, the dominant cardiac pattern is accelerative, rather than decelerative, consistent with the hypothesis that preparation for action, rather than sensory intake, characterizes imaginal processing. It is also instructive to consider the heart rate response that can occur in an anticipatory context: Chase, Graham, and Graham (1968) noted that if the anticipated event requires vigorous motor action, the anticipatory cardiac response is a marked acceleration. Assuming that affective anticipation involves active preparation, potentiation of both autonomic (heart rate acceleration) and somatic motor responses (startle reflex potentiation) might be an expected consequence. When comparing the responses of fearful subjects in anticipation and mental imagery, Lang et al. (1983) noted that, for snake phobics, increases in both skin conductance and heart rate were found both when imagining scenes involving snakes and when anticipating an actual confrontation with an alive snake. One is tempted to conclude that similar cognitive processes, and a physiology primed for action, may characterize both anticipation and imagination of emotional events, prompting similar modulation by emotion for cardiac, electrodermal, and startle responses.

THE NEUROANATOMY OF EMOTION

Understanding the neural circuits mediating the psychophysiology of emotion will depend to some degree on determining which brain structures are important in controlling the peripheral autonomic and somatic responses that together define emotion. Not surprisingly, control systems occur at every level of the central nervous system: from the spinal cord to the brain stem to sub-cortical and cortical structures (for a more extensive discussion, see LeDoux, 1987; Gellhorn & Loofbourrow, 1963; Guyton & Hall, 1996). Thus, for instance, mechanisms in the spinal cord can affect the level of activity in sympathetic and parasympathetic fibers in the absence of supraspinal controls. Among the more important *brain stem* control structures is the medulla oblongata: Electrical stimulation of the rostral portion of this structure evokes sympathetic reactions throughout the body, including heart rate and blood pressure increases, dilation of pupil, inhibition of gastro-intestinal activity, secretion of sweat, etc. Conversely, activation of the vagal nucleus of the medulla oblongata causes a decrease in heart rate and blood pressure and an increase in gastrointestinal activity – reactions associated with parasympathetic activity. Because of its ability to control many elements of autonomic function, the medulla oblongata has been proposed as the final common pathway for autonomic responses associated with defense reactions (LeDoux, 1987).

Cannon originally advocated that key structures in the brain, particularly the hypothalamus and thalamus, were important in controlling peripheral emotional reactions, which was supported by a number of animal studies demonstrating that electrical stimulation of the hypothalamus produced physiological reactions associated with sympathetic activation, and even full motor sequences indicative of emotion, including freezing, piloerection, hissing, and attack (collectively termed the *defense reaction*, Hess & Burgger, 1943), as well as grooming, mating, and feeding/drinking. Lesions of the hypothalamus (Bard, 1934) effectively eliminated these reactions. Despite proposing a much more extensive neural circuit, Papez (1937) also focused on the hypothalamus as a central structure in mediating emotion, particularly bodily responses. Although Papez's circuit is generally considered incomplete today, mainly because it neglects to include structures currently thought important in emotion (e.g., amygdala) and includes structures that are now recognized as more important for memory (e.g., hippocampus; LeDoux, 1987) certain key structures in Papez' circuit, such as the thalamus and cingulate cortex have been implicated in recent neuroimaging explorations of emotional processing (e.g., Breiter et al., 1997; George et al., 1995; Lane, Reiman, Ahern et al., 1997; Lane, Reiman, Bradley et al., 1997).

Prior to the advent of neuroimaging techniques, information regarding the neural circuits mediating emotional experience and expression relied on data from animal studies and patients suffering a variety of brain damage. New technologies for measuring brain activity during emotional processing (including PET, fMRI) now allow an investigation of cortical and subcortical activity during emotional processing in awake alert human participants. The explosion in neuroimaging studies over the past 10 years has produced a burgeoning data base in which new studies are added at an exponential rate, many of these focused on emotion and affect. Making sense of this large data base will rely, again, on careful attention to the specific context of emotional induction in the scanner.

For instance, in a recent meta-analysis of brain activation during emotional processing, data from over 100 PET and fMRI studies were aggregated across a number of different induction contexts (e.g. viewing facial expressions, listening to music, conditioned fear, anticipating pain, and so on (Murphy, Nimmo-Smith, & Lawrence, 2003). When the resulting activation clusters that reportedly varied with emotion were plotted in a 3-dimensional space defined by the Talairach-Tourneau coordinates, a figure eerily reminiscent of the entire brain emerges. Assuming that different perceptual, anticipatory, imaginal, and action contexts prompt activity in divergent and overlapping neural circuits, it may be difficult to understand the neural circuitry of emotion in the absence of making comparisons that control the specific context of emotion induction.

In another meta-analysis (Phan et al., 2004), an effort to control the specific context of the emotional induction was made by comparing neural activation in visual perception, auditory perception, or imagery contexts as they varied with fear, sadness, anger, etc. Across all studies, no specific brain region was reliably activated, consistent with the idea that emotion is not mediated by a specific neural structure. The region most likely to be active across different induction contexts was the prefrontal cortex (medial), a structure highlighted as central in emotion by Davidson (2003), whose work on hemispheric asymmetry indicates tonic differences in resting EEG in frontal regions as a function of affect and temperament (Davidson, 2002).

Regions implicated as active in different affective induction contexts included a greater probability of anterior cingulate and insula activation during emotional imagery, with affective visual perception more likely to additionally include greater activation of occipital cortex and the amygdala. Animal and human patient studies had already noted the potential importance of the amygdala in emotional processing, based, to a large extent, on the same type of data originally invoked to support the hypothalamus as the center of the emotion system. Thus, both lesion and stimulation studies in animals indicate that specific nuclei in this structure mediate specific emotional phenomena, both appetitive and defensive (e.g., Amaral et al., 1992; Gaffen, 1992). Stimulation of the amygdala produces rage, attack and defense reactions similar to those earlier elicited by activation of the hypothalamus and lesions of the amygdala eliminate the fear-potentiated startle response (Davis, 1986), and have been implicated in disrupting appetitive behaviors such as mating, food-getting, and reward learning (Gaffen, 1992).

The amygdala includes multiple afferent and efferent connections to cortical, subcortical, and brainstem structures that have been implicated in mediating the autonomic and somatic responses involved in emotional behaviors (see Davis & Lang, 2003). Inputs to the lateral nucleus of the amygdala include those from unimodal cortical sensory areas, including vision, audition and somatosensory (via the insula) information, as well as from polysensory association cortex. Olfactory input is relayed to the periamygdaloid nucleus (rather than lateral) and gustatory information may also be relayed to this nucleus via its thalamic input. Consistent with this, a number of neuroimaging studies have reported significant activation of the amygdala during perception of aversive visual, olfactory, auditory and gustatory stimuli (see Zald, 2003, for a review).

The outputs from the amygdala are extensive as well, and include almost all of the structures highlighted as important in emotional reactions, including direct connections to the hypothalamus, the central gray, the brain stem, the striatum, and cortical structures including the cingulate gyrus, frontal lobe, visual cortex, and more. The amygdala's central nucleus sends prominent projections to the lateral hypothalamus – a key center activating the sympathetic branch of the autonomic nervous system in emotion (LeDoux, 1987). In addition, direct projections from the lateral extended amygdala go to the dorsal motor nucleus of the vagus, the nucleus of the solitary tract, and the ventrolateral medulla. These brainstem nuclei are known to regulate heart rate and blood pressure (Schwaber et al., 1982), and may thus modulate cardiovascular responses in emotion.

Subcortical structures such as the amygdala and hypothalamus are clearly central in the expression of emotion, particularly in mediating the defensive and appetitive responses that even animal subjects clearly display when under threat or seeking sustenance. With increasing brain complexity, however, the neural circuitry of emotion increasingly includes activation in numerous cortical structures that can modulate subcortical activation, and vice versa. During picture perception, for instance, both unpleasant and pleasant pictures prompt significantly greater activation throughout the visual sensory regions, including middle occipital, inferior occipital, and fusiform cortex, as illustrated in Figure 25.7 (top left; see Lang et al., 1998; Bradley et al., 2003).

As noted by Amaral et al. (1992), in the primate, the amygdala is extensively interconnected with the visual sensory system, with bidirectional connections that could promote both initial amygdaloid access as well as later perceptual modulation through its efferent connections. These projections could potentially "close the loop" with the visual system (Amaral et al., 1992), representing an amygdala feedback circuit that may be significant for the

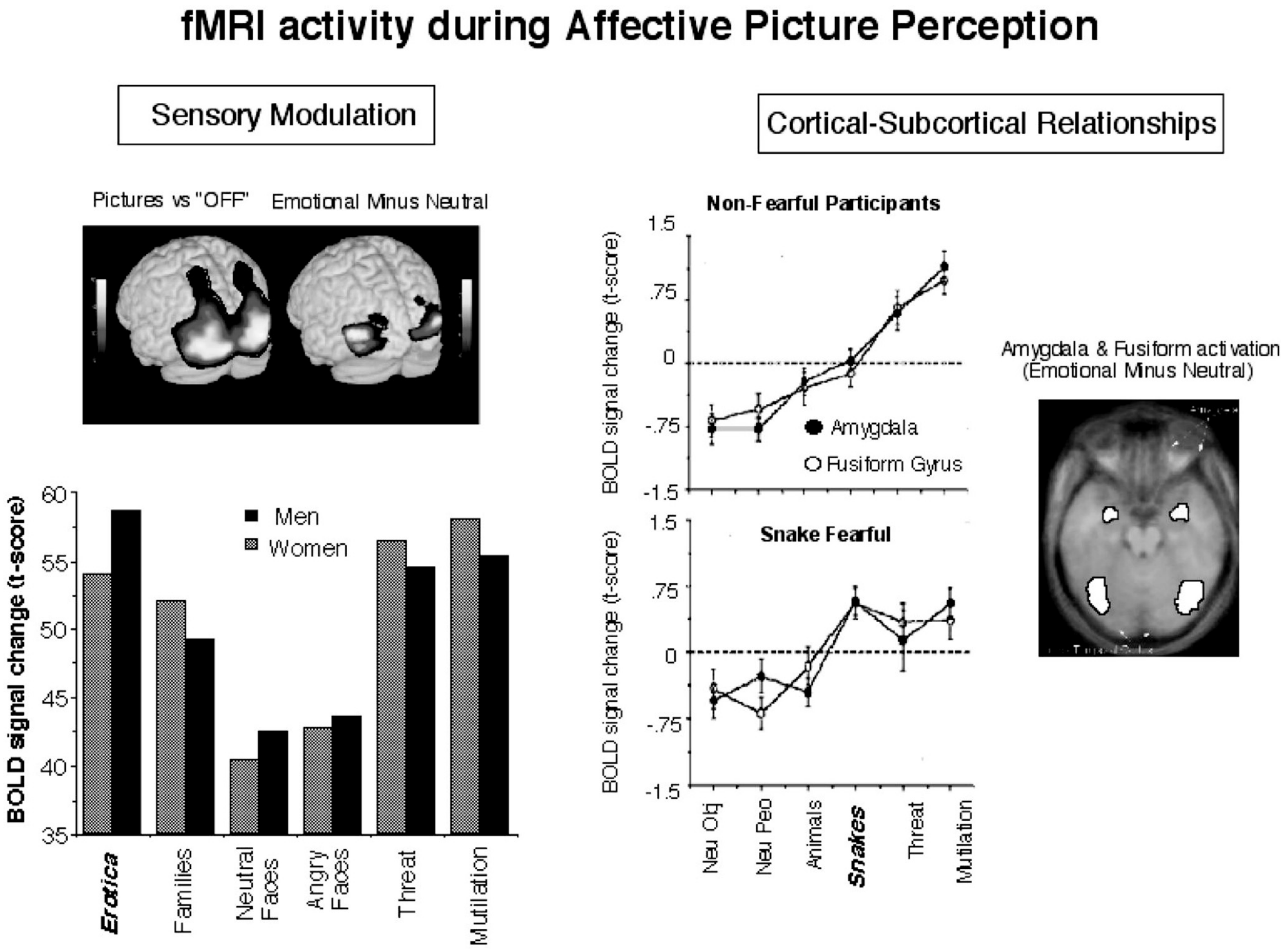

Figure 25.7. Neural activity measured during picture perception using functional magnetic resonance imaging shows greater activity in visual sensory cortex for emotional, compared to neutral, pictures, with men showing greater visual activation when viewing erotica than women. The covariation in activation for sensory fusiform cortex and the amygdala is strikingly high, with snake phobics responding with greater activation in both structures when viewing snakes than non-fearful participants. Based on data from Sabatinelli et al. (2004, 2005).

sustained perceptual evaluation seen in the early stages of emotional processing. Consistent with this, as illustrated in Figure 25.7 (top right), activation in the amygdala consistently and significantly covaries with the magnitude of activation in the fusiform areas (Sabatinelli et al., 2005). Moreover, this effect is even more apparent when snake phobics view pictures of snakes: both the amygdala and the visual fusiform areas show significantly greater activation than for those reporting no fear of snakes (Figure 25.7). These data are consistent with previous PET studies showing greater activation in the occipital cortex when phobics view pictures of phobic objects (e.g., Fredrikson et al., 1993), and furthermore, indicate that increased activity in visual cortex is paralleled by heightened activation of the amgydala as well.

It is now also clear that not only aversive pictures activate the amygdala: Numerous studies have found significantly elevated functional activity in this structure when people view highly arousing pleasant pictures (e.g., Lane, Chua, & Dolan, 1999; Garavan et al., 2001; see Zald, 2003). In fact, the covariation between activity in the amygdala and in visual association areas such as the fusiform cortex when people view erotica is identical to that obtained for highly aversive stimuli (see Figure 7, bottom left; Sabatinelli et al., 2005). Hamann, Herman, Nolan, and Wallen (2004) recently reported larger increases in bilateral amygdala activation (and hypothalamus) when men viewed erotica, compared to women, in a study that included pictures of erotic couples, opposite sex erotica and non-erotic couples. Relatedly, men also show greater functional activity in visual cortical regions viewing erotica, compared to women (Sabatinelli et al., 2004; see Figure 25.7, bottom left). These data are consistent with evaluative and physiological data which find that men rate erotica as more arousing than do women, and also show heightened electrodermal reactions (Bradley et al., 2001b), suggesting differences in the ability of visual cues depicting erotica to engage appetitive activation in men and women.

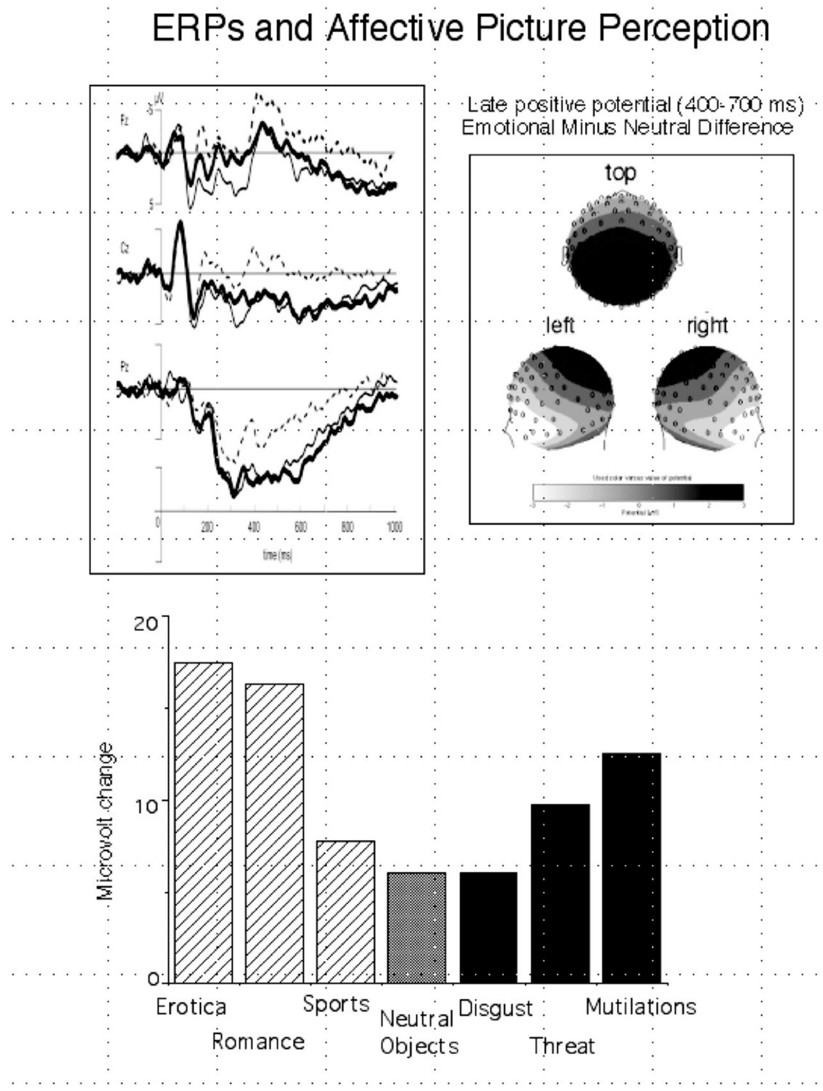

Figure 25.8. The late positive potential elicited 300–1000 ms after picture onset is larger when viewing emotional (pleasant or unpleasant), compared to neutral, pictures, and is maximal over centro-parietal sites (based on data from Keil et al., 2002). The magnitude of the late positive potential is largest for emotional pictures that are rated as highest in arousal (based on data from Schupp et al., 2005).

AU: provide callout

Moreover, taken together, these data suggest a link between the magnitude of physiological reflexes, such as electrodermal reactivity, and the magnitude of cortical and subcortical activation such as the BOLD signal in the fusiform cortex and the amygdala.

In fact, as fMRI, PET and other imaging modalities are used to explore emotion in the brain, the classic psychophysiology of bodily reflexes has an increasingly important role to play. In order to confirm that regional changes in neural activity are in fact related to affect and motivation, we will need to measure the well-established reflex physiology of emotion by simultaneously recording these, if possible, or by measuring these affective reactions in the same participants and paradigm in a simulated imaging context. As emotion researchers well know, evaluative reports are only loosely related to emotion's physiology, varying greatly in their covariation with context as well as with the personality and temperament of the participants, and can not serve as the sole measure of emotional engagement in neuroimaging explorations. Rather, standard practice in neuroimaging studies should be to include a coincident sample of measures that assess hedonic valence (e.g., facial EMG or cardiac response in perceptual contexts) and emotional arousal (e.g., skin conductance; event-related potentials).

The neurophysiology of emotion

A second source of information regarding the neural activity accompanying affective processing is measurement of electrophysiological signals on the scalp, which provide excellent information regarding the timecourse of neural processing. When measuring event-related potentials during affective picture viewing, the most common finding is of a larger late positive potential (Cacioppo et al., 1994) that is elicited 300–1000 ms after picture onset and is maximal over centro-parietal sites. The late positive potential is more pronounced when viewing emotional (pleasant or unpleasant), compared to neutral, pictures (Palomba et al., 2000; Cuthbert et al., 2000), and is largest for highly arousing pictures of erotica, mutilation, and attack (Schupp et al., 2004).

On the other hand, although several studies have reported modulation of earlier ERP components, the nature and direction of the difference are quite variable across studies. For instance, Cuthbert et al. (2000) found that pleasant pictures prompted greater positivity in a 200–300 ms time window following picture onset (at frontal, central, and parietal sites) and a similar pattern of greater positivity over parietal, central, and frontal sites for pleasant pictures in this time window was reported by Palomba, Angrilli, and Mini (1997).

Using dense sensor array, a variety of effects that are maximal over occipital sensors have also been reported in early time windows. Using a relatively slow (1.5 s) presentation, emotional pictures (pleasant or unpleasant) have prompted less positivity over occipital sensors than neutral pictures in a 200–300 ms time window following picture onset (e.g., Schupp et al., 2003). On the other hand, when pictures are presented very rapidly (e.g., 3 per second), a somewhat different pattern is obtained, with emotional pictures prompting greater negativity than neutral pictures over occipital sensors which is again is maximal 200–300 ms after picture onset (Junghofer et al., 2001).

Even earlier effects, in the neighborhood of 100 ms following picture onset have also been reported. Larsen, Norris, and Cacioppo (2003) reported an occipital P1 (about 114 ms after picture processing) that was larger for unpleasant, compared to pleasant, pictures in a design which assessed ERPs to pictures presented in varying hedonic contexts. Keil et al. (2002), on the other hand, found a larger N1 occipitally specifically for pleasant, compared to unpleasant or neutral, pictures. Taken together, the variety of modulatory patterns by hedonic valence and/or emotional arousal very early in the viewing interval suggest that characteristics of specific stimulus sets, subject samples, or task parameters may contribute at least in part to early ERP differences during affective picture viewing, as the pattern of ERP modulation varies widely even in very similar picture perception contexts.

The larger late positive potential for emotional pictures (compared to neutral) is, however, a robust and well-replicated finding. It has also been reliably observed that the amplitude of the late potential increases systematically with the judged arousal of emotional pictures (Cuthbert et al., 2000). According to a biphasic view, motivationally relevant pictures activate reentrant projections from the anterior, basal brain, naturally engaging attentional resources and enhancing processing in the secondary and tertiary centers of the visual system (e.g., Amaral, 19; Davis & Lang, 2003). Consistent with enhanced sensory processing, dipole source localization of the late positive potential highlights occipito-temporal and parietal sites. Using a dense sensor EEG array (129 electrodes), Keil et al. (2002) reported sources over both the occipito-temporal and posterior parietal areas that differed as a function of emotion, with greater source strength over these regions when viewing emotional, compared to neutral, pictures.

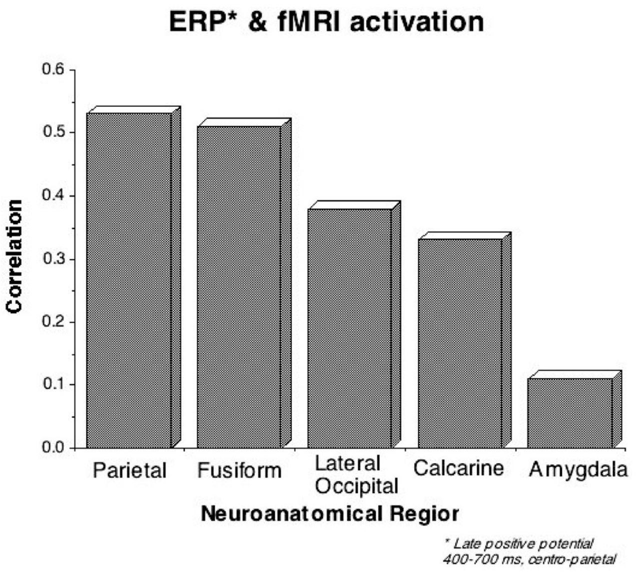

Figure 25.9. The correlation between the magnitude of the late positive potential scored in a window from 400–700 ms after picture onset over centro-parietal sites and the magnitude of BOLD activity in different brain regions, measured in the same participants viewing the same pictures in the scanner and in a simulated scanner using dense sensor (256 channels) EEG measurement.

In a recent study (Sabatinelli, Bradley, & Lang, 2005) ERPs and BOLD measures were monitored in the same experimental participants in the same picture perception paradigm, conducted once in the fMRI scanner and once in a MRI simulator (using dense sensor (256) EEG array). In the analysis of data from the fMRI session, greater BOLD activity for emotional, compared to neutral, picture viewing was found in regions that included the parietal, temporal (fusiform), lateral occipital, calcarine fissure, and amygdala. In the ERP session, the amplitude of the late positive potential recorded over centro-parietal sensors was (as seen previously) greater for emotional, compared to neutral, pictures. When correlations were performed that assessed covariation in the amplitude of the late positive potential and BOLD changes in each region (see Figure 25.9), the late positive potential correlated most strongly with activity in parietal and fusiform regions, and considerably less with either striate cortex or the deeper, more anterior amygdala. The data support the hypothesis that the emotion-related late positive potential is linked to enhanced processing in the dorsal (occipito-parietal) and ventral (occipito-temporal) processing visual streams.

EPILOGUE

Emotion and action

We have speculated that emotion and motivation are related processes, with both involving stimuli and events that move an organism towards action. Animal studies have clearly demonstrated that motivational circuits are initially activated by unconditioned stimuli – those that reflexively active appetitive and defensive systems. New, 'conditioned' stimuli come to activate the same circuits, however, through association with these primary appetitive and aversive reinforcers (e.g., Halgren, 1981). Because humans, as well as animals, learn to respond in adaptive ways to a wide variety of different environmental stimuli and events through this basic learning process, stimuli that activate appetitive and defensive systems through association can be idiosyncratic, not clearly so valenced to bystanders, as well as not obviously related to basic survival mechanisms.

The close link between motivational engagement and overt action has been loosened in humans, presumably due to the evolution of cortical control if these fundamental behaviors (i.e., inhibition and delay), and development of the ability to mentally process, off-line, events that are not currently perceptually prompted. Thus, emotions are most often reported during inhibitory states, when the body is mobilized to respond but action is restrained. Nonetheless, when a provocation is intense (e.g., the attacker threatens), action (i.e., fleeing) is evident, even in humans. Weaker affective cues (e.g., a movie of the same scene), on the other hand, may elicit only small increases in muscle tension, a mere remnant of the original defensive activity. Thus, emotional reactions in humans often involve primarily a disposition towards, or preparation for, action (Frijda, 1986; Arnold, 1970; Lang, 1987), rather than clear overt expression.

Conscious experience of emotion

If emotion is defined in terms of subjective reports, overt behaviors, and bodily responses, one might wonder which measure, if any, taps conscious feelings. The issue of the conscious experience of emotion, and how to approach it scientifically, has posed a number of problems in emotion research. As LeDoux (1995) notes, "... it is understandable why the field of emotion has had so much trouble in solving the problem of emotion – it has set as its goal the task of understanding consciousness" (p. 1059). Animal theorists, in general, balk at using the term 'emotion' in describing motivated behavior in their subjects, mainly because of the added assumption of conscious awareness. The study of motivated behavior, however, does not necessitate taking on the Goliath issue of consciousness, which, in the end, may prove to be more amenable to philosophic, rather than scientific, inquiry.

From a measurement perspective, one solution is to operationally define conscious experience on the basis of evaluative reports: People's reports (verbal or non-verbal) about their emotional experience could be used to index the private, internal state that is usually meant when one speaks of feelings. Some might argue this is unsatisfactory, due to the dependence of personal reports on cultural norms and individual differences in disclosure. In addition, feelings are often held to include the bodily reactions involved in emotional response, such as a racing heart, sweaty palms, and so on. A second solution has been to include 'conscious awareness' as a fourth type of response system in emotion. The difficulty here is that one needs a reliable operational measure of consciousness, and, other than the three-system measures of behavior, physiology, and reports, there are currently no additional methods for directly measuring an internal feeling state. Although clearly central to the personal experience of emotion, the concept of internal states raises more questions than it answers in the scientific study of emotion, as it at can be simultaneously invoked as a cause (e.g., he ran because he felt afraid), an effect (e.g., he saw the bear and felt afraid) or, as James proposed, a consequence of the physiology (e.g., he saw the bear and ran so felt afraid).

Emotion and mood

In this chapter, the emphasis has been on discrete, phasic physiological responses to appetitive or defensive stimuli using cardiovascular, electrodermal, somatic, reflex, electrophysiological, and hemodynamic measures. Such phasic responding is representative of "emotional" reactions, whereas longer-lasting, more tonic changes in physiology are more representative of what is typically meant by "mood." In the laboratory, moods can be induced by sustained exposure to affective stimuli. Using sustained presentation of blocks of unpleasant, neutral, or pleasant pictures, for example, both corrugator EMG activity and the startle reflex increase in magnitude as the duration of aversive picture exposure increases (Bradley, Cuthbert, & Lang 1996; Smith, Bradley, & Lang 2005), indicative of a sustained and increasingly aversive mood state with the duration of exposure. Sustained exposure to pleasant stimuli, on the other hand, was less strongly associated with increasing appetitive activation in both studies.

Codispoti et al. (2003) recently explored neuroendocrine responses in the picture viewing context, using an intravenous catheter to draw blood samples during a 30-minute sustained exposure to mutilation, neutral, or erotic pictures presented in a blocked design on separate days. For unpleasant pictures, significant increases in noradrenaline, cortisol, and ACTH were found, compared to a baseline condition, consistent with previous data indicating that these neuroendocrine changes are associated with sympathetic activation mediated by sustained exposure to stress or aversive contexts (Lovallo & Thomas, 2000). For erotic pictures, these sympathetic changes were not obtained, with the main difference indicating in increase in prolactin from baseline to exposure. Taken together, whereas sustained exposure to aversive stimuli prompts tonic changes indicative of increasing defensive activation, sustained exposure to pleasant pictures is less strongly indicative of increasing appetitive activation.

Arousal and emotional intensity

The concept of arousal in the psychophysiological study of emotion has not fared well over the past thirty years, due in part to Lacey's (1967) observation that physiological responses do not uniformly, and in parallel, increase with increasing arousal. This is supported by more recent data which find that different physiological systems change at different rates, with some (such as startle potentiation) modulated at relatively lower levels of arousal than others (see Lang, 1995). Thus, arousal, or intensity is a critical factor in organizing the *pattern* of physiological responses in emotional (i.e., hedonically valenced) reactions. Emotional intensity presumably reflects the strength of activation in motivational systems subserving appetitive and defensive behaviors, and, as such, has clear ramifications for the amount and type of physiological response.

Theorists reasoning from data on motivated behavior in animals have relied on a proximity dimension to operationalize intensity: Fanselow's (1994) model is based on 'predator imminence' (the distance of the threatening stimulus from the organism), and Miller (1959) also operationalized arousal in terms of distance from an aversive or appetitive goal. Drawing parallels between emotional intensity and imminence, arousal in humans appears to reflect the degree to which a stimulus elicits appropriate appetitive or defensive behaviors. The importance of variations in arousal within separable appetitive and defensive systems points to the necessity of controlling affective intensity in psychophysiological comparisons of pleasant and unpleasant emotion.

Revisiting discrete states: The tactics of emotion

Biphasic and discrete state views of emotion are complementary, rather than mutually exclusive positions, as many theorists recognize (e.g., Mehrabian & Russell, 1974). Not only can a specific state such as fear be categorized along a dimension of aversiveness, but a particular aversive event can be described as involving fear. The issue of how to define discrete states of emotion is central in terms of distinguishing among specific emotions. Ortony, Clore, and Collins (1988) have provided a compelling cognitive analysis detailing the features of situations and stimuli that may differentiate among events people generally label with different emotional terms. Consistent with a biphasic view, the superordinate division in their scheme is one of hedonic valence, differentiating among desirable and undesirable events. Specific features of environmental events are then proposed to control how different hedonically valenced events are labelled. For instance, whereas "distress" labels the *actual* occurrence of an undesirable event, and "joy," the actual occurrence of a desirable event, "fear" and "hope" label undesirable and desirable events that are only *anticipated*.

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

Conclusion

This chapter has explored the psychophysiological study of emotion primarily from a biphasic motivational view. This view posits that human emotions are organized by neural systems of appetitive and defensive motivation that mediate a range of attentional and action reflexes presumably evolved from primitive approach and withdrawal tendencies. Discrete states of emotion, such as fear, anger, sadness, and so on are considered to be based on tactical responses (e.g., freezing, fight, flight) that are deployed by the motive systems in specific environmental circumstances. Rather than physiology being emotion-specific, as James suggested, it was emphasized throughout this chapter that understanding the psychophysiology of emotion will depend on close attention to the context of its occurrence in the laboratory and in life. Common induction paradigms in the psychophysiological study of affect, including perception, imagination, anticipation, and action, generate overlapping and divergent physiological signatures that suggest common motivational determination but which elude easy folk description and instead, demand understanding of the specific sensory, attentional, and action requirements elicited in different emotional/motivational contexts.

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