
The Emotion Probe

Studies of Motivation and Attention

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Emotions are action dispositions—states of vigilant readiness that vary widely in reported affect, physiology, and behavior. They are driven, however, by only 2 opponent motivational systems, appetitive and aversive—subcortical circuits that mediate reactions to primary reinforcers. Using a large emotional picture library, reliable affective psychophysiology is shown, defined by the judged valence (appetitive/pleasant or aversive/unpleasant) and arousal of picture percepts. Picture-evoked affects also modulate responses to independently presented startle probe stimuli. In other words, they potentiate startle reflexes during unpleasant pictures and inhibit them during pleasant pictures, and both effects are augmented by high picture arousal. Implications are elucidated for research in basic emotions, psychopathology, and theories of orienting and defense. Conclusions highlight both the approach's constraints and promising paths for future study.

The purpose of this discourse is to describe a scientific view of emotion that can be explored productively in the laboratory and yet provide a framework for studying practical concerns about emotion in society, the media, and in affective disorder. It begins with a working definition of emotions as action dispositions, describing a database that includes functional behaviors, evaluative and expressive language, and physiological events. These responses all vary enormously within and between emotions; however, it is put forward that this response complexity is orchestrated by simpler, underlying motivational parameters. All emotions can be located in a two-dimensional space, as coordinates of affective valence and arousal. This dimensional conception is applied here to a perceptual task, organizing an analysis of human affective reactions to emotionally evocative pictures.

The concepts of affective valence and arousal are explicated in terms of specific motivational systems in the brain. Following Konorski (1967) and others (e.g., Dickinson & Dearing, 1979; Solomon & Corbit, 1974), it is suggested that affects are driven by two primary motive systems: the appetitive system (consummatory, sexual, and nurturant), prototypically expressed by behavioral approach, and the aversive system (protective, withdrawing, and defensive), prototypically expressed by behavioral escape and avoidance. With respect to the latter, recent animal research is reviewed that (using the tools of pharmacological and neurosurgical mapping) defines the

aversive system's brain circuitry in conditioned fear and specifies its autonomic and somatic output paths. Of particular interest is the manner in which an active aversive system modulates concurrent but independently evoked behaviors. The neurophysiology of this phenomenon is well understood for the startle reflex, which, in animals, is strongly potentiated (is larger) when aversive (fear) motivational circuits are activated.

The subsequent exposition is centered on research using the startle reflex to probe the affective states of human beings. These experiments test a theory of motivational priming or, more specifically, two main corollary hypotheses: (a) Defensive reflexes, including startle, increase in amplitude when an organism is aversively motivated (i.e., when the aversive system is activated and the individual's emotional state is affectively unpleasant); and (b) Defensive reflexes are reduced in amplitude when an organism is positively motivated (i.e., when the appetitive system is activated and the individual's emotional state is affectively pleasant).

The data show very wide support for these hypotheses: Using acoustic probe stimuli and measuring the early blink component of the startle response, the reflex augmentation found in animal studies with shock sensitization and conditioning (anticipation) has been replicated in humans. Furthermore, when humans look at pleasant

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emotional scenes, concurrent startle reflexes are inhibited; the same evoked reflexes are augmented when they occur in the context of unpleasant picture stimuli. These reciprocal effects for pleasant and unpleasant stimuli become stronger as both types of stimuli are judged to be more arousing.

Motivational modulation of the startle reflex is generally robust despite habituation, variations in probe timing and in specific foreground content, or changes in probe intensity and modality. Furthermore, it appears to be specific to startle in the perceptual context, and similar modulation is not observed either for other tested reflexes or for the cortical event-related potential (P300) evoked by the same probe stimulus.

The replicability of startle probe effects commends the method for use in studying special subject populations as a way of assessing affective state: Research suggests that emotional reflex modulation appears very early in human development and persists with aging. There is evidence that when phobic individuals confront phobic objects, they show greater than normal reflex potentiation. On the other hand, when facing stimuli they describe as aversive, psychopathic prisoners fail to show normal startle potentiation. Furthermore, studies of anxiety disorders show significant differences in startle potentiation according to diagnosis (e.g., phobic patients and patients with post-traumatic stress disorder show greater potentiation than patients with panic disorder). These data raise questions about the varying strength of inhibitory and activating circuits in the brain as they modulate attention and emotional expression.

Emotions Are Action Dispositions

William James (1894) once said that emotions are as varied as the shapes of rocks on a New Hampshire farm. Unlike New Hampshire rocks, however, they are not inert granite but more like a protean lava. Emotions are about doing something that is important to the organism (escape, attack, sexual consummation, etc.). On the other hand, curiously, the defining acts may or may not actually occur.

Emotions are systemic responses that happen when highly motivated actions are delayed or inhibited. Or, as Hebb (1949) proposed, emotions result when novel circumstances prevent completion of cued behavior. Thus, emotions quintessentially occur in a behavioral hiatus, as states "experienced," then reported on and evaluated (see Frijda, 1986, on "feelings"). It is in this sense that they are dispositions and not the acts themselves: They reflect central activation and preparation for action.

It is likely that the varied shapes of emotions alluded to by James (1894) have evolved from simpler action tendencies. The behavior of very primitive organisms can be wholly characterized by two responses—a direct approach to appetitive stimuli and withdrawal from nociceptive stimuli (see Schneirla, 1959). This modest behavioral repertoire, sufficient to a flatworm, cannot of course implement the many subgoals of humans nor manage the perceptually richer, more complex environment in which

we live. Elaborate instrumental acts, delay, and inhibition have evolved to facilitate the goal-directed behavior of more complex organisms. Thus, a person's escape from aversive stimuli may be achieved as well by attack or compliance as by flight, and circumspection often rewards an appetite that a direct approach could not satisfy.

It is clear that the contextual tactics of approach and avoidance have become more varied in humans; nevertheless, the strategic frame of appetite and aversion is no less relevant. Emotions are products of a Darwinian development and could be characterized as motivationally tuned states of readiness. In humans, the presumed indices of these "affects" include responses in three reactive systems: (a) expressive and evaluative language, (b) physiologic changes mediated by the somatic and autonomic systems, and (c) behavioral sequelae, such as patterns of avoidance or performance deficits. This is the database of emotion, and a theory of emotion must cope with its breadth and diversity. The task is complicated by the fact that the correlations among and within systems are often quite modest, for example (Lang, 1968; Mandler, Mandler, Kremen, & Sholiton, 1961), when research participants confront a situation designed to evoke a particular affect (e.g., anger, fear, and disgust). Furthermore, the patterns of response that are observed are often unreliable within subjects and across different contexts of stimulation (Lacey, 1958; Lacey & Lacey, 1970). Thus, emotional judgments, physiology, and behavior can present a confusing rock pile that resists a simple classification by specific emotional states.

Affective Valence and Arousal

Although emotional expression is highly varied, many theorists view its motivational basis as having a much simpler, two-factor organization. Konorski (1967, p. 9) advocated a biphasic model that he founded on a typology of unconditioned reflexes. Exteroceptive reflexes were seen to fall into two classes, preservative (e.g., ingestion, copulation, and nurture of progeny) and protective (e.g., withdrawal from or rejection of noxious agents) on the basis of their biological, motivational role. Differentiating his views from Hess (1957), Konorski stressed that activation or arousal modulated both preservative and protective reactions. These reactions were considered to be the behavioral foundation of affects and expressed emotions. Dickinson and Dearing (1979) developed Konorski's dichotomy into two opponent motivational systems, aversive and attractive, each activated by a different but equally wide range of unconditioned stimuli. These systems were held to have "reciprocal inhibitory connections" (p. 5) that modulate learned behavior and responses to new, unconditioned input.

Since Wundt (1896), the view that affects might be organized by overarching motivational factors has also been suggested by researchers studying the emotion reports of humans. Thus, work on natural language categories (Ortony, Clore, & Collins, 1988; Shaver, Schwartz, Kirson, & O'Connor, 1987) suggests that people's knowledge about emotions is hierarchically organized and that

the superordinate division is between positivity (pleasant states: love and joy) and negativity (unpleasant states: anger, sadness, and fear). Osgood and his associates (e.g., Osgood, Suci, & Tannenbaum, 1957), using the semantic differential, showed that emotional descriptors could be in the main distribution along a bipolar dimension of affective valence—from attraction and pleasure to aversion and displeasure. A dimension of activation—from calm to aroused—also accounted for very significant variance. Similar conclusions have been drawn by other investigators of verbal report (e.g., Mehrabian & Russell, 1974; Russell, 1980; Tellegen, 1985) and in early studies of facial expression (Schlosberg, 1952).

The present view integrates these several lines of theory development. It is proposed that two motive systems exist in the brain—appetitive and aversive—accounting for the primacy of the valence dimension. Arousal is not viewed as having a separate substrate, but rather, as reflecting variations in the activation (metabolic and neural) of either or both systems (see also Cacioppo & Berntson, 1994). Tactical demands of context may variously shape affects. All affects are, however, organized around a motivational base. In this sense, valence and system arousal are the strategic dimensions of the emotion world.

Looking at Pictures

The emotional stimuli that are the focus of this presentation are pictures. An effort has been made to collect photographs of people, animals, nature, objects, events, and scenes, sampling as broadly as possible the range of visual representations of the world. The reactions evoked by these picture stimuli do not, of course, mirror all the affects that occur in life. On the other hand, media representations are a central feature of current culture, and icons of religion, family values, beauty, natural disasters, pornography, crime, and violence—in art, film, magazines, and television—are widely held to be powerful emotion generators and significant determinants of societal manners and mores.

Pictures are, furthermore, convenient laboratory stimuli that permit controlled exposure, in timing and intensity, and exact reproduction within and between experiments and laboratories. An aim of this effort is to produce calibrated emotional stimuli that can serve as a measurement standard—analogue to those used in physical metrics—and thus encourage scientific replication in research on emotion.

In the laboratory studies to be described, emotional stimuli were presented either as photographic slides or, when digitized, as displays on a computer monitor. Currently there are over 400 pictures in the International Affective Picture System (IAPS; Center for the Study of Emotion and Attention, 1994). Pictures are initially standardized in groups of 60 slides, using participant samples of approximately 100. In this initial calibration process, participants rate their emotional experience of each picture on scales of affective valence and arousal, using the Self-Assessment Manikin (SAM; Lang, 1980). This instrument is pictographic in form, largely culture free, and

can be rapidly administered (see Figure 1). SAM assessments of pleasure and arousal generally correlate .9 and above with the measures of these judgments, using Mehrabian and Russell's (1974) semantic differential scales (see Bradley & Lang, 1994).

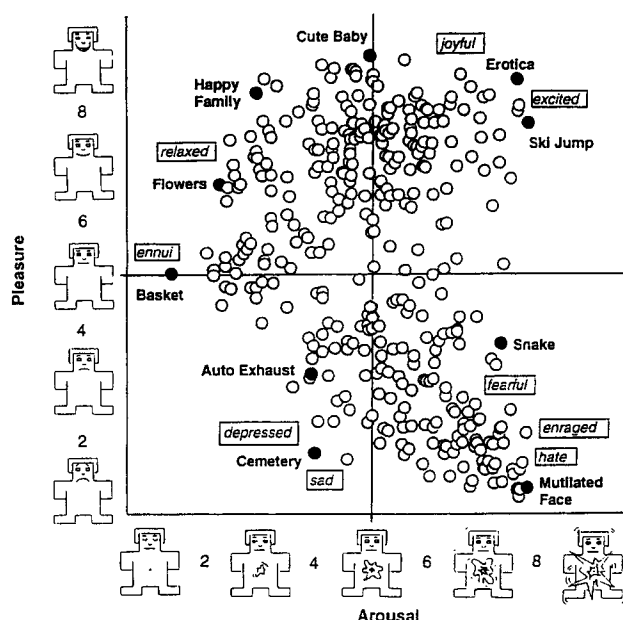
A representative sample of IAPS pictures, distributed in valence/arousal space, is presented in Figure 1. The locations of typical picture content are shown according to coordinates from the initial standardization study. To help orient the reader, the SAM locations of various emotional words noted are obtained from independent rating experiments. The overall boomerang shape of the picture mass (with its two arms seeming to extend from a common calm, no-affect base, towards either high arousal pleasant or high arousal unpleasant locations) is not inconsistent with an underlying bi-motivational organization. Despite efforts to fill its peripheral gaps, this form of the emotion-perceptual space has remained stable over several years of picture collection and research.

In studies of these picture stimuli, SAM-based self-evaluative judgments have shown good stability (Green-

Figure 1

Distribution of 360 Photographic Images From the International Affective Picture System (IAPS)

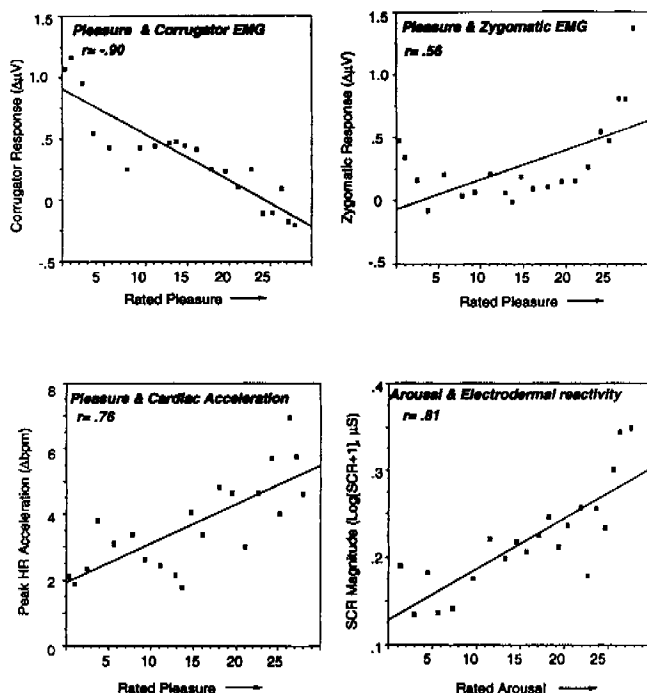
International Affective Picture System



Note. Images are organized in a two-dimensional space, defined by the judged dimensions of valence and arousal. Specific picture contents are indicated for the images denoted by filled circles. Standardization samples of approximately 100 individuals used the Self-Assessment Manikin (SAM; Lang, 1980) to make these judgments. In its paper-and-pencil version, SAM is a 9-point scale, with valence and arousal represented graphically by changes in a cartoon figure (© Peter Lang; see x,y axes above). SAM correlates highly with the semantic differential estimate of these same dimensions (Bradley & Lang, 1994). SAM ratings of various emotion words are located in the same space (see words in italics, in boxes).

Figure 2

Covariation of Affective Valence Judgments

**A Dimensional analysis of EXPRESSIVE PHYSIOLOGY:
Facial muscle, heart rate, and sweat gland activity**

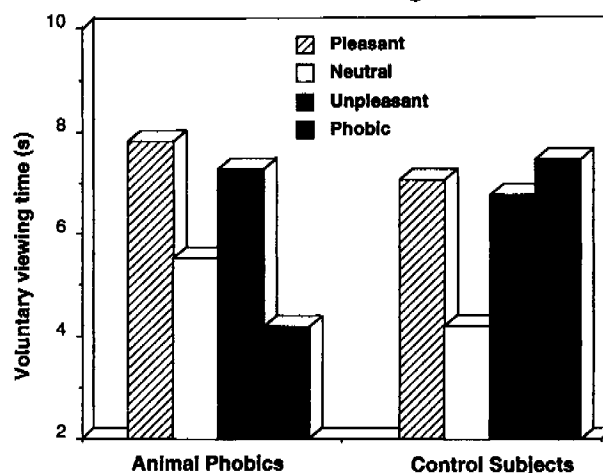
Note. Affective valence judgments covaried with slide response (upper left), zygomatic response (upper middle), peak heart rate acceleration (upper right), and covariation of arousal judgments with skin conductance response (SCR) magnitude (lower left). In each case, judgments are rank ordered for each individual; the graphs depict mean responses at each rank across individuals. (EMG = electromyograph; HR = heart rate; bpm = beats per minute (see Lang et al., 1993).

wald, Cook, & Lang, 1989; Lang, Greenwald, Bradley, & Hamm, 1993). There is little change in the distribution of values from initial standardization to retest in experiment, even with different methods of rating administration (e.g., paper-and-pencil form vs. subject-controlled computer graphic). Furthermore, physiological and overt behaviors in emotion (the other two elements in a three-systems analysis) are modulated in roughly parallel ways over picture contents. Thus, as can be seen in Figure 2, physiological events covary significantly with the parameters of valence and arousal, as defined by evaluative judgments: For a representative sample of IAPS pictures, mean facial muscle activity during viewing correlates strongly with subjects' mean valence ratings (ranked unpleasant to pleasant by picture). Heart rate shows a similar but more modest relationship. On the other hand, mean skin conductance covaries only with judged arousal, increasing monotonically over the stimulus range.

Performance behaviors relevant to emotional picture perception also covary with motivational parameters.

Thus, for example, when subjects discriminate newly presented from previously seen pictures, they key press more slowly to the more arousing images and also react more slowly to new unpleasant pictures than to new pleasant pictures. The valence difference in reaction time is not found, however, for previously viewed pictures. For "old" pictures, only arousal is pertinent, and this time the fastest reactions are to the more exciting images, whether pleasant or unpleasant (Bradley, Greenwald, Petry, & Lang, 1992). Furthermore, when normal subjects are placed in a free-viewing context (see "control subjects" in Figure 3), they tend to spend as much time looking at unpleasant as pleasant pictures. That is, as one might infer from the popularity of "slasher" movies, or the habitual slowing of traffic at a roadside accident, viewing time in normal subjects is correlated with arousal or intensity of evoked emotion rather than pleasantness. Studies of persons with specific fears, however, suggest that this does not follow if pictures evoke very high levels of distress. When phobics viewed pictures of their own phobic objects, a palpable reduction in viewing time was found, consistent with their general avoidant behavior pattern (see "animal phobics," Figure 3).

As the fear data implies, relationships between specific measures can vary widely for individuals and to some extent between particular groups. For example, pleasantness ratings covary more closely with facial muscle activity in females than in males; on the other hand, skin conductance changes are more closely correlated with arousal ratings in males than in females. Overall, however, the motivational variables predominate in organizing the picture perception data. Thus, a factor analysis of various

Figure 3Mean Duration of Free-Viewing for Four Picture Types
Picture viewing time

Note. Pictures included those judged to be (a) highly pleasant, (b) neutral in affect, (c) highly unpleasant by the standardization sample, and (d) consisting of snakes and spiders. Data are presented separately for normal control subjects and for snake and spider phobics (Hamm, Cuthbert, Globesich, & Vaitl, in press).

Table 1
Sorted Factor Loadings of Emotion Measures
on Principal Components

Measure	Factor 1: valence	Factor 2: arousal
Valence ratings	.86	-.00
Corrugator muscle	-. 85	.19
Peak heart rate	.79	-.14
Zygomatic muscle	.58	.29
Arousal ratings	.15	.83
Interest ratings	.45	.77
Viewing time	-.27	.76
Skin conductance	-.37	.74

Note. The factors having the highest loadings for each variable are highlighted in bold.

affect self-report, physiological, and behavioral measures resulted in a strong two-factor solution, with pleasantness ratings, heart rate, and facial muscles loading on one factor (valence) and arousal and interest ratings, viewing time, and skin conductance all loading highly on a second factor (arousal). The cross-loadings for all measures (see Table 1) are very low. Affects are built around motivational determinants.

Motive Systems in the Brain

As proposed at the outset, the structural foundation of these valence and arousal effects is in the brain's appetitive and aversive motive systems. These systems consist of neurophysiological circuits in the brain, largely subcortical,¹ that are primitively activated by primary reinforcement. The present discussion focuses on studies of the aversive system, in part because of its pertinence to psychopathology and in part because the relevant database for this system is larger and the results clearer.

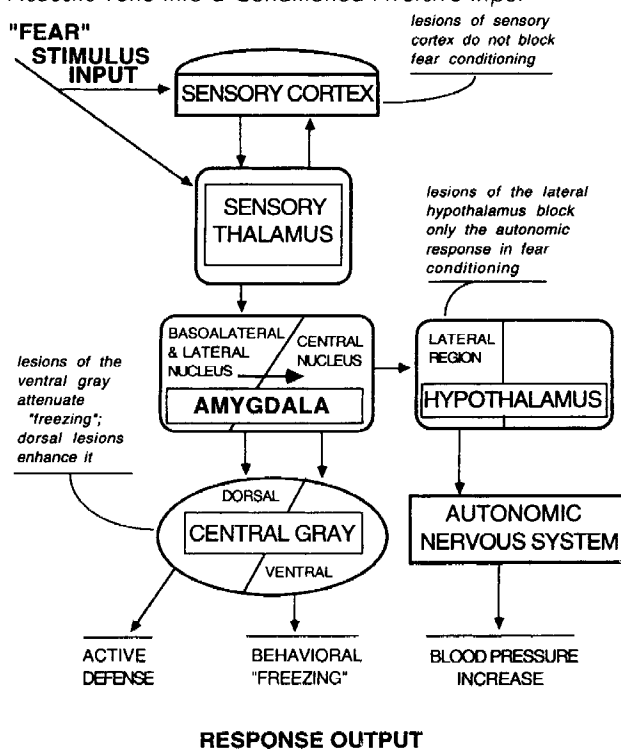
In the main, what is known about the brain's aversive system comes from animal research, particularly from studies of defense reactions and fear conditioning in the rat. In this species, as in man, massive defensive reactions (autonomic and behavioral) are readily evoked by painful stimuli (e.g., electric shock). If such stimuli reliably occur contiguous with or immediately following a previously innocuous stimulus (e.g., an auditory tone), features of the defensive behavior come to be evoked by the formerly innocuous stimulus, presented alone. That is, the new stimulus comes to activate a pattern of emotional responses we call fear.

Investigators are beginning to understand the neural basis of aversive reactivity and associated conditioning phenomenon. That is, using neurosurgical, pharmacological, and electrophysiological tools, the chain of probable neural activation can be traced, starting from the input end in the sensory system—proceeding through the necessary connecting structures, defining the links least prodigal in synaptic connections—to the autonomic and motor effectors. An adumbrated conditioned fear

circuit, with its efferent output paths, is presented in Figure 4.

Input normally passes from the sense organs to the sensory cortex, although simple sensory information (e.g., lights or tones) may require only thalamic processing (e.g., see the cortical lesioning studies of DiCara, Braun, & Pappas, 1970). From the sensory-specific nuclei of the thalamus the circuit proceeds to the amygdala—first to its lateral and basolateral then to its central nucleus (LeDoux, 1990). The bilateral amygdala, located within the temporal lobes of the brain, has long been known as a critical structure in the mediation of emotional expression (see the edited volume by Aggleton, 1992). That is, both stimulation and ablation of this site has reliably al-

Figure 4
Schematic Representation of a Part of the Neuronal Network Involved in the Transformation of an Insignificant Acoustic Tone Into a Conditioned Aversive Input



Note. The conditional stimulus is transmitted to the acoustic thalamus (through the auditory system and shell regions of the inferior colliculus [not shown]). The critical thalamic neurons are in the medial geniculate body of the nearby posterior intralaminar nucleus. "The lateral nucleus of the amygdala receives the acoustic signal from the thalamus and transmits to the central amygdala. Efferent to the amygdala the pathway bifurcates. Projections from the central amygdala to the lateral hypothalamic area mediate the autonomic conditioned emotional response, whereas projections to the mid-brain central gray region mediate the behavioral conditioned response" (LeDoux, 1990, p. 31). Details of the circuit through dorsal and ventral central gray are given by Fanselow et al. (1995).

¹ These circuits may also involve a lateralized cortical component (e.g., Davidson, 1993; Heller, 1993), although the specific, connecting neurophysiology has yet to be defined.

tered a variety of affective/motivational behaviors in both animals and man (e.g., Aggleton & Mishkin, 1986; Everitt & Robbins, 1992; Ursin, Jellestad, & Cabrera, 1981). Furthermore, some evidence suggests that the amygdala may have greater relevance for negative affect and aversion-driven than appetitive behaviors—particularly those controlled by secondary reinforcers (Cahill & McGaugh, 1990).

Efferent to the central amygdala, the aversion circuit branches, with each path apparently governing separate response outputs. Lesioning studies show that different somatic responses, such as “freezing” (immobility in the face of threat) and active fight or flight, and autonomically driven increases in blood pressure are mediated through different neural centers. The autonomic response is dependent on an intact pathway through the lateral hypothalamus (LeDoux, 1990), and the somatic components require an intact midbrain (periaqueductal) central gray area (Figure 4). Furthermore, the ventral central gray is the fear freezing path, whereas the dorsal gray is a critical part of the fight/flight action circuit (see the data and discussion of Fanselow, DeCola, De Oca, and Landeira-Fernandez, 1995, and Depaulis & Bandler, 1991).

It is reasonable to assume neural plasticity in these subcortical circuits. That is, although some subamygdaloid connections might be “hard wired,” the brain “learns” at many levels of its anatomy and functioning. Depending on variations in the built in and acquired weighting of these local pathways, considerable variety in the pattern of affective output could be expected. In fact, the amygdala has been implicated in many aversively motivated responses, that is, in escape and avoidance learning (Ursin, 1965); in defensive/aggressive behavior (Blanchard & Blanchard, 1977; Roldan, Alvarez-Pelaez, & Fernandez de Molina, 1974); and, as is examined in more detail later, in augmenting startle reactions (e.g., Davis, 1989). Furthermore, this same aversive system also prompts varied hormonal and autonomic responses. For example, Iwata and LeDoux (1988) noted that heart rate and blood pressure decrease in response to a conditioned tone (previously accompanied by shock) when animals are physically restrained; on the other hand, these same autonomic responses increase when the conditioned signal is presented to freely behaving animals. These data recall similarly diverse context effects in humans, who show heart rate acceleration while imaging or thinking about unpleasant events (e.g., Vrana & Lang, 1990) but show significant deceleration when shown unpleasant pictures (e.g., Lang et al., 1993).

Overall, the neurophysiological findings suggest that the amygdala is a general mediator of defensive behaviors, for example, a key site in a general aversive motivational system. Structures downstream from the amygdala are implicated in the different forms of defense. Although context dictates that these autonomic and somatic patterns have great variety, they can be functionally organized into two general classes: (a) defensive action, (i.e., contextual variations in fight/flight that are more or less direct responses to nociception or imminent attack) and (b) de-

fensive immobility (i.e., freezing and hypervigilance in which the organism is passive but “primed” to respond to aversive stimulation).

Motivational Priming

Scientists and laypeople agree that the emotions loom large in life. They have, of course, significance as states in themselves, with their own surgent response patterns. In addition, they are held to play an important modulatory role on other behaviors—coloring, inhibiting, or energizing thought, perception, and action—often in contexts that are physically and semantically remote from the apparent source of the controlling affect. It is proposed here that this ubiquitous spread of affection across the behavioral repertory is motivationally mediated.

Emotions reflect the engagement of neural structures and pathways in either the appetitive or aversive motivation systems (e.g., as discussed above). During the period when this subcortical circuitry is active, a modulatory effect is exerted on the brain's other processing operations. Specifically, associations, representations, and action programs that are linked to the engaged motivational system have a higher probability of access (with a concomitantly greater potential output strength) than other information, and conversely, mental events and programs linked to the nonengaged system have a reduced probability and strength of activation. Thus, in the case of an aversively motivated organism (i.e., the affective state is unpleasant), responses to other aversive cues are primed, and at the same time responses to appetitive cues may be reduced or absent. As an example, recent findings (Blaney, 1986; Bower, 1981) suggesting that negative or positive affective moods occasion emotionally congruent verbal associations and memories might be construed to be a result of such motivational priming.

The most primitive and fundamental motivational priming is, however, at the level of unconditioned exteroceptive reflexes. Recall that reflexes can be sorted (Konorski, 1967) according to the primary reinforcement properties of their unconditioned stimuli, either appetitive or aversive, and the consummatory or defensive function of reflex itself. In the priming view, responses to unconditioned stimuli are modulated according to two factors: (a) the classification of the reflex (appetitive or defensive) and (b) the affective valence of the individual's ongoing emotional state. Thus, an independently evoked defensive reflex will be augmented when the organism is already reacting to an aversive foreground stimulus (i.e., is in an unpleasant state); this same reflex will be reduced in amplitude when the organism is processing an appetitive foreground. Finally, both these priming effects—potentiation and diminution of responding—are expected to be enhanced according to the level of affective drive or activation.

Startle Potentiation

In most mammals, any abrupt sensory event will prompt a chained series of rapid flexor movements that can cas-

cade throughout the body (Landis & Hunt, 1939). This startle response appears to be a primitive defensive reflex that serves a protective function, avoiding organ injury (as in the eyeblink) and acting as a behavioral interrupt (Graham, 1979) that clears processors to deal with possible threat.

According to the priming hypothesis, the defensive startle reflex should be considerably faster and of significantly greater amplitude when the aversive motivational system is already active, for example, as in a fear state. This was first examined systematically by Brown, Kalish, and Farber (1951), who compared reflex responses with startle probes (shots from a toy pistol) presented to male rats during neutral or shock conditioned stimuli at extinction. Results conformed to expectation: Animals did indeed react more forcefully—as measured by a stabilimeter in the floor of the cage—when the startle stimuli were presented during fear-conditioned signals (see also Ross, 1961; Spence & Runquist, 1958).

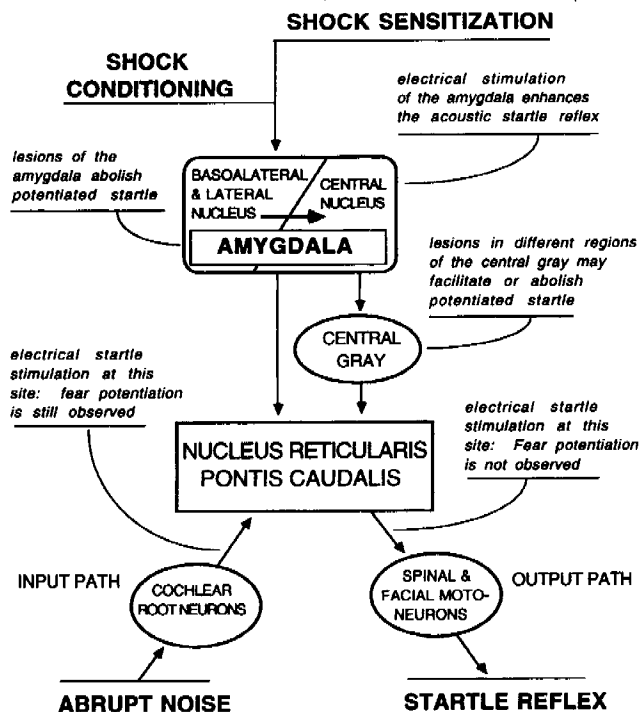
The Rat Brain's Fear-Startle Circuit

Davis and his associates (e.g., Davis, 1989; Davis, Hitchcock, & Rosen, 1987; Lee et al., 1994) and others (Fendt, Koch, & Schnitzler, 1994a) have since gathered considerable evidence that the brain structure mediating fear-conditioned startle potentiation is, at least in the rat, the same aversive system that was previously described. A diagram of the relevant neural paths is presented in Figure 5: Beginning with stimulation of the ear by an acoustic probe (e.g., abrupt noise), the afferent path of the startle reflex proceeds from the cochlear root neurons to the reticular nucleus; efferent connections pass from there through spinal neurons to the reflex effectors. This is the basic obligatory circuit, directly driven by the parameters of the input stimulus (e.g., stimulus intensity, frequency, and steepness of the onset ramp).

The phenomenon of conditioned startle potentiation implies, however, a secondary circuit that modulates this primary reflex pathway. There is now overwhelming evidence that the amygdala, the key structure in aversively motivated behavior, is a critical part of this modulatory circuit. It has been shown that, first, there are direct, monosynaptic projections from the amygdala to the key reticular site, that is, to the structure in the basic circuit on which modulation of the reflex depends; second, electrical stimulation of the amygdala (below the level for kindling) directly enhances startle reflex amplitude; and finally, and most significant, lesions of the amygdala abolish fear-conditioned startle potentiation.

It is important to note that startle potentiation is correlated with freezing behavior in the rat. Thus, for example, foot shocks presented in a destructive environment will prompt both freezing (Blanchard, Fukunaga, & Blanchard, 1976) and potentiated startle (Davis, 1989). Passive freezing (Fanselow et al., 1992), and perhaps potentiated startle as well (Fendt, Koch, & Schnitzler, 1994b), are disrupted by lesions in the ventral periaqueductal gray (Fanselow et al., 1994). Fear potentiated startle, on the other hand, a reflex action, is more likely

Figure 5
Schematic Representation of the Primary Neural Path Between a Startle Stimulus Input and Its Effector Output



Note. Locations along this path are shown where stimulation with microelectrodes will, or will not, produce a potentiated startle response. This procedure isolated the neuronal structure (nucleus reticularis pontis caudalis) where the modulating influence of previous aversive learning impacts on the obligatory startle circuit. The central nucleus of the amygdala (the same central structure as in LeDoux's, 1990, description of an aversive learning network) projects directly to this reticular site, and through the central gray. The fact that lesioning of the amygdala blocks potentiation, and stimulation with microelectrodes potentiates the reflex (in the absence of prior fear conditioning), prompts the conclusion that this structure is a primary component of the aversive motivational system (see Davis, 1986, 1989, in press, for an overview of the neurophysiology).

to be disrupted by lesions in the dorsal pathways (e.g., Fendt, Koch, & Schnitzler, 1994b). Interestingly, when the grosser defense responses (fight or flight) are engaged they appear to activate the dorsal central gray (Fanselow et al., 1992) and interfere with the expected increase in potentiated startle. In fact, lesions of the dorsal central gray can restore potentiated startle in some circumstances (D. Walker & M. Davis, personal communication, March, 1995).

Human Conditioning and the Blink Response

Fear conditioning can be demonstrated in humans, of course, using a visual stimulus-shock paradigm similar to that used in studies of the rat. Furthermore, the phenomenon of startle reflex potentiation can also be addressed in humans, although the methodology for recording the response is somewhat different. As already noted, the whole-body startle reaction is typically re-

corded in animal studies. In research with humans, investigators usually measure only the eyeblink.

Rapid eye closure is one of the first and most reliable components of the behavioral cascade that constitutes the startle reflex. Occurring 30 to 40 milliseconds after stimulus onset, it reflects an abrupt increase in tension in orbicularis oculi—the facial muscle that surrounds the eye. The latency and magnitude of the blink can be measured by monitoring this muscle, using miniature electrodes placed just beneath the lower lid.

In studies with humans, the stimulus used to evoke the blink is relatively modest—typically a 50-millisecond burst of white noise at around 95 decibels, which, although it prompts a clear blink response, rarely interferes with ongoing foreground tasks. Several researchers have confirmed potentiation of the blink response in human aversive sensitization or conditioning that parallels startle studies of the rat (Greenwald, Bradley, Cuthbert, & Lang, 1991; Hamm, Greenwald, Bradley, & Lang, 1993). In brief, the blink muscle response to a startle probe is generally larger after subjects experience electric shock and selectively larger to startle probes presented during exposure to a shock conditioned stimulus than to probes presented during exposure to an unshocked control stimulus. These results, coupled with human neurological evidence linking the amygdala to aversive emotion (e.g., Morris, Bradley, Bowers, Lang, & Heilman, 1991), encourage the hypothesis that similar neural pathways might be responsible for potentiation effects in both rats and humans. In addition, the data suggest that the startle probe methodology might be a valuable tool for assessing the basic view presented here; that is, the aversive and appetitive motivational systems play a fundamental role in organizing human emotional expression.

Probing Emotional Perception

It is proposed that the startle reflex is differentially modulated depending on an individual's ongoing emotional state. More specifically, the amplitudes of blinks evoked by startle probes will vary with the valence of the affective state prompted by a foreground percept. In an unpleasant stimulus foreground the brain is processing negative affective information; the relevant subcortical, aversive system circuitry is contacted; and a defensive reflex is augmented. Appetitive and aversive/defensive dispositions are considered to be opponent states. That is, the active disposition (appetitive or aversive) controls the output processors, and affectively nonconcordant reflexes will not be potentiated and could actually be inhibited. Thus, when appetitive information is the focus of processing, the startle reflex is expected to show relative diminution.

Direct tests of this hypothesis have used stimuli from the IAPS (Center for the Study of Emotion and Attention, 1994), selected on the basis of normative affective ratings and organized into three affective classes—unpleasant (e.g., poisonous snakes, aimed guns, and pictures of violent death), pleasant (e.g., happy babies, appetizing food, and attractive nudes), and neutral (e.g., umbrellas, hair dryers, and other common household objects). Picture viewing is, of course,

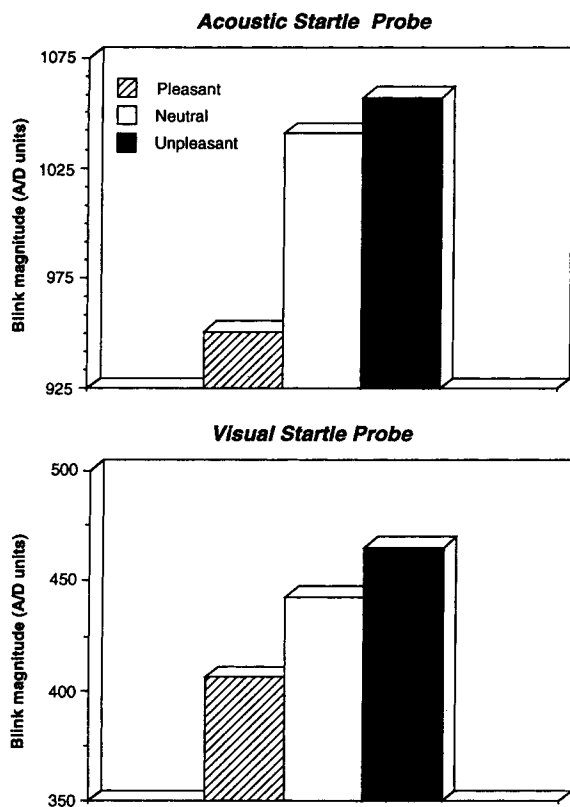
a passive vigilance task in which—like a freezing rat or an attentive predator—viewers are generally immobile. When startle probes are administered in this context, results have consistently conformed to the motivational priming hypothesis: A significant linear trend is reliably observed over judged picture valence, indicating that the largest startle blink responses occur during unpleasant content and the smallest during pleasant pictures (see Bradley, Cuthbert, & Lang, 1990; Greenwald, Bradley, Cuthbert & Lang, 1990; Vrana, Spence, & Lang, 1988).

Bradley, Cuthbert, and Lang (1991, in press) found this affect–reflex effect using monaural rather than binaural acoustic probes and furthermore obtained evidence that the effect may be lateralized (i.e., left ear probes, presumably conferring an advantage in right brain processing, showed the strongest relationship with affective valence). Jansen and Fridja (1994), using evocative video film clips, and Hamm, Stark, and Vaitl (1990), using IAPS slides, obtained the affect–startle effect in European research participants. Finally, Bradley et al. (1990) found the same pattern of affective modulation using both visual and acoustic startle probes (see Figure 6), disconfirming an alternative hypothesis that affective modulation is secondary to differences in modality-directed attention (Anthony & Graham, 1985).

More recent results have further extended and clarified this phenomenon. On the one hand, it has been shown that over many presentation trials of the same picture stimuli, despite a marked general habituation of the startle reflex itself, affective potentiation and inhibition persist (Bradley, Lang, & Cuthbert, 1993). On the other hand, it is now apparent that the general affect–startle effect is more pronounced in the context of more arousing stimuli. Cuthbert, Bradley, and Lang (in press) showed that when unpleasant slides are rated highest in arousal, both skin conductance and probe startle potentiation are greatest. Similarly, as pleasant pictures are judged to be more arousing, skin conductance (indexing sympathetic activation) increases, as for unpleasant pictures. For startle magnitude, however, increasing arousal of a pleasant foreground prompts an opposite effect—greater reflex inhibition. This result is consistent with the motivational priming hypothesis proposed earlier. Arousal does not have an independent, unitary effect on behavior: Modulation of the defensive reflex increases with activation, but the direction of effect is different, depending on the motivational system (appetitive or aversive) engaged.

Other data support the hypothesis that the modulatory pattern described here is specific to defense-type reflexes. For example, a T-reflex probe (activation of the soleus muscle in the leg with a tap to the Achilles tendon) does not prompt a differential modulation by picture valence. Instead, for this neutral posture reflex, a simple arousal effect is observed, with larger responses to both arousing pleasant and unpleasant stimuli relative to the calmer judged neutral content (Bonnet, Bradley, Lang, & Requin, in press). Furthermore, it appears that responses indexing the brain's attentional system—that are not motivationally specific—also do not show modulation according to affect system. Thus, the P300 component of the cortical event-related potential,

Figure 6
Mean Blink Reflex Magnitudes to Acoustic and Visual Startle Probes



Note. Reflex magnitudes are to acoustic (top panel) and visual (bottom panel) startle probes presented during viewing of pleasant, neutral, and unpleasant pictorial slides (Bradley, Cuthbert, & Lang, 1990). (Both the acoustic and visual startle probes resulted in blink magnitudes with similar linear patterns over valence categories [pleasant < neutral < unpleasant]. A/D = analog-to-digital conversion). Adapted from "Emotion, Attention, and the Startle Reflex" by P. J. Lang, M. M. Bradley, and B. N. Cuthbert, 1990, *Psychological Review*, 97, p. 384. Copyright 1990 by the American Psychological Association.

recorded in response to startle probes, shows only an arousal effect, that is, a larger wave form during interesting, affective stimuli than during neutral pictures (Schupp, Cuthbert, Bradley, Lang, & Birbaumer, 1993).

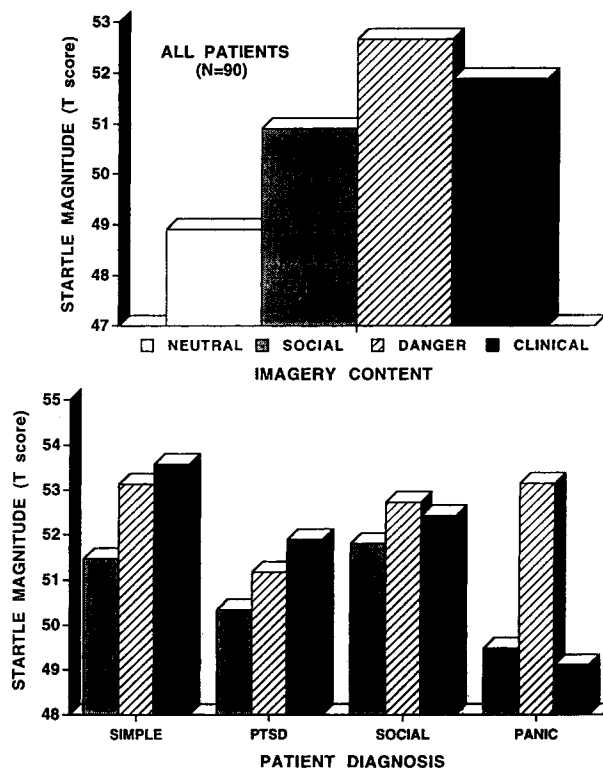
Individual Differences and Psychopathology

The affect–startle effect has an impressive ubiquity. A recent study by Balaban (1995) even found it in five-month-old infants, whose blink responses to startle probes were larger when viewing pictures of angry than when viewing happy faces. An interesting failure to observe the phenomenon, however, occurred in a picture study of incarcerated prisoners (Patrick, Bradley, & Lang, 1993). Whereas inmates without psychiatric diagnoses responded as did college students, psychopathic prisoners failed to show startle reflex potentiation when viewing unpleasant

pictures. Psychopaths did not differ from students or other prisoners in their affective ratings of these pictures, judging them to be arousing and unpleasant. Such response discordance is consistent with the psychopathic diagnosis. In fact, a further analysis of the data showed that the potentiation deficit was not related to criminality per se but was observed specifically in prisoners who, at interview, showed the characteristic emotional indifference and lack of remorse of the classic psychopath (Cleckley, 1976).

As would be predicted, phobic individuals exhibit greater startle potentiation while viewing pictures of their own phobic objects than do nonphobic individuals viewing these or other unpleasant pictures (Hamm, Cuthbert, Globisch, & Vaitl, in press). It does not appear to be the case, however, that all anxiety states show the same pattern of reflex response. Greater potentiation appears to occur most reliably with fears of specific external pain or harm.

Figure 7
Imagery and Startle Probe Magnitude



Note. As part of an initial assessment for treatment, four groups of anxiety patients (overall $N = 90$) were instructed to image the content of specific sentences, involving either routine and affectively neutral events, anxiety evoking social situations (an embarrassing act, a speech performance), situations involving threat of danger (an auto accident or a night time intruder), or situations directly relevant to their specific clinical problem. All patients showed larger startle reflexes to probes presented during fear than during neutral sentence imagery. Overall mean probe startle reflex magnitudes to the different fear imagery contents are shown in the upper part of the figure. Reflex means for the subgroups—simple phobia, post-traumatic stress disorder (PTSD), social phobia, and panic disorder—are shown in the lower part of the figure.

Figure 7 shows the blink reflex responses of four types of psychiatric patients, each group with a different anxiety diagnosis. Probe startle stimuli were presented while the patients imaged neutral scenes and three types of specific fear scenes: (a) events involving their own specific clinical concern, (b) events that would be dangerous or painful experiences for anyone (e.g., a night intruder when home alone or an automobile accident), and (c) events that involved a difficult or embarrassing social performance. Overall, the patients' startle reflexes during fear imagery were largest for scenes that involved potential physical danger and smallest during scenes of social distress. For both social phobics and panic patients, probe responses during the danger scenes exceeded responses during scenes of clinical concern.

These results support the hypothesis that startle potentiation reflects aversive system engagement, that is, subcortical structures related to harm avoidance, which in the rat are activated by primary unconditioned reinforcers, such as electric shock, and by their associated conditioned stimuli. It is not unexpected that simple phobics and post-traumatic stress disorder patients would show large reactions to their own clinical scenes (even larger than to the standard danger scenes). For these phobia and trauma diagnoses, the clinical scene is about a more imminent concern, and (unrealistic though it may be) it is also about physical pain and danger (e.g., threatening animals, falling, blood and injury, assault, rape, or combat). Conversely, social anxieties and the often vague worries and uncertainties found in many panic patients may be more consistent with inhibitory states, as described by Gray (1985), and less an expression of active, goal-specific escape and avoidance motivation. These data suggest that the startle paradigm may prove to be of considerable value in sharpening diagnosis of anxiety states and in relating psychopathology to functional brain activity.

Conclusions

Research Paths and Detours

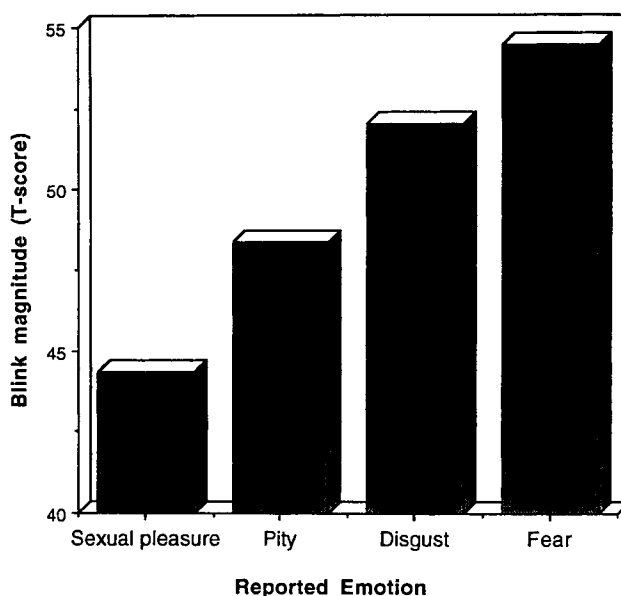
The reader has certainly already discerned the limitations of the model of emotion presented here. For example, the focus has been on action dispositions—on what William James (1894) called the “coarse” affects. This article has not considered more subtle “feelings” or the general factors that block or delay action and thus create the dispositional set. Clearly, the latter factors are of great variety and determine the emotions' varied tactical shapes. They include immediate external factors, for example, the size of an aggressor may be of importance in determining whether an aversive affect is fear (implicit flight) or anger (attack), as well as internal factors that go beyond the current discourse, such as health, biological temperament, and learning.

Dual motives. A further complication may arise when a stimulus context simultaneously activates both motive systems. I have suggested that the appetitive (approach) and aversive (withdrawal) systems compete for

the brain's output processors. However, a stimulus configuration can be multidimensional and doubly evocative. In this case, a conflict theory is assumed (of the sort proposed many years ago by Neal Miller [1944]) in which the behavioral resolution is determined by the relative strength (activation level) of each motive state.

Certain affects, indeed, seem to intrinsically involve dual motivation. In Figure 8 probe startle reactions are shown to picture stimuli that have been rated by an independent sample on separate scales for 10 experienced emotions. For pictures receiving the highest relative score on sexual pleasure (e.g., an attractive, seminude couple), the reflex was smallest, as expected; conversely, both disgust and fear evoked larger responses, with dominantly fearful stimuli showing the strongest reaction of all these picture categories (see also Balaban & Taussig, 1994). In this example, the pictures receiving the highest rating for pity actually exceeded fear pictures in arousal (6.8 vs. 5.7) and were judged lower in pleasure (1.9 vs. 3.6); nevertheless, they showed less probe potentiation (see Figure 8). Interestingly, the pity pictures (e.g., pictures of babies undergoing extreme medical treatments or starving people) were also rated high in nurturance—an approach disposition to help and care for others. The relative startle attenuation observed for pity pictures might represent the algebraic sum of opponent motives, appetitive and

Figure 8
Mean Blink Reflex Magnitudes to Startle Probes
Reported feelings and startle reflexes



Note. Mean blink reflex magnitudes to startle probes presented while individuals viewed pictures that evoked feelings of sexual pleasure, pity, disgust, and fear. Participants rated a large sample of pictures on a group of basic emotion scales. The mean reflex values shown here are for pictures that received consistently high ratings for a specific affect (3–9 pictures per emotion).

aversive—a phenomenon that could be obscured by bipolar affective judgments.

Anticipation, alarm, and helplessness. The dispositional nature of affects imposes another limitation on startle analysis. Recall that potentiated startle in the animal model is found most reliably in fearful, immobile individuals, not in individuals actively avoiding or escaping. The view presented here is similar to that of Masterson and Crawford (1982). They hypothesized a “defense motivation system” in animals that “selectively potentiates or primes a set of innate reactions that include fleeing, freezing, fighting and defensive burying” (p. 664). They conceived the human experiences of fear, anger, anxiety, and apprehension to be evolved expressions of this system. Furthermore, these authors made an important distinction between priming of the defense motivation system and its behavioral sequelae—the “alarm reaction.” When the organism has been defensively disposed, related reflexes are pre-set: “An excited defense response is like a cocked pistol ready to be triggered by supporting stimuli” (p. 664). It is important to note, however, that the “alarm reaction” is not part of this preparatory set. It is a possible sequela of overt action—fight or flight—for which the organism has been mobilized. As noted by Lang, Bradley, and Cuthbert (1990), startle potentiation is to be observed during this first, “cocked pistol,” stage. After the alarm stage has been triggered and the organism swings into action—actively coping or in headlong panic—the harm-anticipatory defense system is overwhelmed. Part of potentiated startle’s neural path is preempted by action,² and blinks no longer reflect affective subtleties.

A further constraint on the affect–startle effect involves states of the organism characterized by somatic or autonomic inhibition. For example, startle potentiation is attenuated by anxiolytic drugs in both animals (Davis, 1986) and humans (Patrick, Berthot, & Moore, 1993). Interestingly, whereas a moderate amount of alcohol reduces overall startle amplitude, it does not prevent emotional modulation (Stritzke, Patrick, & Lang, 1995). Also, startle analysis might not inform, if the individual’s psychological state precluded attention and action. This may be true for affects such as depression. In animals, long periods of punishment can produce “learned helplessness” (Seligman, 1975). The organism is no longer disposed to act—depleted by a persistent stressful context that permits no behavioral recourse. This may also characterize states in which important positive reinforcers have been irrevocably removed, as in grief after great personal loss.³ In these cases, a state of high negative valence exists, but active scanning of the environment is absent. In this circumstance there may be a reduction in reflex response and little evidence of startle modulation.

Stop! Look! Listen!

As the above suggests, affective startle modulation occurs most reliably during states of vigilance, when the organism is stopped but actively orienting. Picture viewing is quintessentially such an orienting task, characterized by

modality and directional tuning of perceptual processors, motor inhibition, and reduced cardiac effort.⁴ According to Sokolov’s (1963) classic analysis, perceptual processing is activated by any change in stimulus input. Thus, each picture presentation should prompt phasic orienting, varying in strength, dependent on stimulus parameters.

Basing his view on studies of simple shocks, tones, and noise, Sokolov (1963) emphasized changes that occur with an increase in physical intensity. In his view, as the loudness of an input augments, orienting first increases and then gives way to a new reaction, the defense response—at first on only some trials and then as a consistent reaction to stimulation. Defense responses reflect a suspension of processing—input rejection—and augur active escape. High auditory intensity is, of course, both aversive and arousing. If one applies the Sokolovian model to startle probe data gathered during emotional pictures, and assumes that intensity and judged arousal are analogous parameters, there are striking parallels.

Frances Graham and others (e.g., Anthony & Graham 1985, Simons & Zelson, 1985) hold that probe startle inhibition indexes attention (i.e., interesting foregrounds use attentional resources thus less are available for probe processing, resulting in reflex inhibition). As can be seen in Figure 9, as pleasant pictures are judged more arousing (and interesting) inhibition does increase. Furthermore, unpleasant stimuli appear to show a similar coincidence of increased picture arousal and startle inhibition—at least in the mid-range. As with Sokolov’s (1963) defense response, however, this effect is reversed for unpleasant stimuli that are farther along the arousal continuum. Indeed, at a certain point, a monotonic increase in startle potentiation is observed.

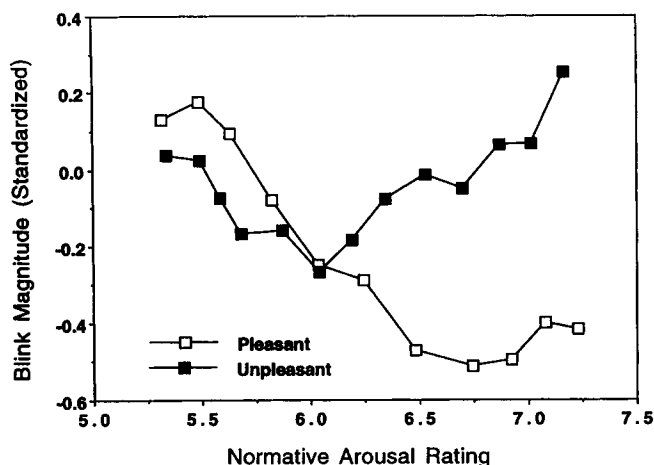
These findings highlight important theoretical issues and signal important directions for research. First, researchers need to know much more about the covariation, and possible interactions, of the various measures of ori-

² Potentiated startle may compete with larger, somatically mediated actions for the pathway from the amygdala through the dorsal central gray area, suggested by lesion studies (M. Davis, personal communication, October 28, 1994).

³ Weiss (1989) has suggested that the inactivity that characterizes depression may be a consequence of norepinephrine depletion in patients with this diagnosis.

⁴ “People look at photographs because it is pleasant and interesting to do so. . . . Observers are invited to attend to such stimuli, but it is generally understood that most instrumental behavior is to be inhibited (or closely regulated) according to learned aesthetic rules. In lay terms, perception occurs across an aesthetic distance, defined by the ‘artistic frame of reference . . . around the work . . . to differentiate it psychologically from reality’” (Gove, 1986, p. 34). “Nevertheless, pictorial information can match the stimulus properties of real object or event referents, activating cognitive representations associated with strong emotional responses. Affective processing, in turn, triggers facial action and visceral motility similar in pattern to that engaged by the veritable stimuli, which can closely parallel evaluations of affective meaning. Because the individual’s aesthetic set generally assures that overt actions (e.g., flight or aggression) are gated out of emotional response programs, residual affective behaviors in the aesthetic context are those related to initiation and choice—assuming that selection of stimuli is freely available—and the active maintenance or termination of stimulus input” (Lang, Greenwald, Bradley, & Hamm, 1993, p. 262).

Figure 9
Changes in Probe Startle Magnitude



Note. The figure shows changes in probe startle magnitude separately for pleasant and unpleasant pictures, as pictures are judged to increase in arousal (IAPS normative valence and arousal ratings). From 38 to 47 subjects contribute to each data point, due to rejected trials and the fact that subjects were not startled during all slides. For clarity, the data were smoothed prior to graphing with a five-point moving average (Rafferty & Norling, 1989).

enting and defense (e.g., as defined by Lacey, 1959; Sokolov, 1963). For example, long after the point on the arousal continuum where defensive startle potentiation begins, heart rate continues to show the decelerative response associated with orienting (Graham & Clifton, 1966). Furthermore, it is now increasingly important to develop a good neurophysiological model of the brain's appetitive system and determine what pathways prompt startle inhibition and how they relate to basic attentional mechanisms. Is the mechanism of inhibition in attention the same as the hypothesized reduction by appetitive motivation? That is as yet unknown (e.g., see Swerdlow, Caine, Braff, & Geyer, 1992, p. 186).

Finally, it is important to know if the phenomena seen in picture viewing can be as consistently observed with other modalities of emotional stimulus presentation. Researchers need to know more about responses to moving pictures, emotional sounds and cries (Bradley, Zack, & Lang, 1994), and reactions when reading narrative text (Spence, Fischler, & Lang, 1994). There are already indications (Bradley, Lang, & Cuthbert, 1991) that reflex modulation may not be the same in memory imagery as in perception. More practically, one can ask what are the implications of this method for emotion evocation and control in clinical treatment and for understanding the social-developmental effects of media?

This is a rich terrain for investigation that offers a plethora of exciting paths to follow. Happily, thanks to many current and past scholars, researchers have a robust theoretical conception, a good neuroscience foundation, and a functional animal model to guide a mapping of the

area. Furthermore, the demonstrated replicability of the basic human research findings, within and across laboratories, encourages the belief that we in the emotion world have at last reached a kind of terra firma. Mindful that the complexities are great and that discoveries often confound cherished preconceptions, we are eager to carry forward this search for new solutions to the old mysteries of human feeling.

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