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Appetitive and Defensive Motivation: Goal-Directed or Goal-Determined?

Peter J. Lang
Margaret M. Bradley
Center for the Study of Emotion and Attention, University of Florida, USA

Abstract

Our view is that fundamental appetitive and defensive motivation systems evolved to mediate a complex array of adaptive behaviors that support the organism's drive to survive—defending against threat and securing resources. Activation of these motive systems engages processes that facilitate attention allocation, information intake, sympathetic arousal, and, depending on context, will prompt tactical actions that can be directed either toward or away from the strategic goal, whether defensively or appetitively determined. Research from our laboratory that measures autonomic, central, and somatic reactions when processing emotional scenes is described which indicates that motivationally relevant cues, whether appetitive or defensive, capture attention preferentially, prompt enhanced perceptual processing and information gathering, and occasion metabolic arousal that mobilizes the organism for coping actions.

Keywords
attention, emotion, motivation

As with many familiar concepts in psychology, the terms "approach" and "avoidance" are used to describe a variety of different phenomena, including: (a) basic directional (often spinal) reflexes (e.g., withdrawal from heat or pain; Grau et al., 2006); (b) interindividual personality/temperament variations (e.g., the stable tendency for an individual to approach or avoid [usually novel] objects; Jones & Gosling, 2006; Larson & Augustine, 2006); (c) directional high-level aims that organize behavior (e.g., seeking promotion, avoiding firing; Thrash & Hurst, 2006); and perhaps most broadly, (d) as directional actions (approach, avoid) that define pleasant and unpleasant affect in humans. It is the latter sense that we address here, proposing that, while behavioral direction may be a defining feature of motivation in simpler organisms, it no longer defines motivational states in humans, for whom specific actions towards (approach) or away from (avoidance) are functional in both appetitive and defensive contexts. Rather than inducing distinctly different behaviors, activation of appetitive and defensive motivation systems induces similar heightened attention and arousal in the service of selecting an appropriate action, whether towards or away from the eliciting cue.

Schneirla (1959) initially noted that, in aplysia, bidirectional actions of approach and withdrawal typify the basic behavioral repertoire supporting survival, with approach associated with action towards stimuli necessary for life, and withdrawal with action away from stimuli that threaten life. It is a truism that more complex organisms, however, survive as individuals and species because a vast repertoire of coping behaviors has evolved from these simple directional actions to defend life and permit its propagation. In the mammalian species, both appetitive and defensive cues call forth a broad range of coping behaviors in which sheer direction (towards or away) of action no longer defines the motivational context.

Rodents, for example, may respond to a perceived threat by active avoidance; or show directionless "freezing"; or, depending on the encounter context, aggressively approach a conspecific (Blanchard & Blanchard, 1989). A wide range of other behavioral options in both mammals and reptiles include defense displays, vocal responses, and alterations in size, shape, or expression that serve the adaptive function of defending against a threat and have no clear directional definition. In appetitive contexts, a similar range of potential actions may be found, depending upon the utility of a specific action. For instance, the predator also often initially freezes, facilitating perception of a distant prey, and the resulting behavior may include strategic withdrawal prior to eventual attack and capture. As in the animal kingdom, so it is for humans—specific

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Corresponding author: Margaret M. Bradley, Center for the Study of Emotion and Attention, University of Florida, PO Box 112766, Gainesville, FL 32611, USA.
Email: bradley@ufl.edu

behaviors in appetitive and defensive contexts are myriad in their variation and not uniform in their direction.

Research suggests that the foundation of response adaptability and diversity is in limbic circuits deep in the cortex and subcortex of the brain that are similar across mammalian species (e.g., Lang & Davis, 2006), and have evolved to initiate and orchestrate the varied processes and actions determined by a primary goal of survival. Although appetitive motivation is active in contexts that promote sustenance (obtaining rewards, water, nutrients, shelter, sexual partners, nurturing the young) and defensive motivation in contexts that threaten life (attack, illness, injury etc.), specific processes of perceptual enhancement, attention allocation, and preparation for action are of general utility in both appetitive and defensive contexts, leading to considerable overlap in the processes and neural structures active in these affective contexts and which are independent of directional differences in behavior.

Motivational Activation

For humans and other animals, the first reaction to a novel cue is a reflexive orientation to the stimulus (Pavlov, 1927) that includes both behavioral and physiological indices of heightened attention and information intake. If the input is motivationally irrelevant, this "orienting reflex" rapidly habituates (Sokolov, 1963). Both appetitive and aversive cues, however, prompt sustained orienting responses that extend perceptual processing and facilitate action selection. For example, an animal orienting to the appearance of a distant predator shows a profound deceleration in heart rate (Campbell, Wood, & McBride, 1997), together with "freezing"—a statue-like inhibition of movement—both of which support increased overall sensory acuity. If the predator approaches, somatic and autonomic activation increases progressively, culminating in defensive action of fight or flight. Interestingly, a similar cascade occurs for the predator: Upon observing potential prey, the predator is likely to freeze, orient, and determine the precise spatial location and nature of potential obstacles before efferent mobilization and a change to goal-directed capture.

Humans also show enhanced attention and action readiness when confronted with appetitive and aversive cues (in life, and in the laboratory) even when the cues are not substantive, but media representations. For example, we have studied pictures that depict a wide variety of the pleasant and unpleasant events encountered in the world, and measured the body's reflex reactions and brain-based activity (e.g., Bradley & Lang, 2007; Lang & Bradley, 2010). The findings indicate that orienting and arousal are similarly enhanced when participants view either appetitive or aversive pictures. A late positive potential measured over centro-parietal sensors is reliably enhanced when viewing either pleasant or unpleasant pictures rated as highly arousing (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000). When explored using a secondary acoustic probe—brief noise bursts presented during the viewing intervals—the evoked probe response in the electroencephalogram (EEG; the P3 component of the event-related potential) is reduced in amplitude when attention is directed to an arousing image. Coincidentally, probe reaction times are also slower when viewing emotionally arousing pictures, suggestive of enhanced attention and orienting (Bradley, Cuthbert, & Lang, 1999).

Interestingly, a secondary startle probe also prompts a reflex that includes the rapid eyeblink. If the picture content is pleasantly arousing (e.g., erotic/romantic content) the reflex is markedly reduced. When viewing arousing unpleasant pictures, in contrast, the same probe elicits a dramatic increase in the startle reaction—a potentiated response that increases as the picture becomes more fearful and threatening, reflecting the startle reflex's evolutionary origins as a defense response (Lang, Bradley, & Cuthbert, 1997). Thus, probe reflexes provide an index of activation of appetitive or defensive motivation: Blinks are potentiated when viewing unpleasant pictures and inhibited when viewing pleasant pictures (e.g., Vrana, Spence, & Lang, 1988).

In addition, measures of general sympathetic activation (e.g., Wallin, 1981), skin conductance, and pupil dilation, evidence increased metabolic load and sensory adaptation (e.g., Janisse, 1977) when viewing either arousing pleasant or arousing unpleasant scenes (Bradley, Miccoli, Escrig, & Lang, 2008), and these physiologically arousing pictures are well encoded and retained, showing superior recall both immediately postexposure and even a year later (Bradley, Greenwald, Petry, & Lang, 1992). Taken together, the motivational states elicited by affective pictures (and the cortical and autonomic substrata underlying their perception) appear to be fundamentally similar to those occurring when other complex animals "stop, look, and listen," sifting through the environmental buzz for cues of danger, social signals, or incentives to appetite, and preparing for goal-directed action.

Predator–Prey: The Defense Cascade Model

Using concepts introduced by Timberlake (1993), Fanselow (1994) analyzed the defensive patterns of prey animals as they changed over three sequential stages of defensive behavior: An initial heightened vigilance when the animal first enters an open foraging area ("preencounter") is followed by freezing and orienting to a specific predator cue ("postencounter"), and culminates with vigorous defensive action when attack is imminent ("circa-strike"). Fanselow's (1994) research suggests that the switch from an attentional mode to active defense is mediated by a change in primary activation from the ventral to dorsal periaqueductal gray. Bandler and others (cf. Bandler & Shipley, 1994) have found, furthermore, that the ventral periaqueductal gray projects to cardiovascular centers mediating bradycardia as well as those involving inhibition of the motor system. In contrast, the dorsal periaqueductal gray projects to centers mediating tachycardia and active behavior.

We have proposed an adaptation of the predator imminence model that accounts for both appetitive and defensive reactions in the human laboratory (Lang et al., 1997). In this view, the model's stages reflect changes in a cascade of adaptive reactions that increase with the imminence of an appetitive or defense-demanding encounter: A participant initially seated in the psychophysiological laboratory is functionally similar to an animal at the *preencounter* stage, that is, moderately alert in an unfamiliar environment. Subsequent presentation of motivationally relevant pictures (*postencounter*) prompts focused attention, "freezing," and sequenced autonomic changes. Physiological indices of attention include pronounced heart rate deceleration, greater skin conductance activity and pupil dilation, and hedonic valence-related modulation of the probe startle reflex. During this static period, however, brain and body are also beginning to mobilize for defensive or consummatory action.

This biological model of emotion suggests that the set of measured responses to an emotional cue will differ considerably at successive stages of motivational activation. The variation broadly reflects a transition from a predominantly attentional posture with motor inhibition to increasing efferent mobilization (closer to the *circa-strike* region) and ultimate action. When defensively motivated, the participant might judge these to indicate a state of fear. Meanwhile, the model's theoretical predator is engaged in a parallel dance mediated by the appetitive system—first freezing and observing quietly the distant prey (food source), followed by stalking actions that tactically vary (towards or away), increasingly mobilized for the *circa-strike* stage, a final rush to capture. Overall, it is a parallel progression from attention to action, with a coincident increment in appetitive arousal. While there is currently little data on the predator's anticipatory pleasures—joy of the hunt, satisfaction in its consummation—the neurophysiological process is likely similar to that observed in defense.

In a previous experiment (Löw, Lang, Smith, & Bradley, 2008), we examined anticipatory brain and physiological reactions in humans using a simulation that was modeled on features of the predator–prey survival scenario. In this simulation, participants observed a stream of briefly presented neutral pictures in a continuous flow, mimicking the serial humdrum of daily life events. Occasionally, however, a cue appeared with defined motivational significance: An offered fistful of money or, alternatively, an attacker's hand pointing a gun at the viewer. These motivationally relevant images were presented in a sequence in which each subsequent presentation loomed progressively larger, simulating movement towards the viewer.

As an image continued its approach, the player was metaphorically in a predator–prey strike zone. At some point in this region, the background of the appetitive or defensive cue changed color, signaling the need for rapid action. On reward trials (money cue), a fast button press resulted in a reward (1 dollar); a slow response produced no gain and an image of money burning up. On threat trials (gun), with a slow reaction the gun appeared to fire and money was deducted from the participant's stake; with a fast response, however, loss was avoided and a steel door slammed shut, blocking the gunfire. As a control procedure, neutral pictures also sometimes appeared to loom, but, when their background color changed, the key press had no functional outcome.

Among the measured indices of attention and emotion were heart rate, skin conductance, event-related potentials (ERPs), and startle blinks. As anticipated, skin conductance increased progressively across both reward and threat sequences. Its amplitude was somewhat heightened, compared to neutral cues, early in the sequence, and for both reward and threat trials it rose dramatically during the final steps that preceded action. Heart rate, on the other hand, showed a modest initial increase (perhaps attributable to vagal release). As possible reward or loss became more certain, however, heart rate decreased steadily to a nadir for the penultimate cue preceding action. This deceleration was followed by an abrupt acceleration immediately prior to the goal signal for escape or capture.

Thus, whether preparing to seize a reward or avoid punishment, the two branches of the autonomic nervous system were coactive: An increase in sweat gland activity suggests progressively augmented *sympathetic* arousal; in contrast, heart rate, mainly under *parasympathetic* control, decreased progressively with closer proximity to the goal. This latter phenomenon has been widely noted in biological studies of prey animals confronting a predator (Campbell et al., 1997), and is coincident with a stance of relative immobility (freezing) and an increasingly focused vigilance. Within the circa-strike zone, however, there is anticipatory parasympathetic release and a sympathetic increase in heart rate that reflects the final mobilization for action.

Startle reactions were probed at various stages throughout the cascade, including when viewing the initial cue, midway through the sequence and just prior to the response cue. Initial exposure to a motivational cue (i.e., a distant threat or reward) yielded the pattern observed in many free-viewing studies—significant reflex potentiation when viewing the threat cue and a relative inhibition for appetitive cues (e.g., Bradley, Codispoti, & Lang, 2006). Consistent with initial heightened attention allocation, the late positive potential was also enhanced, relative to neutral cues, when reward or threat cues were initially presented. However, as the distance to confrontation closed, reflex magnitude was increasingly inhibited for both reward and threat trials, reflecting effects of inhibitory task-focused attention and suppression of irrelevant action, facilitating a final functional response to the motive cue. Consistent with enhanced attention and vigilance, the amplitude of the late positive potential also increased as action became more imminent. Taken together, whether the motivational goal was to obtain reward or avoid punishment, autonomic, central, and somatic reflex measures signaled heightened attention and vigilance together with sympathetically mediated arousal supporting action preparation and initiation in both the appetitive and defensive contexts.

Motivational Circuits

The primitive similarities in appetitive and defensive reactions suggest that the mediating neural circuits are overlapping, involving many of the same neural structures. Brain imaging studies support this view. For instance, when viewing pleasant or unpleasant scenes, a neural circuit that includes enhanced activity in visual cortex (e.g., bilateral fusiform, bilateral occipital cortex), thalamus, orbitofrontal cortex, superior parietal cortex, and bilateral amygdala is reliably found (see, e.g., Sabatinelli et al., 2011, for a meta-analysis). Importantly, BOLD activity in the bilateral amygdala is significantly greater when participants view either erotic or mutilation pictures than for quotidian pictures of neutral people, indicating that the amygdala is activated by emotionally arousing stimuli, whether appetitive or aversive (Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005). When activated, circuit projections modulate afferent systems, increasing stimulus receptivity and perceptual processing, and prompting reflexive changes in efferent systems throughout the body that mediate a broad range of functional behaviors.

Rather than isolated reward and fear centers in the brain, then, more often similar structures are found to be active in both appetitive and defensive contexts, and furthermore, variations in activation magnitude are related more to response vigor than to the direction of action. In effect, motive systems may be conceptualized as circuit patterns of neural connectivity among brain structures, rather than specific anatomical sites or actions that uniquely determine appetite and defense. Although the poetry of the predator–prey interaction can be described as an orchestration of approach and avoidance, the coping behaviors mediated by the brain's evolved motive circuitry are adaptively varied, and not limited to physical approach in the context of appetitive cues or to active avoidance in the context of threat.

Conclusions

Emotional cues activate evolved motivational systems in the brain—defensive and appetitive—that promote the survival of individuals, species, and their progeny. The reviewed research confirms that visual cues that activate appetitive and defensive systems mediate a broad range of reactions that serve two primary functions (e.g., Bradley, 2009; Lang et al., 1997): (a) They capture attention preferentially and prompt perceptual processing and information gathering; (b) they occasion metabolic arousal and mobilize the organism for coping actions. The reflex physiology of pleasant and unpleasant emotional cues and their orchestration in the context of appetitive or threatening stimuli is often quite similar, mediated by many of the same brain structures. Acquiring life's needs and defending against its dangers are evolution's strategic goals. The tactics of their achievement are myriad, however, driven by the varied contexts in which the cues arise.

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