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# A place for emotions in behavior systems research

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## ABSTRACT

Although issues of motivation, including appetitive searching behavior, have been crucial aspects of behavior systems approaches since their inception, as well as in the ethological research and models that inspired them, emotions and affect have been noticeably absent in such analyses. Emotions and affect may have been lying below the surface all the time, however, as motivation, emotion, and cognitive processing are embedded in all aspects of behavior, including conditioning and learning. Here a brief case is made that emotions and related hedonic processes, can and should be explicitly incorporated into behavior systems approaches. Evidence from recent behaviorist, neuroscience, and animal behavior (including human) studies suggest that emotions may, just as motivational drives, lead to appetitive searching and avoidance, both general and focal, as well as theoretical formulations and evaluations, would be timely and extend the reach of behavior systems approaches to a far wider swath of psychological research than it has engaged with hitherto.

#### 1. Introduction

Behavior systems approaches are typically tied to a synthesis of conditioning and ethological models of behavior, with a primary focus on the appetitive behavior - consummatory act distinction as well as the hierarchical organization of behavior. These ideas were first clearly articulated by Wallace Craig (Craig, 1918) and extended through the work of Tinbergen (Tinbergen, 1942, 1950, 1951) and Baerends (Baerends, 1976a,b; Baerends et al., 1970). This historical context in the development of behavior systems has been recently reviewed (Bowers, 2018; Burghardt and Bowers, 2017). In Craig's work and subsequent analyses and models, appetence occupied the central place between endogenous 'drives' and the environmental contexts and behavioral responses. What about the role of emotion, moods, and affective states in these behavioral processes and phases? I will present here a brief precis of why these need integration into behavior systems experiments and analyses. Timberlake, Hogan, Domjan and others included motivation and other internal physiological processes as central factors in their approach to behavior and learning-based alterations of existing organized behavioral systems, but emotional, affective, and hedonic processes, although perhaps implied, do not seem to have been explicitly entertained.

Before proceeding, it is necessary to clarify what I mean by these emotion and affective processes. In spite of a long history of characterizing and theorizing about emotion and affect in psychology, researchers in this area still are contesting basic definitions as well as the processes underlying emotion and their role in behavior. Are emotions causes of behavior or the result of physiological changes in response to environmental events and cognitive appraisal? Should emotions be viewed as relatively discrete phenomena or as markers in a dimensional space along continua such as approach-avoidance, high-low arousal, and predictable-unpredictable? Are some emotions more primary (fear, disgust) and others more derived and thus secondary or tertiary (guilt, pride)? What is the role of learning of either the emotions themselves or the contexts in which they occur? What species have which emotions and is a comparative evolutionary approach, as Darwin (1872) proposed, an ethologically useful starting point, or misleading and ready for the dustbin (Barrett, 2017b)? Should the focus be on behavioral and physiological measures, representing Darwin's expressions of emotions, on the subjective feelings associated with emotions, or on the role of cognition, consciousness, and/or experienced-based 'construction'? Is consciousness or language critical to emotion or measuring it, as behavior can be misleading (e.g., actors; crying when happy)? What is the relationship between emotion and attitude, often being measured on similar scales (Cacioppo and Berntson, 1994)? Are affect and emotion clearly separable, so that a fly demonstrably cannot experience 'fear' but nonetheless may "feel affect" (Barrett, 2017b: 14)?

This is not the place to weigh in on all these topics, or to attempt any resolution or comprehensive definitions. Moors (2009) provides a fine tutorial on the major conceptions of emotion from the James-Lange theory to the present. The recent debate in *Social Cognitive and Affective Neuroscience* between Adolphs and Barrett captures some of the

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contended terrain (Adolphs, 2017a,b; Barrett, 2017a,b). There are also attempts to arrive at synthesis views that may or may not be accepted as the field of emotion research moves forward (e.g., Panksepp, 2007; Mendl et al., 2010; Ekman, 2016; Cerqueira et al., 2017; Gu et al., 2019). For the purposes of this paper, as it derives from ethological and behavior systems studies on nonhuman animals, I use emotion as stated in a recent paper on fish: "the assessment of emotional states in animals has to rely on the occurrence of specific behaviours associated with internal central states" (Cerqueira et al., 2017; 7).

Other terms used in behavior systems and related areas of animal behavior are also still contested. Opinions differ on the characterization of motivation, drive, needs, instinct, learning, reinforcement, and cognition. All of these terms also overlap with operationally derived measures of emotion. This reflects the holistic organization of organisms and that categories can be both fuzzily delimited and scientifically necessary. Here I will make some additional somewhat arbitrary distinctions for some traditional terms before remodeling them somewhat in the next section based on Craig's proto-behavior systems approach. Drives are biologically based motivational systems derived from ancestral survival and reproductive needs. Motivation includes these, but also acquired generalized or secondary 'drives' and those induced by external stimuli: thermal, social, chemical, visual, tactile, auditory, etc. and those labeled incentives. Dickinson and Balleine (1994) provide useful pathways through some of this terrain from a non-behavior systems, animal learning and conditioning perspective. Motivation also includes processes for which we currently lack information as to their physiological bases or origins. Moods are longer lasting less intense and differentiated states that may facilitate emotion arousal (Ekman, 1994). Affect can reflect both mood and momentary emotions, and is more indicated by general demeanor, posture, vocalization, and facial expressions. These are also, like mood, more 'state' than 'event' behaviors. However, Wallace Craig's views actually circumvented some of these terms.

#### 2. Some predecessors to behavior systems

In Craig's initial 'model,' (explored in detail in Burghardt and Burkhardt, 2018), a physiological need underlay the appetitive behavior and the subsequent location of the stimulus situation setting the occasion for the performance of the consummatory act. These resulted in the biologically functional behaviors of drinking, eating, territorial defense, courtship and copulating, nest building, various parental behaviors, predator defense, and so on. As Craig wrote: "An appetite (or appetence, if this term may be used with purely behavioristic meaning), so far as externally observable, is a state of agitation which continues as long as a certain stimulus, which may be called the appeted stimulus, is absent," while an "aversion is a state of agitation which continues as long as a certain stimulus, referred to as the disturbing stimulus, is present" (Craig, 1918: 91). The underlying cause can be viewed as derived from needs resulting from a deviation from homeostasis or a disequilibrium; Craig listed a number of behavioral indicators of appetites and aversions.

While for aversions, "relative rest" was the goal, for appetites it was the performance of the consummatory act, often stereotyped and species typical, that constituted the goal, reward, or in operant terms, the reinforcement (reinforcer); a point also emphasized by Lorenz in his adoption of Craig's ideas (Burghardt and Burkhardt, 2018; Lorenz, 1937/1985, 1950). The reinforcing aspects of consummatory acts have been documented extensively, not only in mammals and birds, but also in other species. For example, ingestively naïve newborn gartersnakes respond to chemical cues from species typical prey (earthworms or fish) presented on cotton swabs with investigatory tongue flicking and predatory strikes at the swabs, which were removed just as the strike commenced. The strike response is an energetically costly unrewarded behavior. Snakes learned to respond more to swabs with chemical cues (odors and vomodors) that led to strikes without food ingestion, but this did not occur with animals that only investigated and did not attack. Furthermore, the attacking snakes increased their responsivity to the experienced prey chemicals relative to chemicals from other salient prey that did not lead to failed attacks (Burghardt, 1968, 1990). In short, the consummatory strike, being unrewarded, did not habituate or extinguish, but served to reinforce an existing prey preference. Consummatory ejaculation seems as rewarding to male *Drosophila* as it is to male humans, and the underlying neural mechanism have been teased out (Zer-Krispil et al., 2018).

Most learning as studied by psychologists takes place during the appetitive phase, and this is where research has focused: maze running, problem solving, place learning, tool use, etc. Even lever pressing and pecking can be appetive. Although the reward or goal may be food, water, mate, or shelter; the 'learning' is in how to obtain them more than what to do with them, which are often a given. Nevertheless, as the Brelands' found out, consummatory actions often affected their training of arbitrary responses in animals (Breland and Breland, 1961) and Bolles extended such limitations to avoidance learning (Bolles, 1970). In short, animal learning researchers could not continue to ignore ethological factors and constraints without reaching the limits of their ability to generalize their research to unfettered animals, however much students of learning wished they could do so. Timberlake was a pioneering psychologist in bridging the gap in developing a viable ethological psychology.

#### 3. Origins of modern behavior systems approaches

Behavior systems research, adapted by Timberlake and others from Craig's analysis and ethological ideas, especially as developed and extended by Tinbergen's early writings (Tinbergen, 1942, 1950, 1951) and Baerends' later ones (Baerends, 1976a,b), were applied to varied and ingenious contexts. What were some of these early ethological applications? Tinbergen applied the hierarchical approach to reproduction in stickleback fish. The reproductive instinct was composed of several sub-instincts involving fighting, nest building, courtship and mating, and parental care. Each of these included a variety of behaviors, each with their appetitive and consummatory phases. Baerends analysis of just one aspect of reproduction, nest provisioning behavior by female digger wasps (Baerends, 1976a), entailed many levels. Inspecting, founding, provisioning, nest closing, and defending each contained several overlapping systems such as digging, hunting, and transporting, with numerous behaviors embedded within these and also overlapping among them.

Timberlake applied this hierarchical scheme to more experimentally tractable settings; an overview of his general scheme is described and depicted in Section 1 in Lucas (2019). One important addition was to divide the appetitive phase into general and focal search stages. The latter occurs when the goal object has been identified and located. The rolling ball bearing studies are classic experiments (Timberlake, 1983b; Timberlake and Washburne, 1989) that incorporated the hierarchical and appetitive-consummatory concepts in more traditional laboratory settings and species (see Lucas, 2019 for an overview). There are numerous fine treatments and applications of behavior systems over the vears (Domjan, 1994; Hilliard et al., 1998; Hogan, 1994, 2001; Shettleworth, 2010; Timberlake, 1983a,b, 1993, 1994, 2001; Timberlake and Silva, 1995). Recent compact and extended summaries (Burghardt and Bowers, 2017; Krause and Domjan, 2017) as well as the other articles in this issue of Behavioural Processes are also available; the recent review by Bowers provides both breadth and historical depth (Bowers, 2018). An important, but often ignored, element of these behavior systems approaches is studying behavior in its natural context and sequential organization. The hierarchical organized nature of behavior sequences also highlights the point that studies focused on single elementary atomistic units of response may miss these essential aspects of behavior.

Viewing learning as always and ultimately a product of primary

drive reduction (hunger, thirst, sex, pain), so basic to studies of learning during the era in which most classic behaviorist approaches were developed, such as those by Tolman, Hull, and Spence (Osgood, 1953) is no longer viable. Studies showing the rewarding properties of object manipulation (Harlow, 1953) and non-nutritive saccharin (Sheffield and Roby, 1950) were among the early findings that discredited primary drive reduction theories. As documented in the paper by Lucas (2019), much of the research by Timberlake and his students further questioned many key findings and interpretations of instrumental and operant conditioning by showing how they were actually isolated pieces of behavior embedded in adaptive and evolved hierarchical sequences. They were able to show how maze running, the Premack principle, superstition, instinctive drift, time horizon, and other phenomena were functionally explicable by deriving experiments from more naturalistic observations, a point made by Tinbergen decades earlier (Tinbergen, 1942, 1951), but often ignored in the heyday of behaviorism, including radical and methodological varients.

Learning experiments of all kinds are now more sophisticated and the importance of comparative studies increasingly recognized. Consider the two major species used in most studies of operant conditioning, domesticated rats and pigeons. Skinner proudly claimed that schedules of reinforcement led to virtually identical stimulus control parameters across all species (i.e., rats, pigeons, rhesus monkeys) as long as differences in their motor and sensory abilities were accommodated, Nonetheless, later researchers have uncovered major differences in even these laboratory warhorse species. Consider suboptimal choice in rats and pigeons where the animals are given a choice between alternatives that provide rewards 20% versus 50% of the time. Clearly, the 50% alternative is most efficient in payoff per effort expended. In experiments with unsignaled reward, both rats and pigeons chose the 50% rewarded alternative, whereas in the context of signaled reinforcement, pigeons chose the suboptimal 20% rewarded alternative. In this issue, Zentall and colleagues review this phenomenon and argue that a behavior systems account can explain these anomalies and lead to novel explanations and research (Zentall et al., 2019). They argue that for rats, the tactile and movement attributes of the lever press activate the focal search stage preceding prey capture, while for pigeons, it is the visual cues that activate focal search anticipating food pecking, and it is this difference in the species typical foraging sequence that underlies the apparently irrational behavior of the pigeons. They point out the importance of considering how foraging is organized sequentially in these two species, the salience of the stimulus modalities used to signal reinforcement, and the difference between general and focal searching in the appetitive phase of behavior.

In Bowers (2018) review, he laments that behavior systems approaches, so rich in applications and insight, are ignored in most areas of behavior study in psychology, biology, and neuroscience, and primarily discussed only in relation to animal learning and conditioning. He also notes that, while Timberlake always acknowledged the intellectual predecessors for his views, especially Craig, Tinbergen, and Baerends, this historical connection of behavior systems to classical ethology is frequently overlooked. Since the main promotors of behavior systems in the United States were Timberlake and Domjan, interested in laboratory studies of animal learning, behavior systems applications became narrowed to conditioning, challenges to traditional approaches to learning, and the hegemony of Pavlovian and operant/ instrumental conditioning, interchangeable stimuli and responses, and schedules of reinforcement. The operant worldview, even when related to more ethological and evolutionary approaches as Skinner (1966) attempted, has changed little in some quarters (Stahlman and Leising, 2018). The neglect of behavior systems is also true of psychology more generally. For example, a powerful call for studying the 'parental care motivational system' (Schaller, 2018) does not have a single mention of behavior systems. However, it does cite old work by Lorenz and McDougall. A similar call for viewing cognition as a motivated activity and integral to dynamical theories of cognition has appeared recently

(Barrett, 2019). Viewing cognition as a branch of ecological psychology and citing Lorenz (1950), this recent paper also completely ignores behavior systems and modern ethology.

Tinbergen strongly argued that studies of learning must consider each species behavioral, motor, and sensory adaptations. As Bowers (2018) has pointed out, the hierarchical structure of behavioral organization along with species typical motivational components were key. However, a less fortunate legacy of Tinbergen was his aversion to studying emotion, play, or other processes he viewed as subjective and beyond the reach of a solid empirical science (Tinbergen, 1951, 1963). While this was an understandable reaction against the purposive and teleological Dutch animal behavior school of his day (Bierens de Haan, 1947), those were no longer major dangers in the British and American biological fields he was operating in after 1945. Indeed, no representatives of such a school were at the seminal Cambridge symposium in 1949 that brought together ethologists, physiologists, and comparative psychologists and which helped shape the succeeding decades of research. However, it was in tune with the then current heyday of animal conditioning and behaviorist dogma, where concerns with emotion, feelings, and species differences were either anathema or ignored by many experimental psychologists.

#### 4. How emotion is already slipping into behavior systems

Returning to Craig: his appetites and aversions paper targeted motivational systems involving food, water, nesting material, courtship, parental care, predators, fighting, and so on. His interest in emotion was also shown by his commentary on the 50th year anniversary of Darwin (1872) and his subsequent interest in aesthetics in birds (Craig, 1922, 1943). At about the time he was first writing, William McDougall was developing his version of instinct theory (McDougall, 1908), where such motivational systems, rather than specific innate behaviors, were key organizing psychological processes. Each of these instincts was associated with a specific emotion (Burghardt and Bowers, 2017). Examples would be flight and fear, pugnacity and anger, parental care and love. Cognition (reason, intelligence), motivation (drives, will) and emotion (feelings, affect), were the tripartite cornerstones of early academic psychology. While distinguishing them is important, there are also important connections among them, and McDougall rightly saw that all had to be incorporated into a viable psychology. Although an outspoken opponent of behaviorism and largely rejected by mainstream psychology, his instinct models were comparable to those of the ethologists and his thinking on emotions was, as we shall see, resuscitated, perhaps unwittingly, by neuroscientists decades later. Note that if instincts are accompanied by emotion, then perhaps the emotions themselves could provide the "state of agitation" central to appetence as used by Craig.

Today we are also seeing that researchers wedded to a behavioral psychology based on reinforcers and contingencies of reinforcement are beginning to revamp some of their distinctive views about core concepts such as reinforcers and 'reinforcement' (rewards) (Killeen and Jacobs, 2017a,b). Since the value of a specific reinforcer can vary with the individual, reinforcers are not intrinsic aspects of things. Rather, reinforcement is a relationship among affordances, the observer, and his/her current state and prior history. Indeed, what is reinforcing is not only dependent on the individual, his/her prior experience and heredity, but also may involve hedonistic and affective properties underlying learning. Thus, Killeen and Jacobs (2017a) claim that the ORG-ANISM needs to be formally inserted into the operant three-term contingency  $(S^d - R - S^R)$  with all its species typical and evolutionary history in addition to the individual animal's own history of reinforcement. That is, it is not enough to view behavior as involving a discriminative stimulus (e.g., light, verbal command) leading to a response followed by a subsequent reinforcer or, perhaps, punishment. They further posit that this is not sufficient either, and prefer Thorndike's term 'satisfier' rather than Skinner's reinforcement. Indeed, in

their final version, for a given animal in a given state, the discriminated stimulus leads to an instrumental (appetitive) response leading to a consummatory response: thus, S<sub>D</sub> – R<sub>I</sub> – R<sub>C</sub>. Furthermore, they refer to 'disposition' as an umbrella term encompassing affective states, motivation, goals, and intentions. They refer to Timberlake and behavior systems, but actually go beyond them in not only calling for neural and physiological data to complement the behaviorist agenda, but anticipate my theme: "Invoking states such as joy, love and satisfaction as part of our understanding of behavior need not be tautological, nor should we fear being labeled mentalists for employing such terms. They are real" (Killeen and Jacobs, 2017a: 27). In actuality, decades ago some applied behavior analysts developed an extensive body of literature on the value of incorporating positive emotional experiences such as love and affection in helping developmentally disabled children, but the field was not ready to embrace their ideas (e.g., Twardosz and Nordquist, 1983). The commentaries on Killeen and Jacobs heretical paper were, however, remarkably positive (Killeen and Jacobs, 2017b). Craig made a similar point: "internal states. . . . are probably exceedingly complex and numerous and similar to the physiological states which in the human organism are concomitants of appetites, emotions, desires" (Craig, 1918: 95). If behavior analysts, perhaps even Skinner, had read and understood Craig, experimental psychology may have developed quite differently.

#### 5. Motivation and emotion in neuroscience

In neuroscience research, as issues of motivation and rewards become tied to neural and physiological mechanisms and are more intimately studied, new ways of conceptualizing motivation, reward, learning, and emotion are being developed. A marker of this is the highly cited distinction made by Berridge and associates between 'wanting' and 'liking' (Berridge, 2004; Berridge and Kringelbach, 2015; Berridge et al., 2009; Robinson and Berridge, 2008). Wanting is, in their terms, incentive salience that "promotes approach toward and consumption of rewards" (Berridge et al., 2009: 67-68) whereas liking refers to the hedonic salience of rewards (both objectively and subjectively measured), whereby "Hedonic hotspots distributed across the brain may be functionally linked together in an integrated hierarchical circuit" (Berridge et al., 2009: 67). While liking is positively hedonic, disliking, measured by disgust reactions is 'negative aversive' (sic). They note that this distinction may be helpful in clarifying neural mechanisms and developing treatments for many aspects of behavior, including pressing social problems such as obesity, drug addictions, mood disorders, depression, and compulsions (cf., Burghardt and Burkhardt, 2018). However, one can also view this distinction as similar to the Craig system where 'wanting' is a prelude to appetitive searching, and 'liking' a possible, but not necessary, consequence of obtaining the stimuli involved in the consummatory act. Berridge et al. (2009) view 'desires' as a more cognitive version of neurologically basal 'wants.' Wanting, in their view, involves both innate and learned components, as Craig (1918) also claimed. They assert that liking includes emotion, mood, and affective components, a hierarchical organization is explicitly entertained, and, I would add, evolutionary analyses are needed as well. For example, addictions have deep evolutionary roots and such wanting has been related to coopted systems of insect-plant interactions and have been studied from an appetitive consummatory framework (e.g., van Staaden and Huber, 2018).

Many emotions or affective states can operate via the same appetitive and consummatory phases as more traditionally studied behavior. Emotions, as in Berridge's papers, are bodily processes that can be measured, in contrast to the 'feelings' that they might engender, but which are impossible to assess linguistically in human infants and nonhuman animals. Such feelings, however, such as the pleasure of eating or orgasm, can be the salient consequences of performing consummatory responses resulting from engaging with the appeted stimulus. While looking for food, mates, nesting material, and so on easily fit Craig's system, including as modified by Timberlake, Hogan, and others, so can aversions. These can include fear, a basal emotion included in virtually every discussion of emotion. Fanselow (1994) has studied the fear emotion from a behavior systems viewpoint for many years. Fear is also being integrated as an essential factor, along with stress, in studies of predator-prey interactions (Zanette and Clinchy, 2017) and antipredator behavior (Mori and Ito, 2017); thus emotion is here already, somewhat disguised, but still openly visible, like the purloined letter in Edgar Allen Poe's classic tale! As Dickinson and Balleine (1994) point out, disgust, also a major emotion category, is a major factor in illness-induced food aversions and they include disgust as a major component in their discussion of Tolman's cathexis theory. Emotions have never been far away from either behavior systems or any other psychological system.

# 6. Emotion is far from a settled concept – an opportunity, not a problem

As mentioned in the introduction, there are several competing versions of viewing emotions. There are the basic discrete emotional expressions that Ekman, building on Darwin (1872), argued were universal such as surprise, anger, fear, happiness, disgust, and sadness, as well as derived expressions, such as contempt (Ekman et al., 1972; Ekman and Friesen, 1975). Much of this research was based on recognition of static expressions from photographs. Eibl-Eibesfeldt took a more dynamic ethological approach by filming social interactions and facial expressions cross culturally, including children born blind or with serious brain malformations. His work showed that the sequential organization of such behavior followed consistent scripts (e.g., flirting, temper tantrums, laughing, grief), even in then still remote tribes (Eibl-Eibesfeldt, 1970). His studies, highly germane to behavior systems and neuroscience research, were almost totally ignored by the emotion research community. In this issue Nelson and Mondloch (2019), although not citing his work, have recognized the value of studying emotion in its natural context in their interactive studies of children and adults peering at emotionally charged objects, using eye monitoring technology. In his book claiming that virtually all emotions found in humans also exist in other species, de Waal (2019) uses a plentitude of examples gleaned from video-recorded interactions. These provide further indications how emotion can, and is formally entering behavior systems research.

Additional evidence for the blurring of motivation and emotion comes from Jaak Panksepp in his influential work trying to balance cognitive neuroscience with affect (Panksepp, 1998). He developed a scheme involving seven major basic systems from which all others are derived, at least in mammals (Panksepp, 2017). These seven are SEEKING, RAGE, FEAR, LUST, CARE, PANIC, and PLAY (caps always used). Panksepp holds that these are conserved "coherent emotional action patterns, as well as rewarding and punishing states" (Panksepp, 2017: 475). The SEEKING system is actually a general exploratory and appetitive system, but in a major treatment it has been viewed as central (Wright and Panksepp, 2012). At least originally, Panksepp's view did not accommodate the Berridge distinction (Burghardt and Cooper, 2012) or take Craig and behavior systems theorists into account. One of the advantages of the Panksepp classification, however, is that it takes parental care seriously as a major category, and it certainly is critical as both a motivational and functional system (Schaller, 2018) in many species, and one with diverse neural components (Cunningham et al., 2017; Kohl et al., 2018). Whereas the Ekman and similar approaches focus on facial expressions, Panksepp views his seven systems as rooted in basal brain regions and the core of instinct. His approach is reminiscent of McDougall's theories. Although rooted in modern neuroscience, albeit one of several approaches (c.f., Adolphs, 2017a), it could be incorporated into a behavior systems approach (Burghardt and Bowers, 2017). There is no clear demarcation implied, nor possible, between the conative and the affective in his system. One of Panksepp's

basic systems, PLAY, has been discussed in terms of behavior systems (Burghardt, 2005) and an extended persuasive analysis is present in this issue (Pellis et al., 2019). Note that play can be viewed as both behavior and as an emotional state. It would seem that love, care, and grief, just as hunger, thirst, and lust, can also be studied from both aspects as well, often simultaneously. All can lead to appetitive searching, both general and focal, as well as consummatory acts and relative rest.

Craig (1918) described jealousy, arguably an emotion, in his doves. Jealously can lead to both general and focal search, leading to attacks on the rival, perhaps even murder, in humans as well as in birds. The consummatory response may lead to momentary, at least, satisfaction. Often the fulfilling of the consummatory act may not bring the reward and satisfaction that was anticipated, or be adaptive or functional for the life of the individual. Consider, overeating, junk food, drug addictions or sadomasochistic sex. Recent experiments in humans show the role of anger on both appetitive dominance seeking and aggression (Cabral and de Almeida, 2019).

The relatively discrete emotions position of Panksepp and others has been criticized on several grounds and alternative dimensional, valence, cognitive appraisal, and other schemes advanced (e.g., Moors, 2009; Barrett, 2017b). These are called core affects and are consciously experienced (Russell and Barrett, 1999), making their application to nonhumans initially suspect. Nevertheless, the dimensional approach has been reviewed in terms of animal emotion and mood (Mendl et al., 2010) and applied to fish (Cerqueira et al., 2017) and bumblebees (Perry et al., 2016). In this approach, two or three dimensions are used to accommodate all emotional states and their subjective components. One dimension is arousal, high or low. Thus, fear, anxiety, joy surprise would be high and being calm, relaxed, and sad low. The dimension of positive or negative valence would put fear and sadness in the negative and joy and relaxed in the positive. These core affect experiences are fitted into quadrants when orthogonally arranged. Imposed on this scheme is the question of whether these core affects are in reward acquisition or punishment avoidance mode. In this way, biologically important behavior may be understood as fitness enhancing, via rewards, or associated with minimizing exposure to fitness-threatening punishers. These dimensions incorporate many emotional and mood states as well as motivational, appraisal, and cognitive states.

There have been attempts to integrate the discrete emotion and dimensional approaches (Mendl et al., 2010; Panksepp, 2007), but some points should be noted. One is that in Craig's (1918) model aversions were there all the time, not just approach responses. In fact, he noted that the same stimulus could change valence due to satiation and excess exposure. Another is that the dimensional approach appears remarkably similar to Thorndike's law of effect and satisfiers and punishers, although not so noted (c.f., Killeen and Jacobs, 2017a). A third point is that a major school opposing ethological ideas of modular, but often overlapping, instinctive systems was the approach/withdrawal theory championed by Schneirla, Lehrman, and others, which ultimately foundered on not being able to effectively account for how behavior is actually controlled and organized (Schneirla, 1965; Burghardt, 1973). Proponents of similar universal schemes in psychology (Approach/Avoid, Positive/Negative) vigorously disagree with one another and no consensus is at hand (e.g., Cacioppo and Berntson, 1994; Russell and Barrett, 1999). A fourth observation is that this approach largely ignores the actual richness and diversity of emotions and motivations, the role of ritualization in their phylogenetic and ontogenetic modification, and the multiple systems that are often activated simultaneously. In fact, motivational conflicts and biological rhythms were integral to much ethological theory (Tinbergen, 1951; Burghardt, 1973) and were clearly described by Craig (1918). Such conflicts can be incorporated into behavioral systems. For example, appetitive focal search could pit an attractive food resource against venturing into a risky environment to obtain it. Different behavioral elements and sequences could become conditioned, habituated, or altered to different degrees. Finally, quite different states can occupy similar space in the proposed quadrants, such as fear, anger, and rage and sadness, depression, and satiation. There is, consequently, a potential to limit innovative research into the diverse behavior systems of animals through lumping not just apples and oranges, but mates, offspring, and tasty food as occupying similar space on an overly simplistic model that might be replicating the errors of the early primary drive theorists.

That being said, neuroscience studies are exploring how different behavior systems are organized in the brain, how they interact with one another, and how discrete and dimensional aspects underlie motivated, affective, and cognitive systems across species. A recent paper brought together several themes in a model of emotion based on neuroscience studies of fruit flies. Drosophila (Gu et al., 2019). Citing many of the sources on emotion used in the present paper, the authors "propose an integrative model of basic emotions" based on neuromodulators subserving internal states, evolution, hierarchical organization, and ethological instinct theory. They develop a primary color model of basic emotions that ties the early evolution of emotion to neuromodulators as seen in flies, viewed as representing ancestral states before things became more complicated in vertebrate brains. They propose three core affects, each underlain by different monoamine neuromodulators. Norepinephrine is the substrate for stress and emotions such as fear and anger. Dopamine is the substrate underlying rewarding emotions such as joy. 5-hydroxytryptamine (5-HT) or serotonin is involved with punishment, losing, and sadness. Neurotransmitters interact with neuromodulators and Gu et al. claim these systems appear functionally conserved throughout evolution, including in mammals. In actuality, they refract their emotion interpretations from basic behavior in the Drosophila during courtship, copulation, aggression, and other activities, even having measures indicative of happiness and surprise! I suspect that the psychological emotion research community (e.g., Barrett, 2017a), will not be amused by such claims. Nevertheless, the work of Gu et al. (2019) on flies, Perry et al. (2016) on bumblebees, and van Staaden et al. (2018) on crayfish are, at the minimum, tapping into neural and behavioral phenomena related to emotional, affective, and hedonic processes that behavior systems may be best situated to explore and explicate for the psychological emotion research community.

De Houwer and Hughes (2018), eminent members of this community, acknowledge that today there is still little consensus on what constitutes emotion and emotional phenomena, that intuition and pet theories prevail, and that much research is "scientifically counterproductive" (p. 61). For them the answer, in their final sentence, is straightforward. "Describing emotional phenomena in terms of behavioural principles will result in a more cumulative science of emotion that has the potential to surpass our initial intuitions and theoretical ideas" (p. 65). All well and good, but their operant-based functionalcognitive approach ignores the claim, advanced here, that both emotion research and behavioral principles need to employ the full ethological arsenal (description, origins, evolution, ontogeny, adaptive function, private experience) to adequately make progress and their valuable empirical focus would benefit by incorporating these considerations.

In conclusion, incorporating affective and cognitive processes into behavior systems approaches in new, rigorous, and imaginative ways, may help bring about a true integrative psychological science that can address the rich diversity and mechanisms of behavior in all species. Such research may also enrich our understanding of emotion and related phenomena and the behavioral, evolutionary, and neural mechanisms underlying them. It is worth exploring these potentials, which would be a lasting tribute to Bill Timberlake and other pioneers in behavior systems.

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reviewers helped clarify my views and presentation.

#### References

- Adolphs, R., 2017a. How should neuroscience study emotions? By distinguishing emotion states, concepts, and experiences. Soc. Cogn. Affect. Neurosci. 12, 24–31.
- Adolphs, R., 2017b. Reply to Barrett: affective neuroscience needs objective criteria for emotions. Soc. Cogn. Affect. Neurosci. 12, 32–33.
- Baerends, G.P., 1976a. The functional organization of behaviour. Anim. Behav. 24, 726–738.
- Baerends, G.P., 1976b. On drive, conflict and instinct, and the functional organization of behavior. In: In: Corner, M.A., Swaab, D.F. (Eds.), Progress in Brain Research Vol. 45. Elsevier/North-Holland Biomedical Press., Amsterdam, pp. 427–447 Perspectives in brain research.
- Baerends, G.P., Drent, R.H., Glas, P., Groenewold, H., 1970. An ethological analysis of incubation behaviour in the herring gull. Behaviour (Suppl. 17), 135–235.
- Barrett, L.F., 2017a. Functionalism cannot save the classical view of emotion. Soc. Cogn. Affect, Neurosci. 12, 34–36.
- Barrett, L.F., 2017b. The theory of constructed emotion; an active inference account of interoception and categorization. Soc. Cogn. Affect. Neurosci. 12, 1–23.
- Barrett, N., 2019. On the nature and origins of cognition as a form of motivated activity. Adapt. Behav. https://doi.org/10.1177/1059712318824325journals.sagepub.com/ home/adb. in press.
- Berridge, K.C., 2004. Motivation concepts in behavioral neuroscience. Physiol. Behav. 81, 179–209.
- Berridge, K.C., Kringelbach, M., 2015. Pleasure systems in the brain. Neuron 76, 646–664. Berridge, K.C., Robinson, T.E., Aldridge, J.W., 2009. Dissecting components of reward:' liking,' wanting,' and learning. Curr. Opin. Pharmacol. 9, 65–73.
- Bierens de Haan, J.A., 1947. Animal Psychology. Hutchinson University Library, London. Bolles, R.C., 1970. Species-specific defense reactrions and avoidance learning. Psychol. Rev. 77, 32–48.
- Bowers, R.I., 2018. A common heritage of behaviour systems. Behaviour 155, 415-442.
- Breland, K., Breland, M., 1961. The misbehavior of organisms. Am. Psychol. 16, 681–684. Burghardt, G.M., 1968. The reinforcement potential of the consummatory act in the modification of chemical-cue preferences. Am. Zool. 8, 745.
- Burghardt, G.M., 1973. Instinct and innate behavior: toward an ethological psychology. In: Nevin, J.A., Reynolds, G.S. (Eds.), The Study of Behavior: Learning, Motivation, Emotion, and Instinct. Scott, Foresman, Glenview, IL, pp. 322–400.
- Burghardt, G.M., 1990. Chemically mediated predation in vertebrates: diversity, ontogeny, and information. In: In: McDonald, D.W., Müller-Schwarze, D., Natynczuk, S.E. (Eds.), Chemical Signals in Vertebrates Vol. 5. Oxford University Press, Oxford, pp. 475–499.
- Burghardt, G.M., 2005. The Genesis of Animal Play: Testing the Limits. MIT Press, Cambridge, MA.
- Burghardt, G.M., Bowers, R.I., 2017. From instinct to behavior systems: an integrated approach to ethological psychology. In: In: Call, J., Burghardt, G.M., Pepperberg, I.M., Snowdon, C.T., Zentall, T. (Eds.), APA Handbook of Comparative Psychology Vol. 1. American Psychological Association, Washington, DC, pp. 333–364 Basic concepts, methods, neural substrate, and behavior.
- Burghardt, G.M., Burkhardt Jr, R.W., 2018. Craig's appetities and aversions as constituents of instinct: a centennial appreciation. J. Comp. Psychol. 132, 361–372.
- Burghardt, G.M., Cooper, M.A., 2012. Seven missteps of desire. Neuropsychoanalysis 14, 40–43.
- Cabral, J.C.C., de Almeida, R.M.M., 2019. Effects of anger on dominance seeking and aggressive behaviors. Evol. Hum. Behav. 40, 23–33.
- Cacioppo, J.T., Berntson, G.G., 1994. Relationship between attitudes and evaluative space: a critical review with emphasis on the separability of positive and negative substrates. Psycho. Bull. 115, 401–423.
- Cerqueira, M., Millot, S., Castanheira, M.F., Félix, A.S., Silva, T., Oliveira, G.A., et al., 2017. Cognitive appraisal of environmental stimuli induces emotion-like states in fish. Sci. Rep. 7 (1), 13181. https://doi.org/10.1038/s41598-017-13173-x.
- Craig, W., 1918. Appetites and aversions as constituents of instincts. Biol. Bull. 34, 91–107.
- Craig, W., 1922. A note on Darwin's work on the expression of the emotions in man and animals. J. Abnorm. Psychol. Soc. Psychol. 16, 356–366.
- Craig, W., 1943. The song of the wood pewee Myiochanes virens Linnaeus: a study of bird music. Bulletin - New York State Museum 334, 1–186.
- Cunningham, C.B., Badgett, M.J., Meagher, R.B., Orlando, R., Moore, A.J., 2017. Ethological principles predict the neuropeptides co-opted to influence parenting. Nat.
- Commun. 8, 14225. https://doi.org/10.1038/nccomms14225. Darwin, C., 1872. The Expression of the Emotions in Man and Animals. Murray, London,
- England.
  de Houwer, J., Hughes, S., 2018. Toward a cumulative science of emotion: a functionalcognitive framework for emotion research. Cogn. Emot. 33, 61–66. https://doi.org/ 10.1080/0269931.2018.1504750
- de Waal, F., 2019. Mama's Last Hug: Animal Emotions and What They Tell Us About Ourselves. W. W. Norton, New York, NY.
- Dickinson, A., Balleine, B., 1994. Motivational control of goal-directed action. Anim. Learn. Behav. 22, 1–18.
- Domjan, M., 1994. Formulation of a behavior system for sexual conditioning. Psychon. Bull. Rev. 1, 421–428.
- Eibl-Eibesfeldt, I., 1970. Ethology: The Biology of Behavior. Holt, Rinehart, and Winston, New York, NY.
- Ekman, P., 1994. Moods, emotions, and traits. In: Ekman, P., Davidson, R.J. (Eds.), The Nature of Emotion. Oxford University Press, New York, pp. 6–58.

- Ekman, P., 2016. What scientists who study emotion agree about. Psychol. Sci. 11, 31–34.
   Ekman, P., Friesen, W.V., 1975. Unmasking the Face: A Guide to Recognizing Emotions from Facial Cues. Prentice Hall, Englewood Cliffs, NJ.
- Ekman, P., Friesen, W.V., Ellsworth, P., 1972. Emotion in the Human Face: Guidelines for Research and an Integration of Findings. Pergamon Press, New York, NY.
- Fanselow, M.S., 1994. Neural organization of the defensive behavior system responsible for fear. Psychon. Bull. Rev. 1, 429–438.
- Gu, S., Wang, F., Patel, N.P., Bourgeois, J.A., Huang, J.H., 2019. A model for basic emotions using observations of behavior in *Drosophila*. Front. Psychol. 10, 781. https://doi.org/10.3389/fpsyg.2019.00781.
- Harlow, H.F., 1953. Mice, monkeys, men, and motives. Psychol. Rev. 60, 23-32.
- Hilliard, S., Domjan, M., Nguyen, M., Cusato, B., 1998. Dissociation of conditioned appetitive and consummatory behavior: satiation and extinction tests. Anim. Learn. Behav. 26, 20–33.
- Hogan, J.A., 1994. Structure and development of behavior systems. Psychon. Bull. Rev. 1, 439–450.
- Hogan, J.A., 2001. Development of behavior systems. In: In: Blass, E.M. (Ed.), Handbook of Behavioral Neurobiology Vol. 13. Plenum, New York, pp. 229–279 Developmental psychobiology.
- Killeen, P.R., Jacobs, K.W., 2017a. Coal is not black, snow is not white, food is not a reinforcer: the roles of affordances and dispositions in the analysis of behavior. Behav. Anal. 40 (1), 17–38. https://doi.org/10.1007/s40614-016-0080-7.
- Killeen, P.R., Jacobs, K.W., 2017b. The modulated contingency. Behav. Anal. 40. https:// doi.org/10.1007/s40614-017-0101-1.
- Kohl, J., Babayan, B.M., Rubinstein, N.D., Autry, A.E., Marin-Rodriguez, B., Kapoor, V., et al., 2018. Functional circuit architecture underlying parental behaviour. Nature 556 (7701), 326–331. https://doi.org/10.1038/s41586-018-0027-0.
- Krause, M.A., Domjan, M., 2017. Ethological and evolutionary perspectives on pavlovian conditioning. In: In: Call, J., Burghardt, G.M., Pepperberg, I.M., Snowdon, C.T., Zentall, T. (Eds.), APA Handbook of Comparative Psychology Vol. 2. American Psychological Association, Washington, D.C, pp. 247–266 Perception, learning, and cognition.
- Lorenz, K., 1937. Über den Begriff der Instinkthandlung. Folia Biotheoretica Series B 11, 17-49. [On the concept of instinctive action]. In: Burghardt, G.M. (Ed.), 1985. Foundations of Comparative Ethology. Van Nostrand Reinhold, New York, NY, pp. 405–432.
- Lorenz, K., 1950. The comparative method in the study of innate behavior patterns. Symp. Soc. Exp. Biol. 4, 221–268.
- Lucas, G.A., 2019. Adaptive systems influence both learning and conscious attention. Behav. Processes 160 this issue.
- McDougall, W., 1908. Social Psychology. Methuen & Co, London, UK.
- Mendl, M., Burman, O.H.P., Paul, S.P., 2010. An integrative and functional framework for the study of animal emotion and mood. Proc. R. Soc. B: Biol. Sci. 277 (1696), 2895–2904. https://doi.org/10.1098/rspb.2010.0303.
- Moors, A., 2009. Theories of emotion causation: a review. Cogn. Emot. 23, 625-662.
- Mori, A., Ito, R., 2017. Antipredator behavior. In: In: Call, J., Burghardt, M, G., Pepperberg, I., Snowdon, C., Zentall, T. (Eds.), APA Handbook of Comparative Psychology Vol 1. American Psychological Association, Washington, DC, pp. 833–852 Basic concepts, methods, neural substrate, and behavior.
- Nelson, N.L., Mondloch, C.J., 2019. Children's perception of emotions in the context of live interactions: eye movements and emotion judgements. Behav. Processes this issue.
- Osgood, C.E., 1953. Method and Theory in Experimental Psychology. Oxford University Press, New York, NY.
- Panksepp, J., 1998. Affective Neuroscience. Oxford University Press, New York, NY. Panksepp, J., 2007. Neurologizing the psychology of affects. How appraisal-based con-
- structivism and basic emotion theory can coexist. Perspect. Psychol. Sci. 2, 281–296. Panksepp, J., 2017. Instinctual foundations of animal minds: comparative perspectives on the evolved affective neural substrates of emotions and learned behaviors. In: In: Call, J., Burghardt, G., Pepperberg, M.I., Snowdon, C., Zentall, T. (Eds.), APA Handbook of Comparative Psychology Vol 1. American Psychological Association, Washington, DC, pp. 475–500 Basic concepts, methods, neural substrate, and behavior.
- Pellis, S.M., Pellis, V.C., Pelletier, A., Leca, J.-B., 2019. Is play a behavior system, and, if so, what kind? Behav. Processes this issue.
- Perry, C.J., Baciadonna, L., Chittka, L., 2016. Unexpected rewards induce dopamine-dependent positive emotion–like state changes in bumblebees. Science 353 (6307), 1529–1531. https://doi.org/10.1126/science.aaf4454.
- Robinson, T.E., Berridge, K.C., 2008. The incentive sensitization theory of addiction: some current issues. Philos. Trans. R. Soc. B 363, 3137–3146.
- Russell, J.A., Barrett, L.F., 1999. Core affect, prototypical emotional episodes, and other things called emotion: dissecting the elephant. J. Pers. Soc. Psychol. 76, 805–819.
- Schaller, M., 2018. The parental care motivational system and why it matters (for everyone). Curr. Dir. Psychol. Sci. 27, 295–301.
- Schneirla, T.C., 1965. Aspects of stimulation and organization in approach/withdrawal processes underlying veretebrate behavioral development. In: In: Lehrman, D.S., Hinde, R.A., Shaw, E. (Eds.), Advances in the Study of Behavior Vol. 1. Academic Press, New York, pp. 1–74.
- Sheffield, F.D., Roby, T.B., 1950. Reward value of a non-nutritive sweet taste. J. Comp. Physiol. Psychol. 43, 471–481.
- Shettleworth, S.J., 2010. Cognition, Evolution, and Behavior, 2<sup>nd</sup> ed. Oxford University Press, Oxford, England.
- Skinner, B.F., 1966. The phylogeny and ontogeny of behavior. Science 153, 1205–1213. Stahlman, W.D., Leising, K.J., 2018. The coelacanth still program selection back to
- the fore in a science of behavior. Am. Psychol. 73, 918–929.
   Timberlake, W., 1983a. The functional organization of appetitive behavior: behavioir systems and learning. In: In: Zeiler, M.D., Harzem, P. (Eds.), Advances in the Analysis

of Behavior Vol. 3. John Wiley & Sons, New York, NY, pp. 77-221.

Timberlake, W., 1983b. Rats responses to a moving object related to food or water: a behavior systems analysis. Anim. Learn. Behav. 11, 309–320.

- Timberlake, W., 1993. Behavior systems and reinforcement: an integrative approach. J. Exp. Anal. Behav. 60, 105–128.
- Timberlake, W., 1994. Behavior systems, associationism. And Pavlovian conditioning. Psychon. Bull. Rev. 1, 405–420.
- Timberlake, W., 2001. Motivational modes in behavior systems. In: Mowrer, R.R., Klein, S.B. (Eds.), Handbook of Contemporary Learning Theories. Lawrence Erlbaum Associates, Mahwah, NJ, pp. 155–209.
- Timberlake, W., Silva, K., 1995. Appetitive behavior in ethology, psychology, and behavior systems. In: In: Thompson, N.S. (Ed.), Perspectives in Ethology Vol. 11. Plenum, New York, pp. 211–253 Behavioral design.
- Timberlake, W., Washburne, D.L., 1989. Feeding ecology and laboratory predatory behavior toward live and artificial moving prey in seven rodent species. Anim. Learn. Behav. 17, 1–10.
- Tinbergen, N., 1942. An objectivist study of the innate behaviour of animals. Bibliotheca Biotheoretica 1, 39–98.
- Tinbergen, N., 1950. The hierarchical organization of nervous mechanisms underlying instinctive behaviour. Symp. Soc. Exp. Biol. 4, 305–312.
- Tinbergen, N., 1951. The Study of Instinct. Clarendon Press, Oxford.
- Tinbergen, N., 1963. On aims and methods of ethology. Zeitschrift für Tierpsychologie 20,

Behavioural Processes 166 (2019) 103881

410-433.

- Twardosz, S., Nordquist, V.M., 1983. The development and importance of affection. Lahey, B.B., Kazdin, A.E. (Eds.), Advances in Clinical Child Psychology 6, 129–168.
- van Staaden, M.J., Hall, F.S., Huber, R., 2018. The deep evolutionary roots of 'addiction'. J. Ment. Health Clin. Psychol. 2 (3), 8–13.
- van Staaden, M.J., Huber, R., 2018. Crayfish learning: addiction and the ganglionic brain. Perspect. Behav. Sci. 41, 417–429. https://doi.org/10.1007/s40614-018-00181-z.
- Wright, J.S., Panksepp, J., 2012. An evolutionary framework to understand foraging, wanting, and desire: the neuropsychology of the SEEKING system. Neuropsychoanalysis 14, 5–39.
- Zanette, L.Y., Clinchy, M., 2017. Predator-prey interactions: integrating fear effects. In: In: Call, J., Burghardt, G., M, Pepperberg, I., Snowdon, C., Zentall, T. (Eds.), APA Handbook of Comparative Psychology Vol 1. American Psychological Association, Washington, DC, pp. 815–831 Basic concepts, methods, neural substrate, and behavior.
- Zentall, T., Smith, A.P., Beckmann, J., 2019. Differences in rats and pigeons suboptimal choice may depend on where those stimuli are in their behavior systems. Behav. Processes this issue.
- Zer-Krispil, S., Zak, H., Shao, L., Ben-Shaanan, S., Tordjman, L., Bentzur, A., et al., 2018. Ejaculation induced by the activation of Crz neurons Is rewarding to *Drosophila* males. Curr. Biol. 28, 1445–1452. https://doi.org/10.1016/j.cub.2018.03.039.