

Current Emotion Research in Psychophysiology: The Neurobiology of Evaluative Bivalence

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Abstract

Evaluative processes have their roots in early evolutionary history, as survival is dependent on an organism's ability to identify and respond appropriately to positive, rewarding or otherwise salubrious stimuli as well as to negative, noxious, or injurious stimuli. Consequently, evaluative processes are ubiquitous in the animal kingdom and are represented at multiple levels of the nervous system, including the lowest levels of the neuraxis. While evolution has sculpted higher level evaluative systems into complex and sophisticated information-processing networks, they do not come to replace, but rather to interact with more primitive lower level representations. Indeed, there are basic features of the underlying neuroarchitectural plan for evaluative processes that are common across levels of organization—including that of evaluative bivalence.

Keywords

amygdala, evaluative bivalence, insula, negativity, neuroevolution, positivity

Evolution has endowed organisms with a highly sophisticated central nervous system that is capable of rapidly evaluating complex situations and determining subsequent behavioral responses. The outcome from such evaluations can manifest in approach or avoidance dispositions whereby individuals actively seek resources or avoid potential threats. In many instances, approach and avoidance dispositions synergistically promote a common behavioral outcome, but this is not always the case as

such dispositions can come into conflict. One salient example comes from situations in which an organism is highly motivated to approach a rewarding stimulus (e.g., water source), even though approach would increase potential threats (e.g., predators). Thus, the organism must approach the goal while maintaining a high level of vigilance for potential threats. The dynamic interaction between positive and negative evaluations and their neurobiological substrates have been a major focus of

psychological research and have recently benefited from technological and theoretical advances. The current review will highlight some of these advances and discuss how such developments have improved our understanding of the psychological and neurobiological mechanisms of evaluative processes. The review will document that evaluative processes are represented throughout multiple levels of the neuraxis and organized in accordance with a cardinal principle of evaluative bivalence (i.e., separable positive versus negative substrates).

Despite the inherent complexities involved in the neurobiological and psychological components of evaluative processes, the behavioral manifestations of these processes are necessarily constrained as, for example, an organism may be unable to simultaneously approach and avoid a target. These physical constraints and evaluative conflicts may obscure the architecture of the underlying neurobiological and psychological processes. Many theories of basic evaluative processes have posited a bipolar model where positivity and negativity are reciprocally regulated along a single evaluative continuum (Osgood, Suci, & Tannenbaum, 1957; Posner, Russell, & Peterson, 2005; Russell, 2003; Watson, Wiese, Vaidya, & Tellegen, 1999). While reciprocal modes of activation can occur, the neurobiological substrates coding for positive (e.g., approach, rewarding) and negative (e.g., avoidance, aversive) affect are at least partially independent allowing for coactivation of both positive and negative evaluations (as in ambivalence). In the present article, we will use positivity (or positive evaluations) and negativity (or negative evaluations) to refer to the underlying valenced affective dispositions. It is important to distinguish between the basic evaluative processes and associated affective states and action dispositions or outcomes. The hedonic states of reward and aversion generally correspond to the basic positive and negative evaluative dimensions, respectively, as do the response dispositions of approach and avoidance. In some cases, however, these latter classes of phenomena may dissociate. We will return to this issue.

In contrast to the bipolar model, a bivariate representation of evaluative space (see Figure 1) with separate positivity and negativity axes may more appropriately capture and represent the dynamic weighting of positivity and negativity across time and context. Neural interactions, behavioral conflicts among levels of processing, and physical limitations on bodily movements may all exert constraints on the relative evaluative distributions across the bivariate surface. These factors are likely to be, at least in part, context dependent, and those contextual constraints themselves provide an important source of information on the operations of evaluative processes. Thus, the mere observation of behavior may not be sufficient to understand the dynamics of the underlying evaluative processes and associated approach versus avoidance dispositions. Based on evolutionary, neurobiological, and psychological considerations, Cacioppo and Berntson (1994; Cacioppo, Gardner, & Berntson, 1999; Norris, Gollan, Berntson, & Cacioppo, 2010) have proposed a more complex, bivariate space model of evaluative processes. This evaluative space model (ESM) recognizes that distinct positive and negative evaluative systems can function in a reciprocal, independent, or coactive fashion, and embraces the multilevel representations

(from spinal to neocortical) of evaluative systems that allow for parallel, partially independent patterns of evaluative processing. Such patterns allow for more flexible outputs, such as cautious approach during anxiety-like states (McNaughton & Corr, 2009). It is also consistent with the fact that people can feel ambivalent when they win some amount but could have won an even larger amount, an event dubbed a *disappointing win* by Larsen, McGraw, Mellers, and Cacioppo (2004).

The ESM is based on the premise that evaluative systems have been shaped by evolution to yield a wide range of adaptive responses to environmental contingencies. As such, the ESM makes predictions regarding the architecture of evaluative processes and how they relate to behavior. Conversely, understanding of the basic neurology of evaluative processes importantly informs and calibrates features of the ESM.

Neurobiological Organization and Rerepresentation

The late 19th-century neurologist John Hughlings Jackson (1884) offered an early description of the hierarchical structure and rerepresentation of function across levels of the neuraxis.

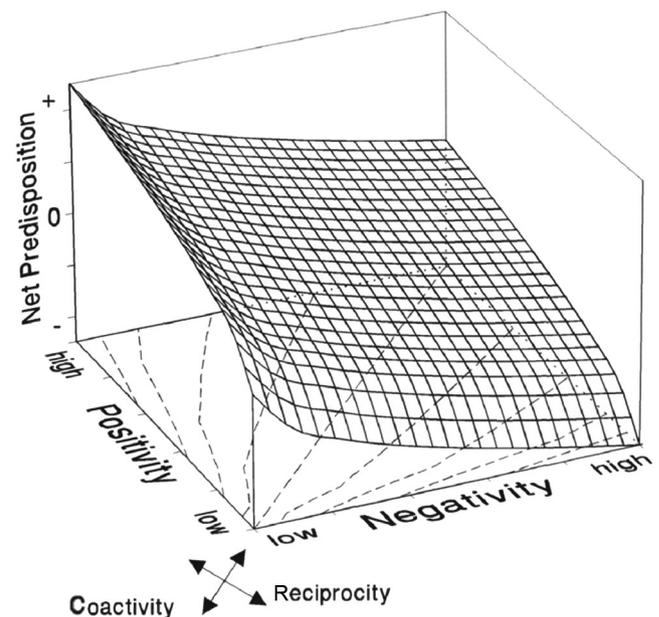


Figure 1. Bivariate evaluative space. The Y axis represents the level of activation of positive evaluative processes (positivity), and the X axis represents the level of activation of the negative evaluative process (negativity). The reciprocity diagonal represents the classical bipolar model of valence which extends from high positivity (upper left) to high negativity (lower right) along a single evaluative continuum. The coactivity diagonal represents an alternative mode where both evaluative dimensions are coactivated (conflict, ambivalence). The arrows outside of the box represent uncoupled changes in positive or negative evaluative processing. This evaluative plane provides a more comprehensive model of evaluative processes that subsumes the bipolar model as one reciprocal.

Although a strict hierarchical model of neural organization is an oversimplification, it remains the case that there is an important hierarchical dimension to the functional organization of the neuraxis. Embellishments of this model that more closely approximate contemporary perspectives on neuroarchitecture will be considered in this article. Central to Jackson's view was that the evolutionary emergence of higher level neural structures did not entail the replacement of more primitive neural organizations. Rather, Jackson noted that the brain was organized in a rerepresented fashion whereby information was simultaneously processed at multiple levels. For example, primitive protective responses to potentially noxious stimuli are apparent in the pain withdrawal reflexes at spinal levels that can operate even in the absence of communication from the brain. Importantly, these primitive protective responses are embellished at progressively higher levels of the nervous system (see Berntson, Boysen, & Cacioppo, 1993; Norman, Cacioppo, & Berntson, 2010). The evolutionary development of the higher level neural systems, such as the limbic system and cerebral cortex, endowed organisms with an expanded behavioral and motivational repertoire able to capitalize on experience-dependent associative knowledge, information-processing networks, and cognitive strategies that anticipate and prepare for environmental contingencies. Thus, the evolution of the central nervous system has maintained primitive lower level responses to potentially harmful stimuli while simultaneously allowing for the development of more integrative and elaborated information-processing capacities at the highest levels of the brain. At progressively higher levels of organization, there is a general expansion in the range and relational complexity of contextual controls and in the breadth and flexibility of discriminative and adaptive responses (Berntson et al., 1993; Berntson & Cacioppo, 2008).

The adaptive flexibility characteristic of higher level neural structures comes at a cost; greater flexibility implies a less rigid relationship between inputs and outputs, a greater range of information that must be processed, and a slower serial-like mode of processing. Consequently, the evolutionary layering of higher processing levels onto lower substrates has adaptive advantage in that lower and more efficient processing levels may continue to be utilized, and may be sufficient in some circumstances. Although reflexes are rather rigidly organized to provide a rapid, limited response, they are also embedded in multilevel networks. Consequently, reflex responses are not immutable, as higher systems can come to modulate or suppress pain withdrawal reflexes (e.g., suppressing flexor withdrawal when receiving an injection). Higher neurobehavioral systems also display multilevel organizations. LeDoux (2003) and Phelps and LeDoux (2005) have documented distinct subcortical (via the amygdala) and cortical routes for processing of fear-related stimuli. These multilevel organizational features are not unique to defensive/protective behaviors, but rather, reflect general neuroarchitectural principles that characterize hierarchical neural systems. Hence, the defensive system and its rerepresentative organization across neuraxial levels offers a model system for conceptualizing neurobehavioral processes generally (Berntson & Cacioppo, 2008).

Accordingly, the ESM considers evaluative processes to be mediated by a network of distributed interacting neural circuits ranging from the spinal cord to the limbic system and neocortex. Although there are hierarchical features to this network, there are also long ascending and descending pathways that bypass intermediate levels, as well as lateral pathways that mediate interactions even within levels (Figure 2). This is a pattern we have termed a neural heterarchy.

Although the activities of the components of the affect system are generally integrated into a coherent cognitive/behavioral stream, the existence of multiple processing levels affords considerable flexibility in behavioral action as well as the potential for interference and conflict. In cases where relatively low-level processing is sufficient, or higher level processing is precluded due to temporal or contextual constraints, lower substrates may predominate in behavioral expression. However, given sufficient information and processing time and capacity, higher level cognitive processes are able to inhibit these lower level responses in order to achieve a goal (allow one to receive the injection containing a vaccine). In fact, although integrated to some extent, the multiple levels of processing may allow response conflicts, with different levels of processing each disposing the individual toward different behavioral responses. These conflicts may facilitate an outcome (e.g., retrieval of a prized possession from a fire, followed by a rapid, spinally mediated withdrawal), or may interfere with it (via hesitancy, vacillation, or indecision). In part, the latter arises from the fact that physical constraints preclude both actions concurrently, as the limb cannot extend or reach out and flex or pull back at the same time. This physical constraint, however, belies the complexity of the underlying dispositions. Although the limb may not be able to extend and flex at the same time, the underlying flexor and extensor muscles can, in fact, be coactivated. This may lead to inaction, but that inaction is not sufficient evidence for a lack of underlying response dispositions. The limb response may be constrained along a single bipolar continuum of flexion or extension, but the underlying neuromuscular machinery is not so constrained and may reveal a broader fundamental bivariate structure. Accordingly, the framework provided by the ESM has the potential to promote theory and research on the affect system both at the level of the individual components and at the level of the integrated network.

Asymmetries in Evaluative Processes: The Negativity Bias and the Positivity Offset

The coexistence of both positive and negative attributes to an object or context does not necessarily result in a neutral dispositional state as might be implied by a bipolar evaluative model. Rather, coactivation of both positive and negative evaluations may yield a nonneutral condition of ambivalence.

In his classic studies on conflict, Neal Miller (1961) used behavioral measures (running speed, the strength of pull on a tether to approach or avoid stimuli, etc.) in order to assess motivational dispositions in rodents. A typical gradient of an

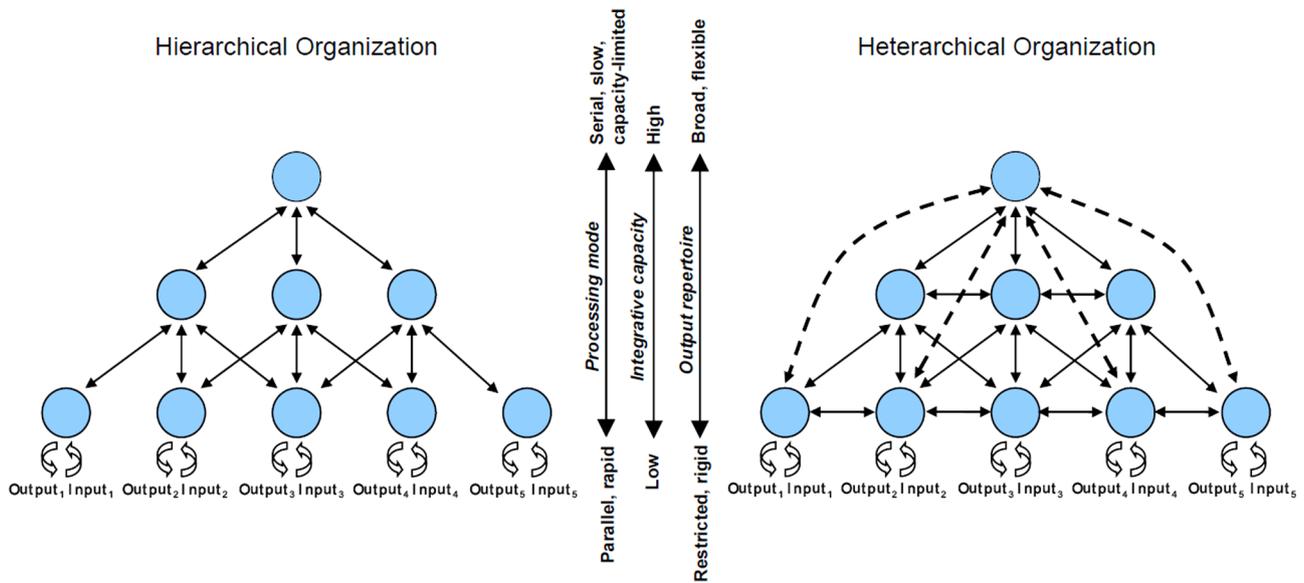


Figure 2. Hierarchical and heterarchical organizations. A heterarchy differs from a hierarchy in the existence of long ascending and descending pathways that span intermediate levels and by the presence of lateral interactions. The ascending/descending pathways allow higher level systems to communicate directly with low levels, in addition to the indirect route through intermediate levels. Lateral interactions allow greater integration within levels. Double-headed arrows illustrate dimensions or variation in functional properties of the levels (processing mode, integrative capacity, and output repertoire) between different levels in the organizations.

approach disposition to a food reward is illustrated in Figure 3; as the animal moves closer to the potential reward (e.g., food) the force exerted to obtain the reward increases. Similarly illustrated is the avoidance disposition away from an aversive stimulus, in this case a shock grid, as measured by the force an animal exerts in order to avoid the aversive stimulus (a shock). Miller observed that the slope of the avoidance gradient generally tended to be steeper than that of the approach gradient, so that at a distance from the goal the approach disposition was greater than the avoidance disposition, and vice versa at proximate locations. The two motivational dispositions of approach and avoidance were then invoked simultaneously, by the presence of both food and shock grid. This introduced what Miller termed an approach–avoidance conflict. The animal would approach the goal box if placed remotely in the apparatus, but as it approached the goal, the relative strength of the avoidance disposition would increase (see Figure 3) and the approach disposition would be overcome by avoidance. At that point the animal was in what Miller referred to as a *stable conflict*. Any further approach would lead to an increment in avoidance, and any movement away would lead to a relative predominance of approach. The equilibrium point of that conflict could be predicted by the relative magnitudes of the approach and avoidance gradients measured independently. In these studies, the joint effect of a positive motivation and a concurrent negative disposition was not a state of evaluative neutrality. Rather, it was a disquieting state of ambivalence, and the animals displayed agitation and vacillation at the equilibrium point. Bipolar models of affect have difficulty in describing this type of approach–avoidance conflict or ambivalent state (see Cacioppo, Berntson, Norris, & Gollan, in press).

The differential slopes of Miller’s approach and avoidance gradients suggest that the evaluative substrates for positivity and negativity are not entirely symmetrical. Organisms tend to be more sensitive to negative or threatening information and generally process such information faster than positive or rewarding information (Ito & Cacioppo, 2000). This *negativity bias* likely emerged as a protective strategy through evolution,

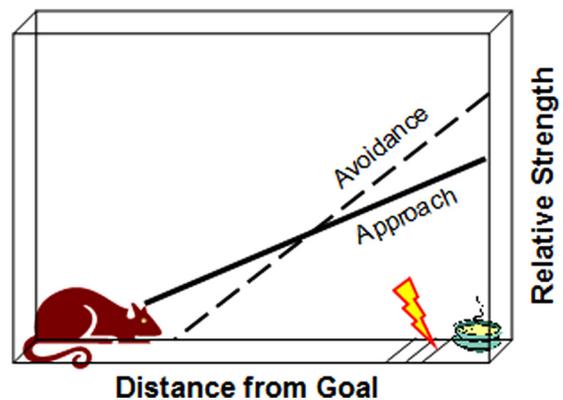


Figure 3. Miller’s approach–avoidance conflict. Approach and avoidance gradients as a function of distance from the goal. Goal items include food (positive incentive) and shock (negative incentive). The avoidance gradient has a steeper slope, and predominates proximal to the goal box (negativity bias), whereas at more remote loci, the approach gradient is higher than the avoidance gradient (positivity offset). The intersection of the gradients represents the maximal conflict point, where approach and avoidance dispositions are equivalent.

since even a single failure to respond adaptively to a survival threat may preclude passing on genetic information. As a potential threat looms, the adaptive response of the brain is to amplify these threats and initiate appropriate behavioral responses, such as fleeing, freezing, or attacking. The negativity bias can be seen across all levels of the neuraxial organization. Another example comes from research on the perception of taste. While humans are capable of tasting sweet, salty, sour, and bitter stimuli, we tend to be more than an order of magnitude more sensitive to bitter stimuli, which are typically experienced as aversive. This may have evolved in part due to the fact that most poisons have a bitter taste. The negativity bias is not limited to sensory systems, as incidental learning of the spatial location of affective stimuli is greater for negative as opposed to positive information (Crawford & Cacioppo, 2002). Other examples of the negativity bias are legion (see Cacioppo et al., in press; Norris et al., 2010).

In addition to the negativity bias, Miller's studies also revealed a phenomenon that has come to be known as the *positivity offset* (Cacioppo & Berntson, 1994; Ito & Cacioppo, 2005; Norris et al., 2010). The positivity offset refers to the fact that the approach gradient often surpasses the avoidance gradient as the distance to the goal increases beyond the equilibrium point (see Figure 3). Therefore, when likely threats are not immediately present, positive evaluations tend to predominate and organisms tend to be characterized by more approach-related behaviors and exploration. The positivity offset is thought to allow an organism to potentially discover new food sources and sexual partners and to gain a more comprehensive understanding of its environment when the probability of threat or attack is low (Norris et al., 2010). With a positivity offset, an organism facing neutral stimuli would be at least weakly motivated to approach and explore, and with the habituation of the initial fear response to unfamiliar stimuli, to display further engagement with the environment. Indeed, the coupling of an initial neophobia and subsequent exploratory tendencies may have appreciable survival value, at least at the level of a species.

From the general perspectives outlined before, the subsequent sections detail illustrative instantiations of evaluative networks at diverse levels of the neuraxis.

Levels of Function: Lower Levels and Spinal Reflexes

As noted above, spinal reflex networks represent the lowest and most primitive levels of organization in the central nervous system. Within the ventral horn of the spinal cord reside all lower motor neurons controlling the skeletal muscles of the trunk and limbs, and all somatosensory information from these structures enters the nervous system at the level of the cord. In addition to serving as the final common pathway for higher motor control of the musculature and a conduit for transmission of somatosensory information, primitive integrative organizations are also present at the level of the cord. Although spinal networks may have limited functions, they offer advantages for

the study of neurobehavioral relations, precisely because of their simplicity. Spinal circuits reveal the basic functional architecture that characterizes neural organizations at all levels of the neuraxis (for historical introduction, see Sherrington, 1906). Higher level neural networks evidence similar organizational schemes and adhere to common functional principles as seen at lower levels, but these schemes and principles may be more difficult to discern and rostral anatomical systems and functional relations may be more elaborate and distributed (Berntson & Cacioppo, 2008; Cacioppo & Decety, 2009).

Spinal substrates of the bivalent flexor/extensor reflexes serve as model evaluative systems. As is the case for higher level evaluative networks, spinal reflexes display a characteristic negativity bias. Flexor withdrawal reflexes are more salient and powerful compared to extensor reflexes, are the earliest to develop, and are the most resistant to disruption. They prevail over extensor reflexes at higher levels of stimulus intensity and associated evaluative activation. Motivational constructs are generally not invoked to account for flexor withdrawal reflexes, as an adequate explanation can be found in the structure of the relatively simple underlying neural circuits and their interactions. Nevertheless, such behaviors represent a well-conserved primitive premotivational disposition to avoid particular classes of stimuli that can serve as a model for understanding higher level adaptive behaviors which entail clear motivational properties. The potency of protective reactions to noxious stimuli is thus readily apparent at the lowest level in evaluative networks, as well as in the overwhelming emotional and motivational effects of pain and the aversive reactions to pain arising from higher neuraxial levels.

Despite this negativity bias, flexor/withdrawal reflexes are not always dominant over their opponent processes as extensor/approach reflexes can take precedence at lower levels of stimulation or activation. Extensor reflexes promote engagement with the environment (e.g., support, locomotion, exploratory responses) and acquisition or consumption of objects (grasping, mouthing, etc.). The disposition toward approach behaviors in the context of low levels of evaluative activation represents a spinal instantiation of the *positivity offset* (Figure 3; Cacioppo & Berntson, 1999; Cacioppo, Larsen, Smith, & Berntson, 2004) that characterizes the operations of evaluative or motivational dispositions at higher levels of the neuraxis.

The opposing actions of flexor and extensor reflexes illustrate the general pattern of bivalence in the neural architecture of evaluative networks. The direct neural circuits underlying these bivalent response systems are distinct and independent, although interacting. They entail distinct receptors and sensory afferents, separate spinal interneuron circuits, and distinct motor neuron pools. As noted above, this relative independence is physically constrained by flexor and extensor muscle insertion and articulation at the joints (Figure 4). In addition to physical constraints, there exist inhibitory neural interactions between the flexor and extensor circuits. Inhibitory interneuron circuits exert mutual reciprocal inhibition between flexor and extensor motor neurons—a principle of neural organization that Sherrington (1906) termed *reciprocal innervation*. Reciprocal

innervation is the property by which spinal reflex networks activating a specific outcome (e.g., limb flexion) also tend to inhibit opponent (e.g., extensor) muscles, which synergistically promotes the target response. This pattern of reciprocal innervation may also characterize the interactions of rostral positive and negative evaluative networks and may constrain the degree of coactivation of these substrates, despite the basic bivalence of the underlying systems.

An understanding of the integrative outputs of spinal flexor/extensor circuits offers a basic neuroarchitectural perspective for models of higher level evaluative networks. Although as depicted in Figure 4, higher level systems are more flexible and elaborated, many of the basic architectural features are shared with those of lower substrates by virtue of their common evolutionary heritage and adaptive functions. Moreover, the extensive interactions between higher level systems and spinal networks, such as in fear potentiation of spinal flexor responses, highlight the heterarchical nature of evaluative systems.

Levels of Function: Intermediate Levels—Brainstem

The primitive approach/withdrawal dispositions characteristic of spinal reflexes are substantially developed and elaborated at the level of the brainstem. Classical demonstrations of the functional capacity of brainstem networks come from studies of experimental decerebration, or isolation of the brainstem and spinal cord in animals and from tragic cases of human decerebration

(anencephaly and hydranencephaly) resulting from failure of rostral cell migration and development (Berntson & Micco, 1976; Berntson, Tuber, Ronca, & Bachman, 1983; Harris, Kelso, Flatt, Bartness, & Grill, 2006; Ronca, Berntson, & Tuber, 1986; Yates, Jakus, & Miller, 1993). Decerebrate animals show highly organized escape, avoidance, and defensive behaviors in response to aversive stimuli as well as approach/ingestive responses to palatable tastes. Similarly, considerable functional capacity is also apparent in cases of human decerebration, although these infants typically do not survive for more than a few weeks after birth. They nevertheless show a relatively intact array of infantile reflexes, including flexor and extensor reflexes, stepping reflexes, and a wide range of brainstem reflexes including tonic neck reflexes, the Moro reflex, and suckling reflexes, among others.

Similar to spinal flexor and extensor reflexes, the basic brainstem substrates for positive and negative evaluative processes appear to be distinct and at least partially independent (Berntson et al., 1993; Berridge & Grill, 1984; Steiner, Glaser, Hawilo, & Berridge, 2001). Brainstem neurobehavioral substrates are more complex and elaborate than the relatively rigid and tightly organized reflex, networks of the spinal cord; however, both decerebrate animals (Mauk & Thompson, 1987; Norman, Buchwald, & Villablanca, 1977) and humans (Berntson et al., 1983; Tuber, Berntson, Bachman, & Allen, 1980) display neural plasticity and associative learning that can modulate neural networks through experience.

Among the more thoroughly studied of brainstem processes are those supporting approach–avoidance action dispositions related to taste hedonics. Similar to the organization of the

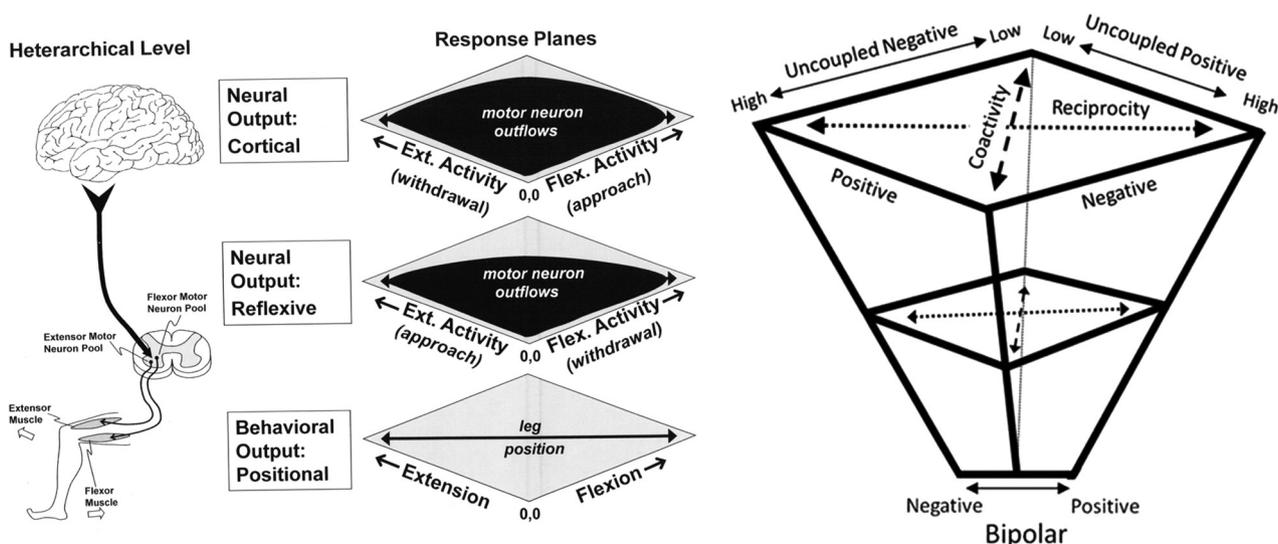


Figure 4. Illustrative levels of organization in somatomotor systems. **Left:** Upper and lower motor neuron regulation of flexion and extension (heterarchical level) and relative output planes (response planes). Arrows and darkened area illustrate the potential patterns of activation or output. At the lowest level, physical constraints limit output to a single continuum from flexion to extension. Broader patterns of output are possible at higher levels of neural organization, which can yield varying degrees of coactivation of flexor and extensor motor neurons (darkened areas of the response planes). **Right:** Levels of evaluative space. Lower (spinal) levels are characterized by bipolar modes of operation whereas higher levels of functioning (e.g., neocortex) are capable of more complex bivariate activation patterns.

spinal cord, the neuroarchitecture underlying positive and negative gustatory hedonics appears to operate in parallel and under independent control in brainstem circuitry (Berntson et al., 1993; Berridge, 2004; Berridge & Grill, 1984; Steiner et al., 2001). Taste hedonics and associated intake/rejection responses offer a prime example of brainstem evaluative systems. Orofacial displays to taste, represented by stereotyped, reflex-like negative rejection/ejection responses to aversive stimuli (gaping, tongue protrusion) and positive intake responses (smiling, licking, swallowing) to palatable stimuli are well conserved through phylogeny and speciation. These responses can be seen early in development and are readily apparent in decerebrate organisms in the absence of more rostral neural tissue.

The positive and negative responses to gustatory stimuli mirror the reflexes of the spinal cord in that they are coupled to opposing patterns of approach/avoidance dispositions, although this is not always the case in higher evaluative networks. Similar to spinal reflexes, the behavioral output of these systems cannot be interpreted as lying along a single bipolar continuum extending from positive to negative or from approach to avoidance. Although a bipolar depiction may account for some features of intake/rejection behavior, it belies the underlying complexity of hedonic processes. Experimental evidence suggests that gustatory hedonic systems are partially independent and do not converge on a single hedonic integrator (Berridge, 2004; Berridge & Grill, 1984).

Just as one can tighten extensor and flexor muscles simultaneously, intake and rejection responses are not incompatible and can be coactive. Although the probability of negative rejection responses to a glucose solution increases with the addition of a bitter compound, this can occur without a reciprocal elimination of positive intake responses (actual consumption may be diminished because of physical interference). Similarly, increasing both bitter and sweet concurrently leads to increases in both intake and rejection responses (Berridge & Grill, 1984). Thus, taste preference, as measured by behavioral consumption and represented on a bipolar scale, may not accurately reflect the underlying bivariate hedonic systems. This does not rule out interactions between hedonic networks, of course, but suggests that mixing positive and negative hedonic stimuli does not simply yield a null average of the two, or a state of hedonic indifference (Berridge & Grill, 1984).

Gustatory hedonics further illustrates the multilevel interactions in heterarchical evaluative networks. Hunger, signaled by higher limbic substrates, can modulate the sensitivity of brainstem gustatory hedonic networks. Similarly, salt deprivation leads to a specific behavioral preference for salty tastes that is related in part to changes in neural sensitivity in brainstem gustatory substrates (Jacobs, Mark, & Scott, 1988). These reflect the extensive ascending and descending interactions in evaluative systems.

Levels of Function: Higher Level Rerepresentations

As one moves from the lowest to the highest levels of the neuraxis, the rerepresentation and elaboration of processes essential

to motivation become increasingly apparent. While brainstem and spinal structure are remarkably sensitive to aversive and hedonic stimuli, they lack much of the behavioral flexibility and adaptability of higher level systems. Although decerebrates may ingest palatable foods, they do not display typical goal-seeking behavior in the absence of a food stimulus, but rather are prisoners of immediate environmental conditions and contexts (see Berntson et al., 1993; Berntson & Micco, 1976). It is with the development of more rostral brain structures, such as the limbic system and neocortex, that one begins to see the emergence of goal-directed behaviors that reflect anticipatory processes and expectancies that are characteristic of higher organisms. Moreover, while lower premotivational substrates may entail simple approach/withdrawal dispositions, higher motivational processes become further differentiated, nuanced, and less directly tied to specific approach/avoidance responses.

Berridge and Kringelbach (2008) characterize the “liking” aspects of motivation as those which entail the hedonic and response-eliciting properties of a stimulus or motivational context. These are apparent in the orofacial intake/ingestive responses to positive hedonic tastes as described above in decerebrates. The decerebrate, however, largely lacks what Berridge terms the “wanting” aspects of motivation, which entail an attentional focus on and goal-seeking behaviors directed toward a desired stimulus or state. This latter aspect of motivational processes is heavily dependent on the increased computational capacity of higher levels of the neuraxis and is mediated by more elaborate neural circuitry. It should not be surprising that the neuroarchitecture of higher evaluative processes entails more complex and distributed networks, which are not as clearly delimited nor as cleanly dichotomized into positive and negative substrates as is the case with lower level representations. Indeed, many computational, attentional, and memorial processes may be routinely deployed for both positive and negative evaluative processing. Systems underlying positive hedonics, reward, and approach may play a role in aversive contexts in guiding behavior toward a positive safety context or outcome (Ikemoto & Panksepp, 1999). Thus, positive and negative evaluative processes may not map as cleanly onto simple motoric approach/avoidance dispositions, but rather into more complex behavioral strategies for goal-directed outcomes.

In line with the heterarchical model, common organizational principles manifest at diverse levels of evaluative functions. Similar to findings with premotivational spinal reflexes, the magnitude of a response of higher level systems to negative stimuli has often been reported to be larger than to positive stimuli (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Pratto & John, 1991). This negativity bias is seen in diverse attentional paradigms such as identification of negative versus positive emotional faces, and in event-related potential markers of the early stages of evaluative processing (Cacioppo et al., 2004; Ito & Cacioppo, 2000; Ito, Larsen, Smith, & Cacioppo, 1998; Öhman & Mineka, 2001). While this negativity bias has been considered obligatory at spinal levels, it may be subject to modulation at higher level motivational and evaluative processes (Berntson & Cacioppo, 2008; Smith et al., 2006).

Neural Substrates of Higher Level Evaluative Systems

Although the findings mentioned above are consistent with a differentiation of positive and negative neural substrates at higher levels of the neuraxis similar to that seen at lower levels, there are added complexities in higher networks. For example, the nucleus accumbens (nACC), a structure historically associated with reward, is comprised of discrete subcomponents with important phenomenological and computational distinctions. The “liking” (positive hedonic effect, reward) and “wanting” (incentive salience, goal-striving) aspects of hedonic states are mediated by distinct anatomical regions of the nACC (Berridge, 1996; Pecina, Smith, & Berridge, 2006). Moreover, the neural network mediating “wanting” is far more distributed throughout the neuraxis, likely attributable to the importance of motivational drive on evolutionary fitness. “Wanting” and “liking” are further differentiated by their neurochemical substrates. The motivational drive (“wanting”) can be modulated by manipulation of endogenous dopaminergic signaling without altering “liking” responses (Berridge & Kringelbach, 2008). Conversely, “liking” appears to be more dependent on opioid, cannabinoid, and GABAergic signaling (Berridge & Kringelbach, 2008). Such complexities caution against the overly simplistic ascription of discrete neural loci to the mediation of complex neuropsychological phenomena (Cacioppo & Decety, 2009). Nevertheless, there remain differentiations between higher neural substrates mediating positive and negative evaluative processes, and this is also apparent in lateral differences in representation of positive and negative evaluative systems (Craig, 2005; Davidson, Shackman, & Maxwell, 2004; Harmon-Jones, Vaughn, Mohr, Sigelman, & Harmon-Jones, 2004; Rutherford & Lindell, 2011).

In contrast to the predominant involvement of the nACC in positive affect, the amygdala has been implicated more in negative affect. Since the classic studies of Walter Rudolf Hess (1954) on brain stimulation in the waking animal, this structure has been implicated in fear and negative affect. In general accord with animal studies, imaging studies in humans have reported amygdala activation during emotion, especially with negative emotions (Critchley et al., 2005; Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005; Zald & Pardo, 1997), and patients with amygdala damage have been reported to show attenuated negative affect (Tranel, Gullickson, Koch, & Adolphs, 2006) and deficits in emotional memory (Buchanan, Tranel, & Adolphs, 2006; LaBar & Cabeza, 2006; Phelps, 2006; Phelps & LeDoux, 2005). In a recent study, Berntson, Bechara, Damasio, Tranel, and Cacioppo (2007) found that patients with amygdala damage were similar to control and normative groups in the ability to recognize and appropriately label the valence of positive and negative stimuli (Figure 5). Additionally, when asked to rate the emotional arousal to each stimulus, patients with amygdala lesions were comparable to control groups in their ratings of neutral and positive pictures. However, when tested on the ratings of emotional arousal to negative stimuli, amygdala patients showed a selective decrease in emotional arousal

to negative stimuli. This is in accord with the report of a selective loss of fear reactions in a patient with bilateral amygdaloid lesions, despite the ability to recognize danger and fear-related conditions (Feinstein, Adolphs, Damasio, & Tranel, 2011). Despite this extensive literature, the role of the amygdala may not be limited to the processing of negative stimuli, as it has also been implicated in arousal, regardless of valence. This may be illustrative of the progressive convergence in neural hierarchies and the complexity of processes underlying higher evaluative processes.

Another rostral system implicated in evaluative and affective processes is the insular cortex. As a polysensory integrative system, the insula has been suggested to serve as a substrate for representation of the state of the body, including both visceral and somatic components (Craig, 2009; Saper, 2002). Over a century ago, William James (1884) proposed that emotions were the perceptual consequences of somatovisceral feedback from bodily responses. Although the construct of emotions as merely the perceptual consequences of somatovisceral feedback is no longer tenable, it is increasingly recognized that visceral afference may importantly modulate affective and cognitive processes (Bechara & Damasio, 2005; Craig, 2009; Critchley, 2009). Visceral afference, for example, has been reported to impact emotional memory and cortical reactivity, in part via ascending relays through an interconnected network of structures including the amygdala, the basal forebrain cholinergic system, and the insula (Berntson, Sarter, & Cacioppo, 2003; Roozendaal, McEwen, & Chattarji, 2009).

This convergence of visceral and somatosensory information in the insular cortex has been suggested to support interoceptive representations, and their segue through the anterior insula may represent a fronto-insular junction linked to networks involved in affective processes, including the prefrontal cortex and the amygdala (Craig, 2009; Critchley, 2009). These and other findings have led to the suggestion that the insular cortex may play a particularly broad role in cognitive/emotional integration and to the subjective guidance of cognition and behavior (Bechara, Damasio, & Damasio, 2003; Craig, 2009; Damasio, 1999; Singer, Critchley, & Preusschoff, 2009). Consistent with this line of reasoning, Berntson et al. (2011) demonstrated that in contrast to the selective effects of amygdala lesions on emotional arousal, lesions to the insula resulted in a more diffuse blunting of valence ratings and arousal ratings to both positive and negative stimuli (Figure 5). Individuals with insula lesions rated unpleasant stimuli as less negative and less arousing and rated pleasant stimuli as less positive and less arousing when compared to amygdala lesion and contrast lesion patients (Berntson et al., 2011). This appeared to reflect a general blunting of the capacity to process positive and negative stimuli, likely related to its extensive connections with higher limbic and cortical mechanisms.

The broad effects of insula lesions on both affect and cognition emphasize the progressively more integrative role of higher neural networks. This increasing integrative capacity tends to obscure, but does not preclude, the separability of positive and negative evaluative networks. The pivotal integrative role of the

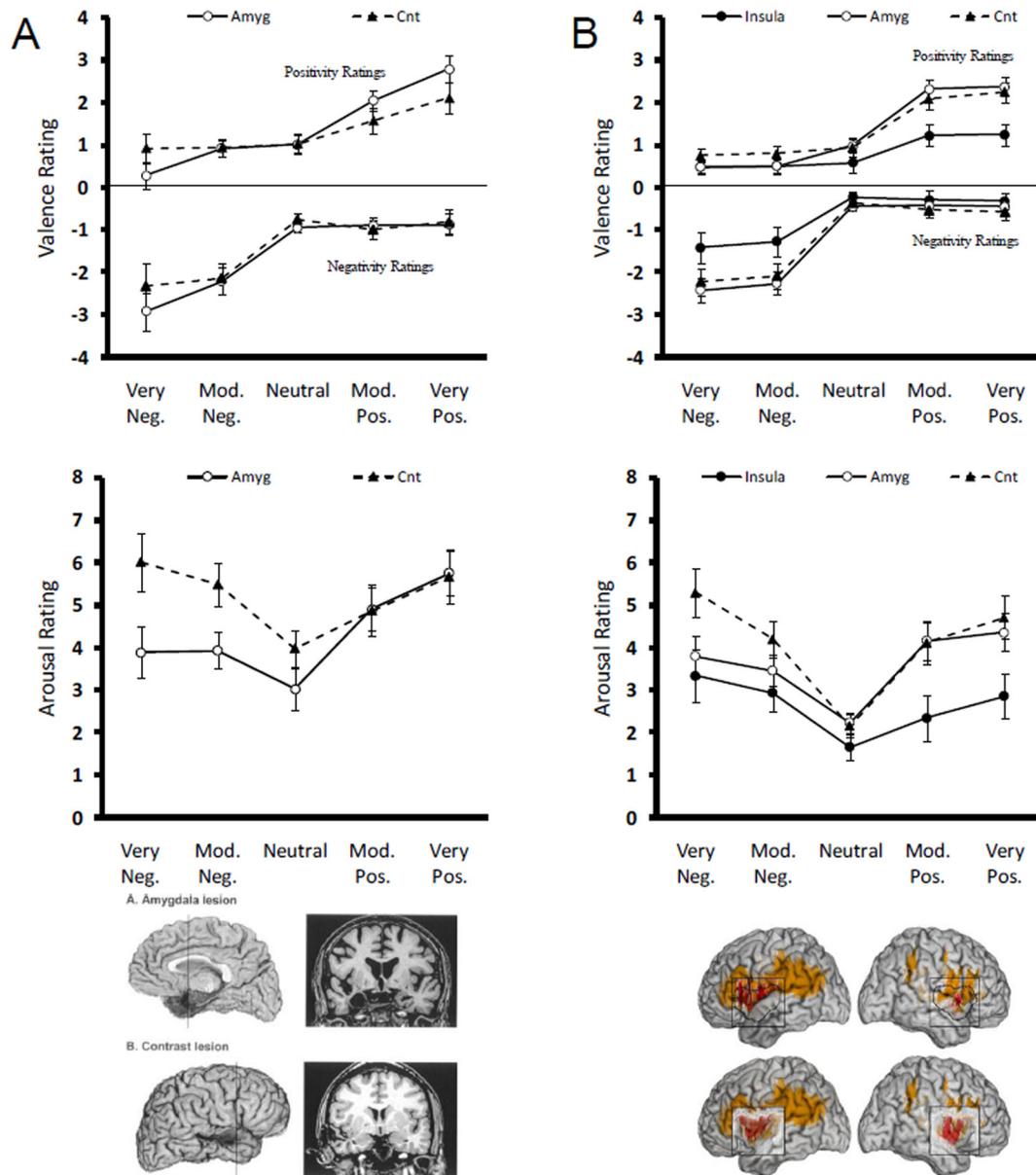


Figure 5. Effects of amygdala and insula lesions on evaluative ratings. **(A)** Ratings (mean, SEM) of valence (upper) and arousal (lower) of picture stimuli ranging from very negative to very positive, by patients with amygdala or contrast lesions. Both groups effectively discriminated and categorized the stimuli. Both groups also displayed comparable arousal functions to positive stimuli, but the amygdala group showed diminished arousal selectively to the negative stimuli. **(B)** Ratings (mean, SEM) of valence (upper) and arousal (lower) to picture stimuli ranging from very negative to very positive, by patients with insula, amygdala or contrast lesions. Patients with insula lesion displayed a global reduction in emotional arousal to both positive and negative stimuli and also showed a blunted ability to correctly identify and/or label such stimuli according to their positive or negative picture content. This suggests a much broader role for the insula in both positive and negative evaluative processing and for both cognitive and affective aspects.

insula via both its ascending and descending projections further highlights the importance of interactions among levels in heterarchical systems (Craig, 2009). In their iterative-reprocessing model, Cunningham and Zelazo (2007) argue for a reciprocal, recurrent communication across distinct spatial and temporal dimensions of neural processing. According to this model, lower level substrates provide affectively laden information

regarding the valence and the arousal dimensions of a stimulus or context that serve to guide higher evaluative processing substrates. Higher level prefrontal cortical systems are then able to utilize this information to subsequently modulate processing at lower levels (see Cunningham & Zelazo, 2007). The multiplicity in heterarchical levels certainly complicates attempts at simple isomorphic mappings between fundamentally bivalent

systems and the underlying neural substrates (Berntson, 2006; Cacioppo & Decety, 2009). Nevertheless, behavioral and psychological approaches continue to document the cardinal principle of evaluative bivalence. Grabenhorst, Rolls, Margot, da Silva, and Velazco (2007), for example, find that positive and negative odors presented separately induce consistent and distinct patterns of brain activation. In accord with the bivariate model, mixtures of positive and negative odors do not diminish or neutralize these activations, but rather result in a more robust activation that includes both general patterns of activation.

Summary

With recent theoretical and technological advances, scientifically relevant conceptualizations of affective processes and their neural substrates are now possible. The bivariate multi-level model of evaluative space allows for the inclusion of new theoretical constructs and empirical evidence which can resolve competing hypotheses, generate new and testable hypotheses, and increase theoretical breadth and depth leading to better conceptualizations of affective phenomena. Theories that assume strictly bipolar models of evaluative processes have difficulty accounting for evidence from the neurosciences that show distinct neural substrates are coactivated in the presence of appetitive and aversive stimuli, nor do these theories incorporate the influence of evaluative mechanisms organized at lower levels of neuraxis. The evaluative space model provides a more comprehensive conception of evaluative processes and subsumes, rather than discards, more limited bipolar models of affect.

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