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BRAIN MECHANISMS
PAPERS IN MEMORY OF ROBERT THOMPSON

Edited by Francis M. Crinella and Jen Yu



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BRAIN MECHANISMS
PAPERS IN MEMORY OF ROBERT THOMPSON^a

Editors

FRANCIS M. CRINELLA AND JEN YU

Conference Organizers

FRANCIS M. CRINELLA AND GARY MORPHIS

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Neurobehavioral Organization and the Cardinal Principle of Evaluative Bivalence^a

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INTRODUCTION

The fundamental dimensions of neuraxial organization likely hold the keys to an understanding of neurobehavioral relationships. Recent developments in neuroscience have made dramatic inroads into the mysteries of neuronal function. These developments are particularly striking in view of the fact that the neuron theory was still being debated 60 years ago (Cajal, 1954 as cited in Reference 1), that neurochemical transmission was documented less than 80 years ago,² and that Hodgkin and Huxley's³ clarification of the ionic bases of neural activity is less than 50 years old. Throughout this development, it has become apparent that the identification of basic principles of cellular function can illuminate a wide range of neural operations. A parallel evolution has also been apparent in our understanding of the operations of neural systems and of the broader organizational features of the brain and spinal cord. Early stimulation and lesion studies of Fritsch and Hitzig⁴ and Ferrier⁵ demarcated sensory and motor areas of the cortex, and case studies of Bouillaud, Broca, and Wernicke suggested a further functional differentiation of cerebral areas. The surgical extirpation studies of Fluorens⁶ further indicated a differentiation of functional contributions across neuraxial levels.

These early findings raised the question as to the fundamental dimensions and organizational principles underlying patterns of neuroanatomical differentiation. While the demarcation of sensory and motor systems has considerable historical and intuitive appeal, as well as clear anatomical and functional bases, this distinction blurs as one proceeds from lower motor or sensory neurons to

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higher processing levels. While an appreciation of basic sensory and motor processes is necessary for the understanding of behavior, it is insufficient. The sensory/motor distinction, for example, is difficult to cleanly impress on perceptual, motivational, emotional, or cognitive phenomena. Indeed, as the level of functional neural organization increases, the expanding complexity poses an increasing challenge to efforts to reduce its operations to elementary dimensions or principles. At the same time, an understanding of the complex operations of higher systems increasingly demands a reduction to more manageable organizing principles. The alternative is the invariable devolution into fact lists and elaborated microtheories with limited generality.

Several salient organizational principles or dimensions have been recognized historically in central neural systems. These principles provide an important conceptual vantage point or structure that can facilitate interpretation of data, guide experimental studies, and foster the development of theory. In view of the complexity of the nervous system, it is not surprising that multiple organizational dimensions are apparent. We briefly outline three broad neuroarchitectural schemas, reflecting hierarchical, concentric, and centrencephalic features of neural systems. These dimensions are not mutually exclusive, but capture distinct aspects of neuraxial structure. We then consider an additional organizational feature of neural systems, representing an orthogonal dimension which cuts across hierarchical, concentric and centrencephalic structures. This dimension manifests itself in evaluatively bivalent behavioral dispositions (positive/negative, approach/avoidance, appetitive/aversive) to environmental stimuli or contexts. This feature permeates all neuraxial levels and organizational dimensions, and itself constitutes an important neurobehavioral organizing principle.

Veridical evaluations of the adaptive significance of environmental objects and events are so central to survival that all species have biological mechanisms for approaching, acquiring, or ingesting certain classes of stimuli; for withdrawing from, avoiding, or rejecting others; and for the establishment of enduring response predispositions toward classes of stimuli. The evaluative dimension has been widely recognized as a pervasive organizing principle that captures the bivalent component of behavior.^{7,8} The evaluative theme has emerged across diverse disciplines, and is represented in theoretical conceptions ranging from the behavioral economics of bees⁹ and the neurobiology of adaptive reflexes,^{10,11} to the social psychology of attitudes.^{12,13} Evaluate processes represent a fundamental aspect of neurobehavioral organization that manifests itself widely in perception, motivation, emotion, learning, and cognition. This principle has arisen repeatedly in the behavioral literature, given its explanatory power. At the same time, the evaluative dimension has also been historically interwoven, explicitly or implicitly, into conceptions of neurological organization. Indeed, the ubiquity of the evaluative dimension of behavior across ontogeny, phylogeny, and encephalization, suggests that this dimension may reflect a fundamental pattern of neural organization. While not providing a complete account of behavior, the ubiquity of evaluative processes in behavioral contexts offers a powerful organizing dimension for the understanding of neurobehavioral relationships.

THREE MAJOR DIMENSIONS OF NEUROBEHAVIORAL ORGANIZATION

The Hierarchical Dimension

The emerging Darwinian perspective of the nineteenth century inspired concepts of a hierarchical organization of neural levels progressively layered through phylogeny.¹⁴ In his essay "Evolution and Dissolution of the Nervous System," John Hughlings Jackson¹⁵ further developed the hierarchical concept of the functional organization of the brain. Based on studies of the epilepsies, and on the consequences of brain damage, Jackson proposed that "higher levels of the nervous system represent and re-represent all lower nervous centers and thus the organism as a whole."¹⁵ Higher levels of the neuraxis were believed to entail a progressive elaboration of functional organizations, which ranged from representations of discrete muscles at the lowest level, to movements and actions, and ultimately to intentions, outcomes and consciousness. According to Jackson, the consequences of injuries to higher level systems could best be understood not by losses of functions, but rather by "dissolution" of functions to more basic representations at lower levels of the neuraxial hierarchy. In accord with the suggestions of Fluorens,⁶ of Fritsch and Hitzig,⁴ and of Ferrier,⁵ Jackson believed that the highest level of this integrative hierarchy resides in the cerebral cortex (especially the frontal lobes). The focus on the cerebral cortex as the highest integrative organ of the brain was perhaps epitomized in Pavlov's "transcortical" theory of association, in which lateral associative connections among cortical analyzers served as the neural substrates for learning and memory.¹⁶ Pavlov's "second signal system" was also believed to be a product of the operations of the cerebral cortex.

The Concentric (Parallel) Dimension

Empirical support for the hierarchical concept of neuraxial organization has continued to amass since the turn of the century. Hierarchical neural organizations have been documented at the anatomical, neurophysiological, and behavioral levels.^{14,17} While vertical hierarchical features of neuraxial organization are well established, deviations from, or additions to this neuro-architectural model have been recognized. A horizontal or concentric dimension of neural organization was suggested by early embryological studies of somitic development in ontogeny, which emphasized the central-peripheral course of neural development.^{14,18} Embodied in this view is the concept of a general, non-differentiated central substrate from which more specialized lateral or peripheral systems emerge through ontogeny. Thus, while embryonic neural crest cells may be functionally pluripotential,¹⁹ differentiation and functional heterogeneity, together with a constriction of potentiality, emerge with outward migration of these cells.²⁰

This generalized-specialized, central-peripheral dimension of neural architecture is manifested within segmental levels by the existence of parallel neur-

axial systems which are clearly apparent in both sensory and motor systems. In now classic studies, Lawrence & Kuypers^{21,22} suggested that descending motor pathways to the cord could be divided into two major functional groups: (1) a lateral system descending in the lateral funiculus (corticospinal, rubrospinal), terminating in the dorsolateral spinal gray, and ultimately influencing motor neurons controlling the distal musculature; and, (2) a ventromedial system descending in the ventral funiculus (reticulospinal, tectospinal, vestibulospinal), terminating in the ventromedial spinal gray, and influencing proximal and axial muscles. Corresponding to these anatomical differences, disruption of these two descending pathways yields distinct functional consequences. Damage to the lateral funiculus and/or the pyramidal tract yielded deficits primarily in independent movement and fine control of the distal musculature, while destruction of the ventral funiculus resulted in deficits in balance and postural control. A similar parallel organization is also apparent in sensory systems, as illustrated by the ascending somatosensory pathways of the dorsal column and anterolateral systems. These parallel systems differ in fiber characteristics, number and properties of synaptic relays, terminal fields, somatotopic organization, and receptive field characteristics.¹ These pathways provide parallel routes to higher neural systems, and subserve differentiated functional roles in somesthesia. A similar example is evident in the multiple, parallel visual pathways to the cortex, which (1) derive from different retinal ganglion cell populations, (2) terminate on segregated geniculate relay neurons, (3) follow alternate processing routes in visual cortical systems, and (4) subserve differentiated functions.²³

The Centrencephalic Dimension

The concept of specialized lateral systems surrounding a less differentiated central neural core was compatible with emerging functional perspectives of the middle of the current century. In 1949, Moruzzi and Magoun published a classic paper describing the widespread activation of the cortical EEG on stimulation of the reticular formation (see Reference 14), and shortly thereafter lesions of the rostral reticular formation were shown to yield EEG and behavioral coma.²⁴ These findings ignited a flurry of studies, and led to the concept of an Ascending Reticular Activating System (ARAS). The ARAS was considered to exert important control over the functional state of the cerebral cortex and other higher neural systems. The apparent association between this reticular substrate and arousal, attention, and consciousness¹⁴ suggested an important executive function for the central core of the brainstem, which strains the Jacksonian hierarchical model of neuraxial organization.

The distinguished neurologist Wilder Penfield offered a potential reconciliation of these findings with the Jacksonian hierarchical model.^{25,26} Penfield states:

Like Hughlings Jackson, our own study of epilepsy and epileptic patients has forced us to the conclusion that there is an area in the central nervous system devoted to the integration of the functions of the sensory and motor areas of the cortex, an area in which is to be found the "neural substratum

of consciousness." But it is not situated in the anterior frontal cortex as he suggested.

(Ref. 26, p. 473)

Penfield pointed to the fact that consciousness may be preserved during ictal episodes of cortical origin, or is lost only after epileptiform activity has invaded widespread brain areas. In contrast, he argued that pure epilepsies of consciousness (*petit mal*) are invariably of subcortical origin. These and other observations led Penfield to the view that it is a subcortical "centrencephalic" system that represents the highest integrative level of the brain:

The vast interconnected network of cells and fibers in the cortical matrix must . . . constitute an essential part of the machinery of the mind. But without the constant selective activating influences of the reticular network of the higher brain stem, the cortical mantle lies dormant. Without an integrated system for control of excitatory and inhibitory effects upon local cortical functions of the two hemispheres, co-ordination of cortical function as a whole would be impossible.

(Ref. 26, pp. 481f.)

Consistent with this suggestion, Thompson, Crinella, and Yu²⁷ have amassed considerable evidence for an integrative contribution of central core systems to problem-solving and "intelligence." On the basis of an extensive series of lesion studies employing a wide variety of tasks, Thompson *et al.* found that lesions of many brain areas, while compromising learning or performance of specific tasks, do not generally impair problem-solving functions. In contrast, lesions of a set of central core structures appear to generally disrupt learning and problem-solving, on a wide variety of tasks, independently of specific sensory or motor impairments. These subcortical structures, including the basal ganglia, substantia nigra, ventral tegmental area, superior colliculus, medial raphe, and pontine reticular formation, are believed to play an important integrative or executive function in neurobehavioral processes.

This centrencephalic dimension of neuraxial organization is not inconsistent with the possibility of hierarchical relationships among neural systems. It does highlight, however, the fact that lower levels of the neuraxis do not necessarily assume a subordinate role in these relationships. The essence of the centrencephalic view is that ascending influences from lower neural levels, in addition to their role in the pre-processing and transmission of afferent information, can potentially exert executive or controlling influences on higher neural mechanisms. Together with the hierarchical principle of neural organization, the centrencephalic concept emphasizes the potentially powerful bi-directional interactions among vertical neuraxial levels.

THE ORTHOGONAL DIMENSION OF EVALUATIVE BIVALENCE

Evaluative processes are so central to survival, so universal through ontogeny and phylogeny, so ubiquitous across environmental contexts, and so pervasive in behavioral manifestations, that they likely reflect a fundamental

feature of neural organization. Evaluative dispositions are apparent in the operations of neural systems extending from the spinal cord to the highest levels of the neuraxis. Indeed, the evaluative dimension appears to cut across the hierarchical, concentric, and centrencephalic dimensions of neural organization.

The Evaluative Dimension in Behavior

As considered here, evaluative processes entail an explicit behavioral or incentive valence, which disposes the organism toward or away from specific environmental stimuli or contexts. Two features characterize evaluative dispositions, and differentiate these dispositions from other types of response biases or tendencies. The first is an explicit evaluative categorization of a stimulus into positive or negative valence classes. This classification may be based on an evolutionary heritage, through which neural systems come to be constitutionally turned to adaptively significant stimuli. Alternatively, learning processes based on environmental experience may endow stimuli or stimulus classes with evaluative significance.²⁸ The second defining characteristic of evaluative processes is the invocation of behavioral dispositions, which entail bivalent tendencies toward (e.g., approach, acquisition, or consumption) or away (avoidance, escape, or rejection) from the stimulus. At lower levels of behavioral organization, evaluative dispositions may be closely tied to highly specific responses (e.g., pain-withdrawal reflexes). In other cases, especially those related to higher organizational levels, evaluative processes may be expressed in a wide range of highly flexible behavioral manifestations (e.g., attitudes).

At higher levels of behavioral organization in humans, evaluative dispositions may be characterized by subjective descriptors (pleasurable, painful, desirable, disagreeable). While these subjective components may reflect perceptual reactions to evaluative dispositions,²⁹ they are not a necessary feature of those dispositions. Indeed, evaluative dispositions can be operative, even in humans, in the absence of consciousness awareness.^{30,31} Moreover, specific affective or "hedonic" reactions to taste stimuli, closely tied to the palatability of the stimuli, can be identified even in decerebrate organisms.^{10,32}

The utility of the evaluative dimension derives from the fact that behavior, at diverse functional levels, often organizes along evaluative lines. Thus, the chemical senses literature has historically retained the concept of affective (positive/negative) reactions, given its utility in characterizing responses to gustatory stimuli.^{10,33} The highly stereotyped oro-facial reactions of normal and anencephalic neonates to olfactory and gustatory stimuli further suggest a basic organization of these dispositions.³⁴ The evaluative dimension has also proven to be a powerful factor in accounting for the contextual modulation of basic defensive reflexes, such as eyeblink to a startle stimulus.¹¹ At more complex levels of behavioral organization, perhaps the best known research addressing the centrality of evaluation in humans is Osgood, Suci, and Tannenbaum's³⁵ classic research on the factors or dimensions underlying people's representation and understanding of the world. Across multiple studies and cultures, the

evaluative dimension (e.g., good/bad, positive/negative) was found to be primary. The evaluative dimension has also emerged as a dominant organizing factor in cross-cultural, multidimensional scaling studies of the conceptual organization of emotional words;³⁶ ratings of emotionally evocative pictures;³⁷ facial expressions of emotion;³⁸ facial electromyographic responses to mildly evocative pictures;³⁹ similarity judgments of emotional facial expressions,⁴⁰ and possibly even the responses of single neurons to facial expressions.⁴¹ While the evaluative dimension may account for only a proportion of the variance of behavior in a given context, its ubiquity offers considerable potential for behavioral accounts. This generality may be especially appealing, as the increasing recognition of behavioral complexities has fostered the contemporary proliferation of (albeit sophisticated) microtheories.⁴²

The Evaluative Dimension in Neural Organization

The universal appearance of evaluative dispositions, reflected in approach/avoidance tendencies or appetitive/aversive reactions, is likely attributable to their survival advantage. Elementary approach/withdrawal reflexes represent basic mechanisms for stimulus evaluation and response disposition. Organisms are constitutionally endowed with an array of adaptive reflexes that support ingestion of required nutrients, promote escape from noxious stimuli, or foster other survival-related behaviors. Protective flexor-withdrawal reflexes to pain stimuli are apparent even in the isolated spinal cord, and both decerebrate humans and rats evidence stereotyped oro-facial ingestion/ejection reflexes to relevant gustatory stimuli.^{10,34} While of apparent constitutional origin and relatively stereotyped in form, reflexive responses may nevertheless demonstrate a sensitivity to motivational variables. Oro-facial ingestion reflexes, for example, can be primed by glucoprivation or other metabolic deficits, and can be modulated by conditioned taste aversions, even in the decerebrate organism.^{10,32} These inherent dispositions allow an organism, even at early stages of development and without prior experience, to adaptively respond to important classes of environmental stimuli.

While adaptive reflexes may be functionally limited, they represent only a single level in what appears to be a continuity of evaluative mechanisms. The primary response to pain stimuli in the spinal organism is a reflexive withdrawal of the stimulated limb, although other limbs may be involved through proprio-spinal pathways.⁴³ These reflexes are relatively focal in manifestation, fixed in form, temporally stimulus-bound, and tuned to simple stimulus dimensions (e.g., intensity, somatic locus). Nociceptive signals, however, are also conveyed to brainstem and higher neuraxial levels. In addition to simple withdrawal reflexes, the mesencephalic decerebrate shows a much more global and organized reaction to pain, which includes general sympathetic discharge, piloerection, vocalization, escape-like activity, and isolated clawing and/or biting responses.^{17,44} The behaviors of the decerebrate, however, lack many features of those of the intact organism (e.g., persistence, directedness, adaptability). Similarly, while decerebrate organisms display oro-facial ingestion/ejection respon-

ses to gustatory stimuli, they do not evidence normal appetitive goal-seeking behavior.^{10,17} With involvement of additional subcortical structures, such as the limbic system and striatum, the reactions of the decorticate animal to pain stimuli entail additional response components, and evidences greater directedness, integration, serial coherence, and contextual adaptability.^{17,45} Moreover, the ingestive behavior of the decorticate is more fully responsive to metabolic signals, and appetitive or goal-seeking components are now apparent.^{17,45} These findings suggest that evaluative mechanisms are not localized to specific neuroaxial levels, but evidence a hierarchy of representation throughout the central nervous system. With progressively higher organizational levels in evaluative mechanisms, there appears to be a general expansion in the range and relational complexity of contextual controls, and in the breadth and flexibility of adaptive response.^{17,45,46}

Manifestations of evaluative processes are not limited to constitutionally endowed responses. A general characteristic of organisms is the ability to acquire or modify evaluative reactions based on experience, and even the isolated spinal cord can display conditioned withdrawal responses to otherwise neutral stimuli,⁴⁷ or conditioned alterations in reactivity to pain stimuli.⁴⁸ In fact, the distinction between inherent and acquired dispositions is blurred by apparent constitutional or preparedness for specific patterns of acquired behavior.⁴⁹⁻⁵¹ Examples include conditioned taste aversions^{49,50} and selectively tuned perceptual mechanisms for specific vocal signals in birds,⁵² monkeys,^{53,54} and chimpanzees.^{55,56} These perceptual mechanisms appear to predispose the organism toward specific defensive or protective responses^{53,56} or to the acquisition of specific vocal patterns.⁵²

The examples above entail rather limited responses that are closely linked to relatively simple stimuli. At higher levels of neurobehavioral organization, however, evaluative dispositions are also apparent to more complex categorical or relational stimulus features, and may be manifested in a broad range of behavior and choice. Indeed, manifestations of evaluative processes extend from simple reflex-like responses to discrete stimuli, to inherent motivational reactions associated with homeostatic deficits, to acquired dispositions toward broad classes of complex stimuli. Included within the lattermost are what have been termed attitudes, or the generalized tendency to evaluatively respond to a set of stimuli, events or individuals as a class.¹² Indeed, evaluative processes appear to permeate all dimensions of neurobehavioral organization.

Evaluative Processes and Neurobehavioral Organization

The studies outlined above suggest that evaluative processes may be characteristic of all vertical levels in neurobehavioral hierarchies. Evaluative processes also cut across the concentric or parallel dimension of neurobehavioral organization. The response of an intact, or even a decerebrate organism to a pain stimulus is not restricted to postural or motor adjustments, but is manifested widely in autonomic activation and general behavioral arousal. Indeed, the integrated activation of primitive reticular substrates and parallel somatic and

autonomic systems illustrates the generality of evaluative reactions across the concentric or horizontal organizational dimension.

The parallel organizational plan is also apparent within evaluative mechanisms, and the bivalent character of evaluative dispositions may reflect a manifestation of this parallel organization. Brainstem systems for oro-facial reflexes, for example, entail functionally distinct (although interacting) mechanisms for ingestion and ejection responses, which are differentially sensitive to the effects of deprivation and of conditioned taste aversion.^{10,32} Similarly, the neural substrates and neurotransmitter systems underlying reward and aversion appear to be relatively distinct.⁵⁷⁻⁶⁰ Thus, while the nucleus accumbens has been heavily implicated in reward processes, the central nucleus of the amygdala appears to be more selectively involved in affective/aversive reactions.⁶¹⁻⁶³ While the reward and aversion systems are relatively distinct and can be independently manipulated, they typically evidence an opponent interaction. Thus, non-contingent stimulation of "reward" sites in the hypothalamus appears to generally facilitate approach behaviors, while suppressing escape or withdrawal responses.⁶⁴ Conversely, stimulation of "aversive" systems yields the opposite enhancement of escape reactions and inhibition of approach responses.

The bivalent character of evaluative dispositions likely reflects, at least in part, the existence of parallel organizations, which dispose the organism in opposing directions. In some cases, these opposing dispositions may be subject to reciprocal central control. An illustration of this pattern of neural control can be found in Sherrington's⁴³ concept of *reciprocal innervation* of lower motor neurons controlling antagonistic muscles. While distinct primary spinal pathways mediate the opposing extensor and flexor stretch reflexes, these systems are reciprocally innervated by afferent inputs and higher order reflex influences. This reciprocal innervation is characterized by the activation of one circuit and the concurrent inhibition of the opponent reflex. This pattern of reciprocal innervation is also apparent at higher levels of reflex organization, and is manifest in the reciprocal excitatory/inhibitory influences on opponent muscles in locomotion and other postural reflexes.⁶⁵ Similarly, the two divisions of the autonomic nervous system often exert opponent influences on a single organ, and reciprocal controls over these divisions are apparent in brainstem autonomic mechanisms.^{66,67} Opponent features are also clearly shown in motivational processes.^{68,69}

While reciprocal central control is frequently exerted over opposing neural mechanisms, this reciprocity is not invariably manifested. Despite Sherrington's demonstration of reciprocal innervation in spinal networks, concurrent increases in tension can be generated in extensor and flexor antagonist muscles. Moreover, in spite of a degree of reciprocity in the central control of the autonomic divisions, independent changes in one division, or coactivation of both autonomic divisions can be observed in some behavioral contexts.^{66,67} Similarly, while evaluative dispositions in some cases may be subject to reciprocal control, this is by no means a universal feature. A clear exception is in conflict behaviors, which are characterized by the concurrent activation of opposing dispositions. Indeed, within parallel (or horizontal) organizations, opposing evaluative mechanisms may achieve rather independent expression. Moreover, the patterns

of interaction across vertical levels can be even more complex, and can display features of centrencephalic organization. It is to these issues that we turn next.

SIGNIFICANCE OF THE MULTIPLICITY OF EVALUATIVE PROCESSES

The significance of the conception of a continuity of evaluative mechanisms lies in the probability that multiple levels may be expressed in a given context. Importantly, the multiplicity of evaluative representations does not reflect a simple redundancy. Because the capacity for stimulus processing differs across neuraxial levels, these evaluative mechanisms may be sensitive to distinct or only partially overlapping features of the behavioral context. Moreover, because evaluative mechanisms may have differential access to response systems (or levels of organization within response systems), their behavioral manifestations may be rather disparate (and possibly even discordant). Thus, Bolles and Fanselow⁷⁰ consider fear and pain to arise from separate motivational systems, and these states may be differentially reflected in measures of autonomic response and escape behavior.⁷¹ This is consistent with the multiplicity of pavlovian conditioned reflexes (CRs) apparent in conditioning contexts, and with the AESOP (affective extension of the sometimes-opponent-process) theory of Wagner and Brandon.⁶⁹ Pavlovian conditioning can yield both focal conditioned somatic responses (CRs, such as an eye blink or limb withdrawal), and more generalized fear reactions or conditioned emotional responses (CERs, as evidenced by autonomic activation, or suppression of ongoing operants). The interstimulus-interval (ISI) functions for these distinct manifestations, however, may differ substantially. The optimal ISI for eyelid conditioning in the rabbit is < 1 sec, and little conditioning is seen with ISIs beyond 2 sec or so.⁷² In contrast, the optimal ISI for heart rate conditioning in this species is considerably longer (2–3 sec), and conditioning can still be observed beyond 7 sec.⁷² Extended ISI functions have also been reported for CERs and fear potentiated startle.^{8,72,73} Moreover, cholinergic blockade⁷² or cerebellar lesions⁷⁴ can disrupt the eyelid CR, leaving the eyelid unconditioned response (UR) and conditioned heart rate responses undiminished. Similarly, while aversive stimuli can promote both avoidance behavior and freezing, these manifestations are differentially sensitive to variations in intertrial intervals and may reflect distinct components of the conditioned reaction.^{75,76}

The existence of evaluative components of Pavlovian conditioning⁶⁹ is also congruent with two-process theories of avoidance conditioning,^{77–79} which hold that affective Pavlovian components serve to motivate instrumental avoidance responses. While the focus of the present proposal is not explicitly on associative processes, the results outlined above illustrate the ubiquity of the evaluative dimension across behavioral contexts and neurobiological levels. The multiplicity of evaluative processes gives rise to three principal theses:

- (1) Evaluative dispositions arising from different neuraxial levels may be differentially sensitive to specific aspects or features of the stimulus environment.

- (2) The operations of separate evaluative levels may be manifested in different aspects of behavior, and thus may be optimally indexed by different response measures.
- (3) The concurrent activation of multiple evaluative levels establishes the conditions for potential interactions among these mechanisms.

INTERACTIONS AMONG EVALUATIVE DISPOSITIONS

The multiple levels of evaluative processes, their differential sensitivities to features of the environmental context, and their divergent behavioral manifestations all raise the possibility of complex interactions among evaluative dispositions. As discussed above, such interactions may occur across horizontal or parallel evaluative dispositions. Moreover, hierarchical features of neural organization are consistent with clearly documented descending biases exerted by higher systems on lower evaluative mechanisms. Finally, ascending influences can also be seen among evaluative levels. In some cases, the latter may entail the pre-processing and transmission of relevant afferent information. An example can be found in brainstem systems for pain transmission, which can enhance or inhibit the somatosensory afference to rostral neural systems. Equally importantly, however, are ascending influences which assume centrencephalic features. These influences can effect the directional reactivity of higher bivalent evaluative mechanisms.

In an early approach to the study of bivalent conflicts, Miller⁸⁰ proposed an analysis of behavior as a resultant of unitary opposing approach and avoidance dimensions or gradients. While these analyses were elegant, they may have presented an overly simplified account of the dynamics of opposing dispositions. Moreover, this approach is limited by its focus on interactions at a single organizational level (i.e., horizontal interactions). If multiple levels in evaluative mechanisms are concurrently activated in a given behavioral context, there is also the potential for interactions across these levels (vertical interactions). Importantly, these vertical interactions may not be readily reducible to single opposing gradients. Thus, while both fear and pain entail negative dispositions, they may arise from distinct but interacting motivational systems.^{70,71,81} The multiple evaluative dispositions invoked by an environmental stimulus or context may necessitate attention to multiple, interacting evaluative levels.

It is quite clear that the operations of higher evaluative substrates can bias or modulate lower reflex mechanisms. One example is the priming of reflexive startle responses by aversive stimuli or contexts, as suggested by Brown, Kalish, and Farber,⁸² and more recently investigated by Davis,⁸³ Hoffman and Ison,⁸⁴ and Lang and colleagues.¹¹ While the necessary pathways for the primary startle response lie entirely within the brainstem,⁸³ higher limbic mechanisms appear to be essential for startle potentiation associated with conditioned fear.^{11,83} Direct stimulation of the amygdala, for example, can enhance startle reflexes.⁸³ Moreover, lesions of this structure (or infusions of NMDA antagonists) can block conditioned fear-potentiation of startle responses, without altering non-associative potentiation due to sensitization.^{83,85-87} While originally considered

to result from a generalized effect of drive, more recent studies have demonstrated that startle potentiation is relatively specific to aversive reactions.^{84,88} Indeed, appetitive contexts may yield an opposite attenuation of startle responses.¹¹

An additional illustration of the descending priming of basic reflexes comes from studies of predatory behavior in the cat. Electrical stimulation of the hypothalamus and related areas, which induces predatory attack, has been found to sensitize distinct and lateralized receptive fields for basic brainstem response components.^{89,90} Receptive fields for jaw-opening, biting, pawing and lunging reflexes expand, in proportion to stimulation intensity, primarily on the side of the body contralateral to the stimulation electrode.^{89,90} This reflex priming appears to play a pivotal role in the consummatory components of attack, since sensory denervation of these receptive fields abolishes terminal attack components. These studies reveal that higher limbic mechanisms for evaluative or motivational response can exert a potent bias on lower sensory-motor reflex mechanisms.

Descending influences can also modulate ascending afferent transmission, which could not only impact lower reflex substrates, but could do so on information received by higher evaluative mechanisms. One example is hunger-induced priming of gustatory transmission, which can be seen at the level of the primary central neurons (nucleus tractus solitarius) of the gustatory pathway.³³ An additional example derives from the marked reduction in pain sensitivity and reactivity which can be observed following uncontrollable aversive stimuli.^{91,92} This hypoalgesia appears to be mediated, at least in part, by descending opiate and non-opiate pathways to the spinal cord.⁹³ Both the degree of hypoalgesia and the relative contributions of opiate and non-opiate systems have been shown to be dependent on psychological factors, including the predictability and controllability of the aversive event.^{91,92} The effects of these psychological variables appear to be mediated by both associative and non-associative factors, and depend in part on the inherent response dispositions of the subjects to the aversive stimuli.⁹⁴⁻⁹⁶

It is now clear that relatively primitive evaluative dispositions can have notable impact on complex, acquired behaviors. An example is the "instinctive drift" as noted by Breland and Breland,⁹⁷ which entailed the unexpected intrusion of inherent response tendencies into an explicitly reinforced operant chain. More recent concepts of species-specific defense responses,^{70,98} preparedness and contrapreparedness,⁹⁹ and selective associations⁵⁰ all reflect the dispositional biases that, beyond the explicit experimental contingencies, shape the likelihood of a given response or association in an experimental context.

A well-documented example of selective association or preparedness is the preferential associability between taste stimuli and visceral malaise in conditioned taste aversions.^{49,50,100} Moreover, in classical fear conditioning paradigms, Öhman and colleagues¹⁰¹ and Cook *et al.*¹⁰² have demonstrated that human subjects show enhanced electrodermal conditioned responses to a conditioned stimulus (CS) having inherent "fear-relevance" (e.g., slides of spiders or snakes), compared with neutral or "fear-irrelevant" stimuli (e.g., flowers or mushrooms). A constitutional basis for such dispositions in monkeys is sug-

gested by studies of Cook and Mineka,^{103,104} reporting enhanced observational learning of fear responses to a toy snake or crocodile, in contrast to flowers or a toy rabbit. Importantly, the subjects in these studies had no experience with the experimental stimuli prior to testing. Moreover, all stimuli were shown to support comparable appetitive conditioning, ruling out explanations based on general differences in salience or conditionability of the stimuli. While it remains possible that nonassociative processes may contribute to this selective pattern of response,^{50,104} it is clear that basic evaluative dispositions can influence the development or expression of fear-like behavior in monkeys.

Similarly, the operations of lower evaluative mechanisms can influence the activity of higher systems. In some cases, this may entail the regulation of ascending afferent information. An example is the conditioned hypoalgesia associated with aversive stimuli, which can be seen even in the isolated spinal preparation.⁴⁸ This conditioned suppression of pain transmission could, in the intact organism, modulate or shape the afferent information available to higher evaluative levels. Moreover, the expression of lower evaluative dispositions may also exert a more direct executive bias on higher systems. Thus, it has been shown that task-irrelevant collateral somatic activity associated with approach or withdrawal responses can bias preference judgments toward otherwise neutral stimuli in human subjects.^{105,106}

These findings suggest that notable interactions may occur among evaluative mechanisms at all functional levels within neurobehavioral systems. The existence of such interactions across evaluative levels would necessarily limit behavioral analyses restricted to a single organizational level. A comprehensive understanding of the behavioral consequences of evaluative processes may require attention to multiple evaluative levels and organizational dimensions. Indeed, the findings outlined above reveal interactions across hierarchical, concentric, and centrencephalic organizations.

THE CHIMPANZEE AS A MODEL FOR THE STUDY OF EVALUATIVE PROCESSES

The evaluative dimension has proven useful in organizing behavioral and psychobiological data on adaptive reflexes, emotion, motivation, and conditioning. Evaluative processes have proven especially indispensable, however, in the study of human attitudes, which entail generalized, valenced dispositions toward classes of stimuli.¹² Unfortunately, there has been relatively little integration of the attitude literature in humans with that on evaluative processes in animals. Attitude researchers have generally focused on more complex and generalized evaluative dispositions, which are difficult to parallel in standard laboratory animals. Until recently,¹³ the attitude literature has paid relatively little attention to lower evaluative processes,¹⁰⁷ or has relegated these processes to limited "incentive" analyses.^{108,109} Thus, the potency of classical conditioning in visceral and affective reactions to individuals, objects and events^{109,110} stands in stark contrast to the limited coverage it receives in reviews of contemporary attitude theories¹⁰⁷ and attitude texts.^{111,112} In contrast to the work with humans,

the animal literature on evaluative dispositions has typically focused on specific behavioral processes or paradigms, and a general theoretical conception has not emerged. In view of these considerations, an animal model is desired which could bridge these two literatures.

Chimpanzees, probably the closest extant relatives of humans, may represent an ideal species for such an effort. Chimpanzees evidence a level of cognitive capacity that rivals or exceeds that any other non-human animal.¹¹³⁻¹¹⁸ Moreover, the complexity of evaluative processes of chimpanzees approaches that of humans. Chimpanzees, but apparently not monkeys^{119,120} (but see Reference 121), for example, are capable of establishing attitudes based on the attribution of knowledge or intentions to others.^{117,118,122} Moreover, these animals evidence a rich social structure,¹¹³ which permits approaches to the study of the social dynamics and social transmission of evaluative dispositions—a dimension that figures so prominently in the human attitude literature. At the same time, inherent dispositions are striking in chimpanzees,¹¹³ and these animals display seemingly paradoxical islands or pockets of rigidity and behavioral constriction that likely reflect primitive evaluative dispositions. This species therefore may offer a potentially powerful model for the study of evaluative processes and their interactions, and may represent an ideal bridge between the human and animal literatures.

Evaluative Dispositions in Chimpanzees

The potency of evaluative dispositions as determinants of functional reactions in the chimpanzee is illustrated by an investigation of photograph recognition in this species.¹²³ Within the early months of life, human infants are able to discriminate between human faces, as well as photographs of faces, displaying a preference for faces of caregivers.¹²⁴ To examine face recognition in apes, we recorded heart rate responses of a juvenile chimpanzee to photographs of human faces. The subject was a 3.5-year-old female, Sheba, who had formed strong social bonds with her two primary caregivers in the course of involvement in the Ohio State University Primate Cognition Project. Facial photographs were repeatedly presented by slide projection, while concurrent heart rate responses were obtained.¹²³ The photographic stimuli consisted of a blank control slide, slides of Sheba's two primary caregivers, two unfamiliar individuals, and two familiar individuals with whom Sheba had not interacted. Importantly, no task demands were imposed, and Sheba had no previous experience or training with these or other photographs.

As expected, the slide stimuli were associated with an orienting-like or attentional response, characterized by cardiac deceleration. Considerable differences were apparent, however, in the magnitude of cardiac responses across stimulus categories, with the photographs of caregivers yielding significantly larger responses than other stimuli. Heart rate responses to slides of caregivers averaged -9.4 beats per minute (bpm), compared to -0.7 bpm for the control slide, -1.2 bpm for the slides of familiar individuals, and -0.3 bpm for the slides of strangers. Since the slides were all matched on simple physical parameters

(luminance, color balance, etc.), the larger cardiac responses to caregivers appeared to derive from the evaluative significance of the stimuli, attributable to the established social bond between the subject and her human caregivers.

This paradigm was extended to photographs of conspecifics.¹²⁵ The experimental stimuli consisted of slide photographs of three chimpanzees; an unfamiliar animal, a familiar playmate, and a familiar animal who had been consistently aggressive to the subject (Sheba). To the extent to which Sheba could recognize the individuals depicted, we expected the photograph of the aggressive animal to invoke an aversive reaction or defensive-like response characterized by heart rate acceleration, while responses to other stimuli were expected to be deceleratory. Results confirmed these expectations. Cardiac responses again significantly differentiated among the photographs, with the photograph of the abusive animal yielding a notable heart rate acceleration, while other photographs resulted in negligible or deceleratory responses. These results confirm the impact of evaluative processes on the functional reactions of the chimpanzee to adaptively relevant stimuli. These findings provide the first clear evidence that perceptual representations in the chimpanzee, generated by photographs of individuals, entail an affective or valenced component corresponding to the recognition of the individual depicted. In these cases, the evaluative significance of the stimuli were based on the social history and experience of the animal. Some evaluative dispositions in this species, however, may also be constitutionally endowed.

In contrast to the view that primate vocalizations are egocentric and relate simply to internal states, it is now clear that primate utterances can evidence intentionality, convey information concerning environmental referents, and display a syntactical organization.¹²⁶⁻¹²⁸ While learning certainly plays a part in vocal signalling, there appear to be notable constitutional features to both vocal production and vocal perception in primate species. To explore the early ontogeny of vocal perception, we used cardiac measures to examine the perceptual response of infant chimpanzees and orangutans to brief periods of chimpanzee vocalizations. For a variety of reasons, all subjects had been separated from their mothers at, or shortly after, birth. Cardiac responses of the chimpanzees to the white noise control stimuli and to most vocal stimuli were predominantly deceleratory, reminiscent of the orienting response. In contrast, cardiac responses to threat-barks were more characteristic of defensive responses, entailing a progressive cardiac acceleration. This pattern of response was comparable at all ages tested, and was apparent within the first 48 hours of birth. This distinct cardioacceleratory response reflected a perceptual reaction to the specific acoustic pattern of the threat vocalization, since other stimuli were matched on simple physical parameters (intensity, duration, frequency spectrum, and shape of the acoustic envelope). In contrast to the results from chimpanzees, cardiac responses of the orangutans to all chimpanzee vocalizations, including threat, were predominantly deceleratory and similar to their responses to white noise. Together, the data suggested that the cardioacceleratory response to threat barks in the chimpanzee (1) reflected a defensive or aversive reaction characterized by sympathetic activation, and (2) may have arisen from a species-specific perceptual endowment for the evaluative processing of adaptively relevant vocal stimuli.

Studies outlined above document notable evaluative dispositions to adap-

tively relevant stimuli in chimpanzees. These evaluative processes are manifest in differential functional (autonomic) responses of the organism, in the absence of a performance context, explicit training, or specific task demands. In some cases, these dispositions may be constitutionally endowed, while in other instances they appear to arise from social learning. One of the advantages of the chimpanzee as an animal model is the sophistication of the cognitive origins of evaluative dispositions. Gallup¹²⁹ argues that chimpanzees, but not monkeys, have a contextually transcendent concept of "self." This may support the apparent ability of the chimpanzee to attribute knowledge states or intentions to others.^{117,118,122} Similar attribution processes are prepotent in attitude formation and change in human subjects, and their presence in the chimpanzee greatly enhances its potential value as an animal model. Indeed, preliminary data from our laboratory (Povinelli and Boysen, unpublished data) suggest that these attributional processes can support the establishment of enduring attitudinal dispositions to others.

Briefly, we employed an "intercom" system, by which the subject could call one of two collaborators by pressing a button next to the individual's photograph, and the selected collaborator would then deliver juice to the subject. After baseline preference tests, an experimental manipulation was imposed on single trials, in which the collaborators spilled the juice during delivery. One collaborator tripped and spilled the juice (the "clumsy" collaborator), and on another trial, the other ("intentional") collaborator walked to the same point and deliberately poured the juice on the floor. In neither case did the animal receive the juice reinforcer. After this single experimental manipulation, the animal subject never again called the "intentional" collaborator over subsequent test trials. Moreover, after the experimental trials, the animal displayed notable aggressive overtures to the "intentional" collaborator, while responses to the "clumsy" experimenter were unchanged. Tests with additional pairs of collaborators yielded similar results.

These preliminary findings suggest that chimpanzees can establish enduring attitudinal dispositions toward specific individuals based on an interpretation of the intentionality of a behavioral act. This is perhaps not surprising in view of the likely survival pressure for predicting the actions or identifying the behavioral state of another organism. This is especially true for a competitive and aggressive species like the chimpanzee, with a highly structured and dynamic social hierarchy. Indeed, attributions of states or dispositions to others may be more fundamental, and may emerge earlier in phylogeny, than the development of a self-concept and self-attributional processes. In any event, it is clear that chimpanzees are capable of many of the processes that underlie human attitudes. At the same time, the existence of striking inherent evaluative dispositions makes the chimpanzee an ideal species for the study of evaluative interactions.

Evaluative Interactions in the Chimpanzee

In spite of the cognitive sophistication of chimpanzees, primitive evaluative dispositions in this species can exert a powerful influence on behavior. This is

documented by a recent study from our laboratory, initially designed to explore the possible use of social deception by chimpanzees. The original experimental design entailed a cooperative task, in which one animal, who was aware of the location of a reinforcer but unable to obtain it, could signal its location to another animal who had instrumental access to the reward but was unaware of its location. The apparatus consisted of large box with a series of pull-rods at one end, linked to stimulus/reinforcement pans. The subjects were restricted to the two ends of the apparatus, and the visibility of the stimulus pans could be controlled by barriers. The subjects were already familiar with this apparatus from a previous study.¹²² In preliminary training, one of the subjects (Sheba) could see the reinforcement pans, and the other (Sarah) was ultimately to have access to the control levers. Two pans were baited with different quantities of candies on each trial, and Sheba was to signal which rod to pull. In the training phase, however, the experimenter controlled the delivery of reinforcements. A reversed reinforcement contingency was implemented—Sarah received the food that Sheba had selected, and Sheba received the remaining, non-selected candy reinforcers. Thus, it was in Sheba's economic interest to select the smaller of the two candy arrays in order to obtain the remaining, larger quantity. She was unable to do so.

After more than 450 training trials extending over 33 sessions, Sheba persisted in selecting the larger quantity, and thereby received the smaller reinforcement. In fact, Sheba's performance was significantly *below* chance (31% correct; $\chi^2 = 14.8$, $df = 1$, $p < .001$). Moreover, her performance became less optimal at higher reward ratios, where she stood to benefit the most. To examine the possibility that this suboptimal performance was idiosyncratic to Sheba, we reversed the social roles, so that Sarah now selected among the reward options. She also failed to learn this simple task. This was a striking outcome, since these were two of the most highly trained chimps in the world, representing probably the most intelligent animal species, but were unable to master a simple response strategy. Premack's Sarah is perhaps the most celebrated chimpanzee in the animal cognition literature, with demonstrated competence (for example) in ratio judgments and analogical reasoning.^{117,118} Sheba has the documented ability to count from 1 to 9, employ transitive inference, accurately derive the sum of two quantities, and flexibly utilize number symbols.^{114,115,130} Yet neither of these animals could pick the smaller of two candy arrays, even after hundreds of training trials. In view of these findings, we abandoned the deception study, and sought to further understand the nature and origin of this dramatic performance deficit.

A powerful interference effect appeared to be operating in this paradigm, likely related to the inherent evaluative disposition toward the candy arrays which served as the task stimuli. This dispositional imperative may have interfered with the acquisition of the underlying rule structure of the task, or with the behavioral implementation of that associative structure. To examine these alternatives, we capitalized on Sheba's existing competence with numerical symbols. Sheba was again allowed to select among two stimulus alternatives. Rather than using food arrays as stimuli, however, we substituted placards with corresponding Arabic numerals. The rest of the task was unaltered—the num-

eral picked by Sheba resulted in a corresponding number of candies going to the observer animal, while Sheba received the amount specified by the non-selected numeral. With this change, Sheba responded correctly on the very first trial, and her performance remained significantly above chance over the ensuing three sessions (75% correct response, $\chi^2 = 9.0$, $df = 1$, $p < .01$). The immediate shift to above-chance performance suggested that Sheba had, in fact, acquired the rules of the task. This associative knowledge, however, may have been obscured in the previous sessions by a potent competing disposition arising from the intrinsic incentive properties of the candy arrays.

It is also possible, however that Sheba was simply "ready" to learn at the point we introduced the number stimuli. The candies were re-introduced, and her performance in the first session fell immediately to 17%. Candies and numerals were then alternated as stimuli (*abba* counterbalanced order) for the next six sessions. Over these sessions, her mean performance with candies was 17%, while her performance with the symbolic stimuli was 72%. These differences in performance were both stable, and highly significant. For confirmation, and to further examine the stability of these performance differences over time and testing, an additional series of eight sessions were run with food arrays and Arabic numerals. All possible combinations of stimuli from 1 to 6 were tested, except for equivalent pairs. The results of this series is illustrated in FIGURE 1 (top). Again, performance differences were stable and highly significant. During sessions with Arabic numerals, Sheba's performance was significantly above chance ($\chi^2 = 8.0$, $df = 1$, $p < .01$), but with food arrays as stimuli, her performance fell significantly below chance ($\chi^2 = 18.0$, $df = 1$, $p < .001$).

Clearly, the disposition to respond to the larger food arrays did not appear to have precluded learning of the rules of the task. Rather, a competing evaluative disposition arising from the candy arrays appeared to have interfered with the task performance. As illustrated in FIGURE 1 (bottom), this interference increased with increasing arithmetic disparity between the candy-array choices. This interference function may reflect the evaluative gradient associated with the incentive disparity between the paired task stimuli. In contrast to the results with arrays, Sheba's performance improved as a function of arithmetic disparity with Arabic numerals as stimuli (FIG. 1, bottom). This positive slope likely reflects the alternate response disposition related to the associative or response-contingent features of the task. Thus, it appears that two dispositional gradients were operative in this task, that (1) arise from distinct antecedents, (2) manifest differentially in performance, and (3) interact. The associative gradient arising from the reinforcement contingency appeared to be masked or overridden by the competing non-associative disposition related to the intrinsic incentive properties of the candy-array stimuli.

In summary, it appears that the intrinsic incentive properties of the candy-array stimuli invoked an evaluative disposition that interfered with optimal performance. In the present task, however, while this dispositional bias impacted on behavioral choice, it did not appear to preclude acquisition of the rule structure of the task. By liberating the animal from the dictates of this potent evaluative disposition, symbolic stimuli permitted the expression of that associative knowledge of rule structures. Indeed, part of the power of symbolic

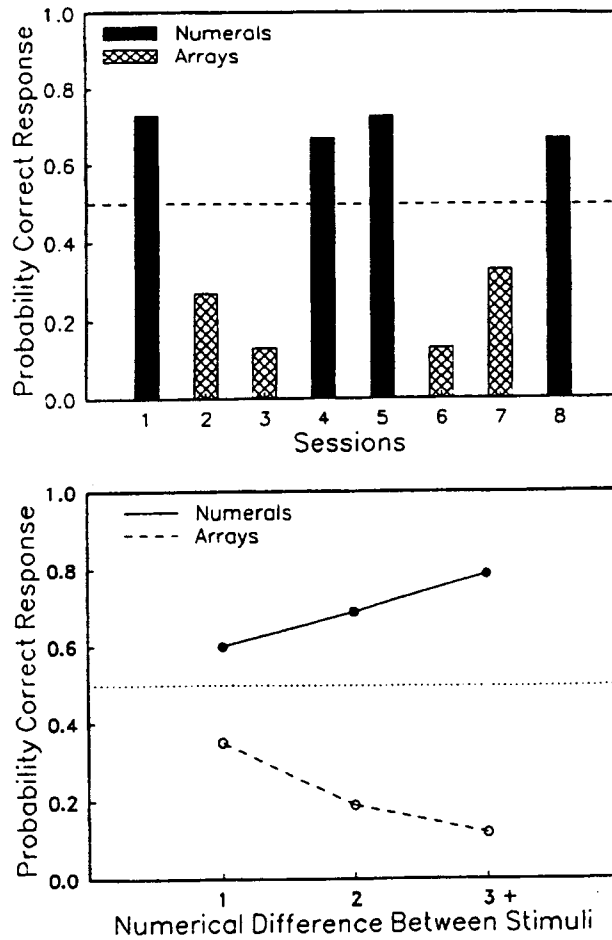


FIGURE 1. Performance of a chimpanzee on a paired-choice selection task with a reversed reinforcement contingency in which the subject received the non-selected array, and an observer animal received the selected array. *Top.* Performance across sessions, as a function of the stimulus type (candies vs. symbolic stimuli). *Bottom.* Performance as a function of the arithmetic disparity between the two array choices.

representations, including language in humans, may relate to the ability of these representations to capture selected aspects, dimensions, or relationships among their real-world referents.

STRATEGIES AND FUTURE DIRECTIONS IN THE STUDY OF EVALUATIVE PROCESSES

In view of the ubiquity of evaluative processes in behavioral contexts, and the wide range of their behavioral manifestations, it is not possible to lay out a singular strategy for future studies. Nevertheless, some general questions and

issues arise relative to evaluative processes. As outlined above, two defining features differentiate evaluative dispositions from other types of response biases or tendencies. The first is an explicit evaluative categorization of a stimulus into positive or negative valence classes.²⁸ This excludes a wide range of perceptual, cognitive, and behavioral biases, such as those related to habituation, associative learning, and orienting and attentional responses. While in each of these cases, evaluative dispositions could be invoked, they are not inherent to these processes. As discussed above, Pavlovian conditioning can yield both discrete somatic CRs (such as eyeblink) which appear to be evaluatively neutral, and affective CERs (such as conditioned fear) which entail the evaluative dimension of the inherent unconditioned stimulus-unconditioned response (US-UR) link.⁶⁹ These two conditionable components can be differentially manipulated by conditioning parameters, and may be present to varying degrees in conditioning contexts.⁶⁹ Similarly, orienting or attentional responses to novel stimuli may be evaluatively neutral in some instances, but may both reflect and be influenced by evaluative dispositions in other cases (as discussed for chimpanzees).

The second defining characteristic of evaluative processes is the invocation of explicit response dispositions, which entail bivalent tendencies toward or away from the stimulus. This distinguishes evaluative dispositions from other classes of response tendencies or biases, including postural adjustments to proprioceptive stimuli, execution of trained or skilled motor acts, reactions to environmental occasion-setters,^{131,132} place or side biases, and behavioral alternation tendencies. In some cases, especially at lower levels of neuraxial organization, evaluative dispositions may be closely linked to specific responses (e.g., flexor-withdrawal reflexes). In other instances, especially at higher levels of functional organization, these dispositions may be expressed in a wider range of manifestations (e.g., generalized attitudes).

These two defining characteristics, and the mechanisms underlying them, offer a structure for future studies. These can be cast in terms of general experimental questions which address the principle theses outlined above (see "Significance of the Multiplicity of Evaluative Processes," above):

- (1) What are the *antecedents* of evaluative processes, and how might they differ across hierarchical, parallel, and centrencephalic dimensions of neural organization?
- (2) What are the *consequents* of behavioral manifestations of evaluative processes, and how might they differ across hierarchical, parallel, and centrencephalic dimensions of neural organization?
- (3) What are the *mechanisms* underlying evaluative processes, and what is the nature of the interactions among these mechanisms within and across organizational dimensions?

The questions outlined above address the broader issues of how evaluative dispositions arise from neurobehavioral organizations, the laws and principles that govern their invocation, the determinants of their manifestations, and the functional patterns of integration among these mechanisms. The importance of the experimental pursuit of evaluative processes is that these processes are

general features of behavior which appear to represent a fundamental dimension of neural organization. Consequently, illumination of the psychobiology and neurobiology of evaluative mechanisms will contribute not only to our understanding of behavior, but to our understanding of the functional organization of the brain. Clearly, answers to many of the questions outlined above will require a combination of behavioral and neurobiological methods, and an appreciation of the underlying neural mechanisms will ultimately be necessary for a comprehensive explication of evaluative processes.

SUMMARY

The principle of evaluative bivalence asserts that behavioral processes often organize along the evaluative dimension, due to a fundamental pattern of bivalent neurobehavioral organization extending throughout the neuraxis. This principle offers a powerful approach to the explication of complex behavioral relationships and the integration of diverse literatures. It also offers a guiding conceptual framework for the study of neurobehavioral relationships which holds the promise of integrating rather than diversifying the study of neural mechanisms for disparate behavioral phenomena.

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