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What is This?
Laterality and Evaluative Bivalence: A Neuroevolutionary Perspective

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Abstract

Rutherford and Lindell (2011) review an extensive literature on lateralization of emotion. As they note, an important issue surrounding this question is the nature of emotion, which bears on what, precisely, is lateralized. The present comments are intended to broaden the context of the review, by considering lateralization from the standpoint of a bivariate model of evaluative processes and a neuroevolutionary perspective.

Keywords
emotion, evaluative bivalence, evolution, lateralization

As noted by Rutherford and Lindell (2011), the literature on lateralization of emotion is complex. To the extent to which lateralization of function obtains, an important question arises as to what, precisely, is lateralized. This is perhaps generally less problematic for lower sensory and motor functions than for more complex psychological processes, but even in the sensorimotor domain, the question of what is lateralized is nontrivial. Certainly, anatomical pathways may display a high degree of laterality, but the associated functional laterality may not always be so readily apparent. This is especially true for emotional processes, as our understanding of the functional lateralization is highly dependent on our theories and concepts of emotion. Even the origin and significance of lateralization itself is far from settled.

A common perspective is that lateralization is an evolutionary initiative that maximizes and optimizes processing capacity by parsing functions to emerging, differentiated and specialized networks. Lateralization has a long evolutionary heritage as lower vertebrates and even invertebrates show striking lateralization of behavioral and motivational processes, as well as sensorimotor functions (e.g., see Bisazza, Rogers & Vallortigara, 1998; Vallortigara & Rogers, 2005). Indeed, the lowest and most evolutionarily conserved central nervous system structures, such as the spinal cord, are among the most lateralized networks of the mammalian nervous system. There is considerable evidence that evolutionary development of the mammalian forebrain is characterized primarily by an increased interhemispheric communication, rather than an emerging isolation and specialization of lateralized systems. In fact, primitive mammals, the marsupials (opossum, kangaroo), have no corpus callosum at all, this having its evolutionary origin in placental mammals (Aboitiz & Montiel, 2003). A broader confluence of information would be expected to enhance integrative cognitive processing, albeit perhaps at the expense of interference or attentional/processing-capacity bottlenecks. Both humans and nonhuman primates with transections of the corpus callosum can process information concurrently in the two hemispheres more rapidly and efficiently than intact subjects (Gazzaniga & LeDoux, 1978), likely the result of reduced cross-hemispheric interference. This parallel processing mode is highly efficient, but the cost is a loss of hemispheric integration. The latter is an important function of the emerging commissural pathways of the corpus callosum. Although lateralization of emotion is of interest regardless of whether the lateralization is seen as emerging or fading through evolution, theoretical perspectives on that lateralization may be quite distinct. Although this issue cannot be fully resolved here, it is an important consideration for understanding laterality in emotional as well as other processes. We will return to this issue.

But what are the precise dimensions of emotion that are lateralized? Rutherford and Lindell (2011) adopt an approach–avoidance motivational framework to consider this question. This is certainly in keeping with much of the literature. It is also compatible with the universal manifestations of approach and avoidance behaviors across a wide range of species and...
contexts. Evolution has endowed organisms with the adaptive disposition to seek out and approach positive, rewarding or appetitive stimuli and to avoid potentially damaging, noxious or aversive stimuli. These dual dispositions are fundamental to survival, and while these dispositions are further developed and elaborated on by higher neural systems, the more primitive, lower level instantiations are highly conserved through evolution. This is apparent at the level of the spinal cord, where simple neural circuits support flexor withdrawal responses to strong or noxious stimuli (pain withdrawal reflex). Flexor reflexes are not dependent on higher neural systems (although they may be modulated thereby), but represent a primitive avoidance system that serves to protect the organism from exposure to noxious stimuli. In contrast, extensor reflexes to moderate tactile stimuli promote limb extension, locomotion, engagement, and acquisition of potentially rewarding stimuli. The extensor engagement reflexes are distinct from flexor reflexes, having separate afferent, efferent and interneuron pathways. Flexor and extensor reflexes support low-level evaluative processing of somatosensory stimuli.

While not generally considered psychological manifestations, these spinal reflexes in fact represent the initial level of evaluative information processing and foster associated approach or avoidance dispositions. At this low level of organization, there is virtually a 1:1 mapping between the neural evaluative computations of the stimulus significance and the adaptive response of flexor withdrawal or extensor engagement. That is, the evaluative computation gives rise to a reflex action disposition (mobilization of efferent substrates), and those dispositions are translated rather directly into extensor (approach) or flexor (avoidance) responses. As noted above, these spinal evaluative networks are highly lateralized, each side of the cord receiving information from, and controlling skeletal muscles on, its respective (ipsilateral) side of the body. With the development of more elaborated rostral evaluative systems, this high degree of laterality will give way to progressive neural integration across the two sides of the body. This represents an evaluative homology to sensory and motor system evolution. The lateral corticospinal pathways, arising from the so-called Betz cells in layer V of the primary motor cortex, are highly lateralized in their (crossed) projections to lower motor neurons controlling distal muscles of the arms and legs. Thus, lesions of the primary motor cortex in the precentral gyrus yield largely lateralized (contralateral) motor deficits. As one moves to more secondary and tertiary motor areas, coextensive with the posterior prefrontal cortex (supplementary motor cortex and supplementary frontal eye fields), there is a progressive increase in bilateral projection and representation of motor processes, and damage in these areas yields deficits in the bilateral organization of movements (Penfield & Jasper, 1954).

Lateralization of the direct flexor and extensor reflex circuitry in the spinal cord is largely complete, although integrative spinal networks do support what Sir Charles Sherrington referred to as the alliance of reflexes and long-spinal reflexes (Sherrington, 1906). At the spinal level, there is not a notable differential lateral representation of flexor and extensor reflexes, as the lateralized representation of the two sides of the body is sufficiently complete that each side has its complement of flexor and extensor reflexes. Laterality, however, is only one of the multiple dimensions of differentiation and specialization within the nervous system; another is the dorsal/ventral dimension (see Berntson, Boysen, & Cacioppo, 1993). The latter is apparent in the dorsal (sensory) and ventral (motor) representation in the spinal gray matter. Even within the ventral (motor) horn of the gray matter, one sees a differentiation and specialization of motor neuron pools for flexor (more dorsally in the ventral horn) and extensor (more ventrally) reflexes. This parallels the hemispheric laterality of the primary motor cortex—a laterality that fades as one moves to secondary and tertiary motor areas. Similarly, one sees a loss of the dorsal/ventral differentiation of flexor/extensor motor control with the emergence of higher evaluative systems, where integration among these motor systems is essential for the more complex evaluative networks and adaptive responses. These primitive evaluative networks exemplify what we have termed the cardinal principle of evaluative bivalence—a fundamental characteristic of the organization of evaluative systems (Berntson et al., 1993; Berntson & Cacioppo, 2008; Norman et al., 2011). This follows the general trend of increasing integration among neural substrates at higher levels of the neuraxis.

While the relative independence of spinal flexor and extensor reflexes and association avoidance and approach dispositions is discussed above, it remains the case that a limb can display a flexor response or an extensor response, but not both simultaneously. This represents a physical constraint on expression of the basic neural substrates. While flexor and extensor reflexes do interact, they are based on distinct specialized circuits that are differentiated along a critical dorsal/ventral dimension, and are sufficiently distinct that they can both show coactivation (as in a stiff arm). The latter can result from descending modulations by higher level behavior and motor systems which have a greater degree of integrative control over both flexor and extensor muscles.

Thus, although somatic flexor and extensor responses are constrained to a bipolar (flexor or extensor) pattern of expression, the underlying neural substrates display a bivalent organization. These primitive evaluative networks exemplify what we have termed the cardinal principle of evaluative bivalence—a fundamental characteristic of the organization of evaluative systems (Berntson et al., 1993; Berntson & Cacioppo, 2008; Norman et al., 2011).

An additional example of the progressive integration of bivalent evaluative systems comes from work on decerebrate humans and animals lacking a functional forebrain (Berridge, 2004; Berridge & Grill, 1984; Steiner, Glaser, Hawilo, & Berridge, 2001). Evolutionarily conserved reflex mechanisms for gustatory hedonics and stereotyped oro-facial intake/rejection responses are organized at the level of the brainstem and are displayed by decerebrate organisms. Sweet or other palatable tastes trigger consummatory responses (licking and swallowing), whereas bitter or sour tastes trigger a characteristic rejection response (gaping and tongue protrusion). These oro-facial intake/rejection responses arise from independently organized, bivalent evaluative systems, as evidenced by the
fact that simultaneous intake and rejection responses can be coactivated by a mixture of bitter and sweet solutions. Again, however, with the emergence of higher motivational and behavioral substrates, there is a progressive integration and control over these brainstem substrates, so that we are able to take bad-tasting medicine or walk away from unhealthy sweets (at least to some extent).

With the development of higher neural networks, one sees a dramatic increase in the complexity of evaluative systems and the flexibility of associated cognition and behavior. While specific structures such as the amygdala and nucleus accumbens appear to make a differential contribution to the positive and negative evaluative processing, there is a great deal of integration among these structures, and other networks, such as attentional and memorial systems, play a common role in both processing dimensions (see Norman et al., 2011). Adding further complexity is that a given structure, such as the amygdala, may show a lateralization in its relative contributions to affective processing (Gläscher & Adolphs, 2003). Despite this complexity, the Rutherford and Lindell (2011) review underscores the basic bivalent structure of higher evaluative processes. Although the answer to the question of what, precisely, is lateralized may require further research and theory, the evolutionary viewpoint offers some perspectives. Although spinal evaluative reflexes map tightly onto approach/avoidance responses, the greater complexity and flexibility of rostral evaluative networks preclude such a tight coupling between basic evaluative computations and specific motor actions. As noted by Rutherford and Lindell (2011), anger presents a problem for a simple mapping between approach/avoidance and positive/negative affective responses. Umweg (detour) tasks, which require the subject to move away from a goal object in order to obtain it, complicate simple neural mappings of approach/avoidance responses. Of special note is that performance on these tasks is substantially degraded by hemispheric lesions, supporting the view that higher level neural systems expand the range of flexibility and permit “avoidance-like” responses as part of a goal acquisition strategy (Coutant, 1974). These and other findings caution against a fundamental hemispheric coding of approach/avoidance behaviors, per se. It is perhaps more likely that the observed laterality of emotional processes reflects the fundamental bivariate structure of positive and negative evaluative substrates. This is consistent with considerable data indicating that the left hemisphere (especially the insula) is associated with parasympathetic activity related to nourishment, positive affect and appetitive/affiliative states, whereas the right hemisphere is more linked to sympathetic regulation and negative affect, aversive reactions and defensive behaviors (Craig, 2005). Despite the ultimate resolution of this issue, emerging theories of emotion can benefit by recognition of the fundamental bivalent dimension of evaluative processes and the multilevel evolutionary perspective.

References