14. BMIs raise new neuroethics questions, which need to be considered together with the benefits provided by BMIs to people with injury or disease.

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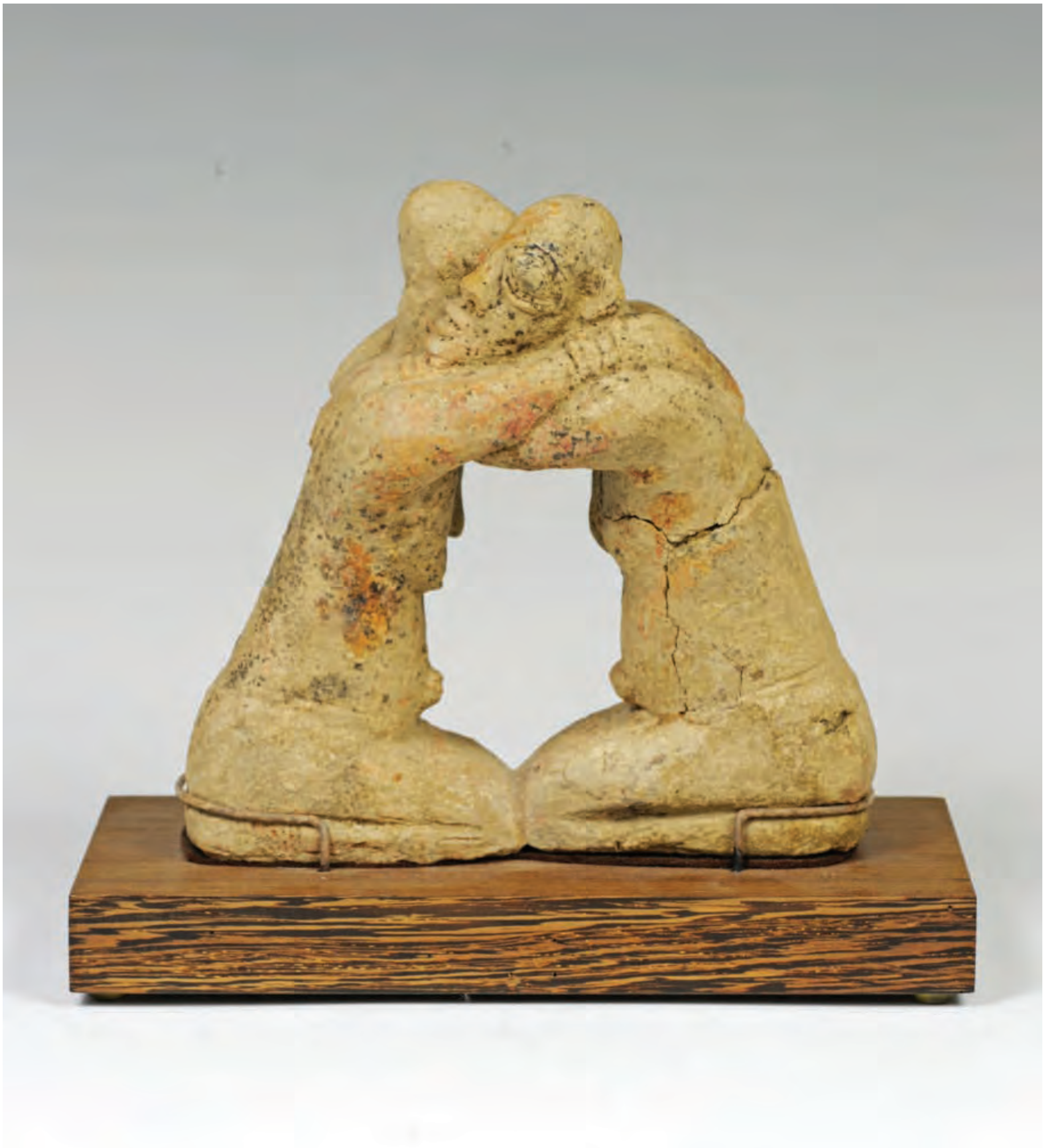
Part VI



Preceding Page

Embracing couple mourning someone's death, perhaps buried in a nearby funerary urn. (Mali, Djenné style. Inland Delta of the Niger River, 13th–15th centuries AD. University of Iowa Stanley Museum of Art, The Stanley Collection of African Art. X1986.451.)

VI The Biology of Emotion, Motivation, and Homeostasis

Emotional and homeostatic behaviors all involve the coordination of one or more somatic, autonomic, hormonal, or cognitive processes. Subcortical brain regions concerned with a range of functions—including feeding, drinking, heart rate, breathing, temperature regulation, sleep, sex, and facial expressions—play a critical role in this coordination. Subcortical brain regions are bidirectionally connected with cortical brain areas, providing a means for reperesentations of internal state variables (eg, visceral information) to influence cognitive operations, such as subjective feelings, decision-making, and attention, and for cognitive functions to regulate or extinguish neural representations in subcortical brain areas that help coordinate behavior reflecting emotional states.

Our consideration of these systems begins with the brain stem, a structure critical for wakefulness and conscious attention on the one hand and sleep on the other. The significance of this small region of the brain—located between the spinal cord and the diencephalon—is disproportionate to its size. Damage to the brain stem can profoundly affect motor and sensory processes because it contains all of the ascending tracts that bring sensory information from the surface of the body to the cerebral cortex and all of the descending tracts from the cerebral cortex that deliver motor commands to the spinal cord. Finally, the brain stem contains neurons that control respiration and heartbeat as well as nuclei that give rise to most of the cranial nerves that innervate the head and neck.

Six neurochemical modulatory systems in the brain stem modulate sensory, motor, and arousal systems. The dopaminergic pathways that connect the midbrain to the limbic system and cortex are particularly important, because they are involved in processing stimuli and events in relation to reinforcement expectation, and therefore contribute to motivational state and learning. Addictive drugs such as nicotine, alcohol, opiates, and cocaine are thought to produce their actions by co-opting the same neural pathways that positively reinforce behaviors essential for survival. Other modulatory transmitters regulate sleep and wakefulness, in part by controlling information flow between the thalamus and cortex. Disorders of electrical excitation in corticothalamic circuits can result in seizures and epilepsy.

Rostral to the brain stem lies the hypothalamus, which functions to maintain the stability of the internal environment by keeping physiological variables within the limits favorable to vital bodily processes. Homeostatic processes in the nervous system have profound consequences for behavior that have intrigued many of the founders of modern physiology, including Claude Bernard, Walter B. Cannon, and Walter Hess. Neurons controlling the internal environment are concentrated in the hypothalamus, a small area of the diencephalon that comprises less than 1% of the total brain volume. The hypothalamus, with closely linked structures in the brain stem and limbic system, acts directly on the internal environment, through its control of the endocrine system and autonomic nervous system, to achieve goal-directed behavior. It acts indirectly through its connections to higher brain regions to modulate emotional and motivational states. In addition to influencing motivated behaviors, the hypothalamus, together with the brain stem below and the cerebral cortex above, maintains a general state of arousal, which ranges from excitement and vigilance to drowsiness and stupor.

The neurobiological investigation of emotion has relied on experiments that define emotions in terms of specific measures ranging from subjective reports of feelings in humans, to approach or defensive behaviors, to physiological responses such as autonomic reactivity. Charles Darwin observed in his seminal book *The Expression of the Emotions in Man and Animals* that many emotions are conserved across species, making clear the relevance of studying emotions by using animal models to probe neural mechansisms. In experimental frameworks, emotional states are thereby considered to be central brain states that can cause coordinated behavioral, physiological, and cognitive responses across species.

In recent years, much work on emotion has focused on the amygdala, which can orchestrate different responses via its connections to the cortex, hypothalamus, and brain stem. Lesions of the amygdala in humans impair fear learning and expression, as well as fear recognition in others, due to decreased allocation of attention to features of faces that communicate fear. Symptoms in a variety of psychiatric disorders—ranging from addiction to anxiety to social deficits—likely involve amygdala dysfunction. However, the amygdala is only one component of a larger set of brain regions that includes parts of the hypothalamus, the brain stem, and cortical areas also responsible for coordinating emotional responses. In particular, the medial and ventral prefrontal cortex and amygdala are closely interconnected. Dynamic processing within and between these structures likely subserves many functions beyond coordinated emotional behavior, including extinction, the cognitive regulation of emotional states, interactions between social and emotional domains, and the influence of the amygdalar representations on decision-making and subjective feelings.

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Part VI

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