Interoception: The Inside Story—A Model for Psychosomatic Processes

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Objective: To comprehend psychosomatic processes, it will be necessary to understand the brain’s influences on bodily functions and also the body’s afferent sensory input to the central nervous system, including the effects of this input on behavior and cognitive functions, especially emotion. The objective of this Presidential Address is to review what is known circa the year 2000 of the processes and mechanisms of visceral sensory psychobiology, often called interoception. Methods: Over 1000 publications that have appeared since the 19th century were reviewed to prepare this review, including a group that are specifically cited here. Results: Factors and data were reviewed that were identified as germane to understanding interoception. These included definitional issues, historical roots, the neural basis, studies and results in the cardiovascular-respiratory and alimentary-gastrointestinal systems, studies of emotion, and studies in people with mental disorders. Drug and hormone effects, pain, proprioception, and phantom limb or organ factors, and the role of awareness were briefly described. Methodological issues, methods of study including functional imaging, and possible future directions for study were identified. Conclusions: Understanding the physical basis of psychosomatic processes, including the so-called mind-body problem, will require a detailed understanding the psychobiology of interoception. Key words: interoception, visceral sensation, psychosomatic, emotion, psychobiology, mind-body problem.

ARAS = ascending reticular activating system; CS = conditioned stimulus; EEG = electroencephalogram; GSR = galvanic skin response; IBS = irritable bowel syndrome; NTS = nucleus of the solitary tract; US = unconditioned stimulus.

The assumption of the existence of psychosomatic processes and psychosomatic disorders is predicated on the belief that psychological or mental functions can interact with physiological or somatic functions—that the mind can affect the body and vice versa (1). Although the philosophical controversy remains as to whether or not mental processes are a fundamentally different “stuff” than are physical processes, most would not dispute the belief that mental processes occur in, and require, the presence of a highly evolved nervous system. (The main alternative is that the mind is not a substance—a “stuff”—at all but rather refers to the brain in action, what the brain does. In other words, the confusion and controversy is due to a category mistake. Mind appears to be a noun but actually is a verb. Of course, this alternative also requires a sophisticated nervous system.) Thus, any theory that proposes to explain psychosomatic functions must involve an explanation of how the brain and the body interact, in both directions: how the brain affects the body and also how the body affects the brain (2).

The afferent or sensory side of this hypothesized closed-loop psychosomatic system involves all of the anatomical, chemical, and physiological mechanisms by which information from the body is transmitted to the brain (3, 4). The study of these mechanisms from a psychological point of view—that is, not just the physiology per se but also the involvement in higher mental processes such as emotion, conscious awareness, and behavior (with or without awareness) (5–8)—has focused on afferent information from the viscera (heart and gastrointestinal tract, primarily, but also respiratory and genitourinary systems, and sometimes including other systems such as the endocrine, as well as chemical, osmotic, and volume changes) and is usually called interoception (9–13). A broader and potentially more useful definition of interoception for the purpose of the investigation of psychosomatic functions should include the afferent information that arises from anywhere and everywhere within the body—the skin and all that is underneath the skin, eg, labyrinthine and proprioceptive functions—not just the visceral organs.

Sherrington used the word “interoceptor” 100 years ago, referring to sensory nerve receptors for stimuli that originate inside the body. Even before him, Sechenov, writing about bodily sensations, referred to “dim feelings,” “faint sensations,” and an “obscure muscular sense” at the border of consciousness. Recent dic-

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tionary definitions of interoceptor include “a receptor, esp. of the viscera, responding to stimuli originating from within the body” and “a specialized cell or end organ that responds to and transmits stimuli from the internal organs, muscles, blood vessels, and the ear labyrinth.” Interoceptive conditioning has been defined as “...classical conditioning in which either the conditioned stimulus (CS) or the unconditioned stimulus (US) or both are delivered directly to the mucosa of some specific viscus.” The present article will provide a brief review of what is known circa the year 2000 about interoception defined in this broader fashion. Understanding interoceptive processes provides data and a model with which to further understand an essential component of psychosomatics—how the body talks to the brain.

In the present article, a variety of issues related to interoception have been addressed. These include 1) the relevance of emotion and motivation to interoception; 2) the roots of interest in interoception in Russian and Eastern European Pavlovian conditioning studies, learning theory, and biofeedback research; 3) the anatomy of the visceral afferent (sensory) neuronal processes; 4) the data produced by studies expressly addressed to interoception in the cardiovascular-respiratory, alimentary-gastrointestinal, and endocrine systems (including drug-induced states); 5) visceral pain, proprioception, and phantom limb and organ phenomena, and their potential relationships to interoception; 6) disorders of interoceptive functions; and 7) consciousness and body schema and their relevance to interoception. Several more detailed expositions and citation bibliographies on the topic of interoception can be found among the cited references, especially Cameron (9), which is a far more detailed expansion of the issues and topics reviewed here.

Historical Roots

The original sources of the study of what is now called interoception cannot be specified precisely, of course, but a good place to start would be with the description of the concept of the milieu interieur by Bernard approximately 150 years ago. Bernard’s idea was that there was an identifiable set of physiological parameters that defined the normal internal state of the organism. Implied in this theory was the hypothesis that the body would seek to maintain these parameters. Several decades later, Cannon (14) called this maintenance process homeostasis. Also implied in both the ideas of the milieu interieur and of homeostasis is the existence in the body of mechanisms by which the organism can track the moment-to-moment fluctuations of these physiological parameters. Without highly reliable afferent information traveling from the body to the nervous system, no control or maintenance of this homeostatic milieu interieur would be possible. Although it is now known that most, if not all, of these physiological parameters are not normally completely static, the theory that there are optimal physiological conditions that vary across organismic circumstances is correct. The afferent pathways that carry the sensory information from the body to the brain provide a potential means not just to control such purely physiological processes as the reflex control of breathing or blood pressure but also a source of information about the state and function of the body that could influence so-called higher mental functions and behavior—ie, interoception.

One very important milestone in theories of the potential importance of interoceptive processes is the James-Lange theory of emotion. Lange was a physiologist who focused his ideas on the possible role of vasomotor changes in emotional reactions, whereas James was a psychologist and philosopher whose ideas more broadly entailed the effects on emotion of feedback from the body more generally. To quote James, from his Principles of Psychology (15), he stated his theory as follows:

“Our natural way of thinking about these coarser emotions is that the mental perception of some fact excites the mental affection called the emotion, and that this latter state of mind gives rise to the bodily expression. My theory, on the contrary, is that the bodily changes follow directly the perception of the exciting fact, and that our feeling of the same changes as they occur IS the emotion. Common-sense says, we lose our fortune, are sorry and weep; we meet a bear, are frightened and run; we are insulted by a rival, are angry and strike. The hypothesis here to be defended says that this order of sequence is incorrect, that the one mental state is not immediately induced by the other, that the bodily manifestations must first be interposed between, and that the more rational statement is that we feel sorry because we cry, angry because we strike, afraid because we tremble, and not that we cry, strike, or tremble, because we are sorry, angry, or fearful, as the case may be. Without the bodily states following on the perception, the latter would be purely cognitive in form, pale, colorless, destitute of emotional warmth. We might then see the bear, and judge it best to run, receive the insult and deem it right to strike, but we should not actually feel afraid or angry.”

“I now proceed to urge the vital point of my whole theory, which is this: If we fancy some strong emotion, and then try to abstract from our consciousness of all the feelings of its bodily symptoms, we find we have nothing left behind, no ‘mind-stuff’ out of which the
emotion can be constituted, and that a cold and neutral state of intellectual perception is all that remains.”

It is essential to understand that James was not proposing that the bodily feeling was the sum total of the reaction, eg, of fear. What he hypothesized was that the feedback from the body produced the feeling part but not necessarily the perceptual-cognitive or behavioral parts. Furthermore, a careful reading of James reveals that his theory did not assert that the bodily reaction came first. Rather, the perceptual-cognitive processing in the brain came first, which led to behavior, which in turn led to bodily sensations that were fed back to the brain, thus producing the feeling part of the emotion: I see the bear (perception), I run (behavior), I am afraid (emotion). James’s theory has been criticized on several grounds, especially by Cannon (14). Although some of the critical comments appear to be correct, and James’s theory in its original form is probably not completely correct, the role of bodily sensations in emotion (and in the control of behavior more generally)—ie, interoception—is undoubtedly very important (16, 17).

The James-Lange theory is about emotion. Emotion is a concept closely related to the concept of motivation. Both are about the “why” of behavior—what prompts an organism to act. Another major aspect of the control of behavior is the “what” of behavior—which behaviors the organism engages in. That relates to learning processes and conditioning. As the James-Lange theory demonstrates, interoceptive processes are closely related to emotion and thereby to motivation more generally. This linkage is clearest in aversive or fearful emotional states. Interoceptive processes are also conceptually linked to conditioning, especially to so-called classical or Pavlovian conditioning, but also to instrumental or operant conditioning. These linkages arise in relation to the issues of Pavlovian conditioning of the functions of visceral organs and the controversy of one-process vs. two-process learning theory, which will be discussed below. These topics have strong historical relevance to the study of interoception and highlight the fundamental need to understand afferent sensory functions in order to understand efferent motor functions.

Pavlov first described the learning process now known as Pavlovian or classical conditioning approximately 100 years ago, and he and his students developed the methods and theory of this conditioning method mostly in the first quarter of this century (18). They called it the conditioned reflex. The first study that used these methods, which demonstrated interoceptive conditioning, was apparently reported in Russian by Bykov and Alekseev-Berkman in 1926, in which both the unconditioned stimulus (kidney function and diuresis) and the conditioned stimulus (infusion of fluid into the gastrointestinal tract) were interoceptive (19).

Pavlovian conditioning is fundamental to interoception because it has been demonstrated repeatedly that changes in function of visceral organs can be effected with Pavlovian procedures, and it seems unlikely that visceral conditioning (change in organ function produced and controlled by the brain) could occur without ongoing sensory input from the organ in question—ie, without interoception. In other words, the brain could not effectively control an organ’s function without moment-to-moment afferent sensory input from the organ as to its functional status.

Interoceptors have traditionally been divided into four major types on the basis of the kind of stimulus they respond to, including mechanoreceptors, chemoreceptors, thermoreceptors, and osmoreceptors (20). Proprioceptors, including vestibular function, and nociceptors (responsive to painful stimuli) are usually included as well. “Multimodal” receptors, which respond to more than one type of stimulus, have been described. Along with overall phylogenetic development, there has been increasing differentiation in the interoceptors, and along with this increasing differentiation in the interoceptors themselves has been greater development in the central nervous system structures that receive this afferent sensory information. Cross-organ interoceptive responses can occur, which are most likely mediated at higher central nervous system levels.

Interoceptive responses have been demonstrated in heart rate, respiration, blood pressure, urine production, and alimentary motility, among others. Associated changes such as the EEG, GSR (sweating), and changes in pupil size have been observed. There are multiple combinations of stimuli and responses that have been studied in both animals and humans. For example, in the case of stimuli, both the conditioned stimulus and unconditioned stimulus could be interoceptive, or one could be interoceptive and the other exteroceptive. Drug-induced states have been used successfully as interoceptive stimuli (see below).

Investigators of interoception and Pavlovian conditioning have been interested in the brain mechanisms involved in these processes (21, 22). For both theoretical and methodological reasons, the midbrain reticular region and the cortex were foci of particular interest. The EEG has been a commonly used method because it is measured from the cortical surface, indicative of activity at that level of the brain, but also because the origin of diffuse cortical desynchronization in the EEG is significantly affected by the midbrain ARAS.
One example of this type of research is the investigation of conditioned effects of carotid stimulation. Initial dilation of the carotid sinus sends afferent impulses that reach the central nervous system and affects the EEG, ie, reaching those brain regions from where the EEG signal is obtained. In other words, carotid dilation had effects in the higher brain centers even before conditioning, and this unconditioned sensory information affected brain function up to the level of the cortex. Once habituation to this unconditioned effect occurred, conditioned responses in the EEG could also be demonstrated.

There is additional evidence for the importance of the reticular formation in visceral sensory processes in addition to the EEG. Electrical stimulation of the reticular formation appears to facilitate the conduction of exteroceptive and proprioceptive information to the cortex but to inhibit interoceptive (which might relate to the relative lack of interoceptive information in reaching conscious awareness).

Pavlov believed that involvement of the cortex was necessary for conditioning to occur. This, of course, is not completely correct, because even invertebrate organisms do not have cortices can show Pavlovian conditioning. There have been reports of conditioning in decorticate dogs and cats. Unilateral surgical removal of the sensorimotor and prefrontal cortex of the dog after establishment of interoceptive conditioning either produced a partial decrement in conditioning or did not substantially disrupt the conditioned reflex. In contrast, studies with pigeons that removed both hemispheres led to loss of the ability to demonstrate conditioning.

Interoceptors are not morphologically different from other sensory receptors and generally seem to follow the same laws of Pavlovian conditioning as exteroceptors, such as extinction, differentiation, etc. There are also differences, however; interoceptive conditioning generally takes longer to establish, but, once established, there is more resistance to extinction and a greater tendency toward disinhibition. There is also evidence for interactions between interoceptors and exteroceptors; the presence of an exteroceptive conditioned motor response seems to facilitate the development of interoceptive motor conditioning, whereas the existence of the conditioned interoceptive motor reflex sometimes tends to inhibit the exteroceptive response.

When either stimulation of mechanoreceptors in the gastrointestinal tract or electrical stimulation of the uterus in humans were used, it was found that EEG desynchronization occurred at stimulation levels that initially were not subjectively detectable. However, with verbal reinforcement, the threshold for subjective awareness became more acute and approached the level at which desynchronization occurred. A second experiment with patients who had undergone colostomy supported this finding. Thus, it appears that nonconscious visceral afferent impulses can be made conscious with verbal reinforcement or feedback. Visceral sensation was described as at the “borderline” of conscious, but that learning can improve awareness. The apparent (at least relative) silence of visceral sensations in one’s consciousness does not imply silence in affecting behavior (or thought processes).

Six principles of interoceptive Pavlovian conditioning have been articulated: 1) Interoceptive stimulation leads to largely unconscious reactions. 2) Interoceptive conditioning is readily obtainable. 3) Interoceptive conditioning is a built-in function, constantly generated and regenerated. 4) Interoceptive conditioning is slower to form but more resistant to extinction. 5) Interoceptive conditioned reactions are dominant over exteroceptive. 6) Exteroceptive and interoceptive stimuli with the same conditioned reaction tend to decrease the intensity of the conditioned effect (23).

The importance of Pavlovian conditioning to interoception, as has already been noted, is that the functions of visceral organs can be modified by this form of conditioning, and visceral afferent sensory (ie, interoceptive) processes undoubtedly are involved in this conditioning. Whether or not the other major form of conditioning—operant or instrumental conditioning—also can influence the functions of the visceral organs was the subject of early biofeedback research and is an issue in the competing theories of one-process vs. two-process learning (24–27). (The term “biofeedback” now has a much broader, more clinical usage than it originally had—it is almost a synonym for a wide variety of behavioral techniques used in the treatment of a wide variety of clinical disorders and largely independent of understanding of underlying mechanisms.)

Briefly, the idea of two-process learning is that different types of learned responses or behaviors can and must be conditioned by the two different laws or methods of learning. Within this context, it is hypothesized that so-called control of voluntary muscular or skeletal responses is biologically separate and distinct from control of so-called involuntary autonomic or visceral responses and that the skeletal responses are conditionable only by the operant techniques, whereas the visceral responses are conditionable only by the classical conditioning methods. Although the major distinction in two-process theory is between types of responses (ie, efferent effects), types of stimuli (ie, afferent effects) related to these responses is of fundamental importance, which relates directly to interoception. One-process theory, on the other hand, argues that these fundamental differences are not real and
thus that visceral conditioning could be produced by both conditioning methods (interoceptive processes would be involved here as well). This theory seems to have arisen to a significant extent from the observations that operant methods affect skeletal responses whereas Pavlovian conditioning affects visceral-autonomic responses, along with the subjective experience in humans that the skeletal responses seem to be voluntary whereas the visceral seem not to be.

Early attempts to condition visceral responses with operant methods appeared in the 1960s. In some of these studies, muscle relaxants were used in an attempt to prevent possible mediating voluntary muscular responses, because if these occurred it would appear that visceral conditioning had occurred with operant methods, but that conclusion would be incorrect. Other studies did not use muscle relaxation. In those studies, if learning did occur, it would not be clear whether learning of the visceral function itself had occurred or whether learning had occurred of a nonvisceral function that then mediated the visceral function through unlearned mechanisms.

At the time that that research was being performed, there were two competing theories about what role external biofeedback (ie, external stimuli) plays in visceral conditioning. The first was that it externalizes internal sensory functions such that such functions can be perceived, because (the theory hypothesizes) these internal functions cannot be perceived directly. The other theory hypothesizes that feedback in not an externalization but rather is an enhancement of internal cues. Interoception research has shown that internal stimuli can be perceived, thus lending support to this second hypothesis.

A number of the initial studies reported positive results. However, over about a decade the inability to replicate many of the early findings that involved muscle blockade became apparent, and interest in this research waned. These failures to replicate do not mean that biofeedback methods do not work. They mean that the possibility of mediating somatic responses cannot be excluded as the possible underlying mechanism. Regardless of the ultimate resolution of the controversy noted above about the role of externalization vs. enhancement of internal cues, in either case, the ability to condition visceral responses strongly indicates the existence of visceral sensory processes that send afferent impulses not just to the brain but specifically to those parts of the brain involved in learning.

Neural Basis of Visceral Sensation

It was known more than 300 years ago that nervous input contributed to the control of heart rate. More than 100 years ago, 1) it was recognized that differences existed in function of the “visceral” from the “somatic” and the “vegetative” from the “sympathetic” aspects of nervous system function, 2) identification of specific nerves and ganglia occurred, and 3) the physiological and pharmacological aspects of autonomic function were studied. In the first half of the 20th century, chemical transmission of nerve impulses in the heart was demonstrated, and acetylcholine was identified as one of the autonomic nervous system neurotransmitters. Adrenaline was identified and isolated from the adrenal gland, and norepinephrine was recognized as a neurotransmitter in sympathetic nerves. Recognition that there were multiple receptors for many of the neurotransmitters was an important step, along with the development of specific agonist and antagonist drugs.

It was determined approximately 100 years ago that there were two separate branches of the efferent or motor aspect of autonomic function (now called sympathetic and parasympathetic) and that they had different neurotransmitters and different (often opposing) effects. It was also recognized that there were visceral or autonomic sensory nerves, but these were not studied in any detail until more recently. (The existence of afferent fibers running in autonomic nerves was verified in the 1920s and 1930s.) The early focus on the efferent aspect of the autonomic system had the effect of, de facto, defining the autonomic nervous system as a motor system, a functional definition that has been widely perpetuated even to the present. It was also recognized that the gastrointestinal tract has an endogenous, relatively autonomously functioning enteric nervous system, which is often considered a third branch of the autonomic system.

Connections between autonomic function and cerebral function was noted as early as the middle of the 19th century, when visceral changes associated with seizure activity were described. Research in the first half of the 20th century repeatedly demonstrated that lesions or stimulation of various parts of the central nervous system produced various types of changes of visceral-autonomic function.

Within the realm of sensory function, investigators generally focused on the external senses, ie, those that mediated the interactions between the organism and its external environment, but it was acknowledged that there was also an internal environment between skin and nervous system. Furthermore, it was recognized that some sensory functions resided at the margin be-
between the internal and external environments. For example, proprioception is about the position and movement of the body in external space but is about the body. Taste is about things in the external world but about to enter the body, as is smell in many cases. Pain can be about either realm. An understanding of visceral sensation and these related processes requires an understanding of the neuroanatomy, physiology, and pharmacology of visceral afferent pathways and mechanisms. The anatomy will now be briefly reviewed, and reviews of the physiology and pharmacology are available (28–31).

Visceral sensory receptors are divided into free-nerve-ending pain receptors (nociceptors), and physiological receptors that monitor ongoing function of visceral organs and mediate visceral reflexes such as baroreception. There are also specialized visceral receptors such as chemoreceptors, osmoreceptors, and thermoreceptors. The sympathetic nerves more commonly contain pain fibers, whereas fibers from physiological receptors (as well as some pain receptors) are more common in parasympathetic nerves. Visceral afferent fibers are generally more abundant in parasympathetic nerves. Stimulation of the receptors that control visceral reflexes typically do not produce conscious awareness.

The afferents in the parasympathetic cranial nerves synapse in the brain stem, including cranial nerves VII, IX, and X, on the nucleus of the solitary tract. All other afferents enter the central nervous system and synapse at the level of the spinal cord.

The NTS in the brain stem is an essential structure in the visceral afferent pathways. One part of the NTS receives input from the spinal tract (the spinosolitary tract), which is believed to be involved in visceral-somatic sensory integration. The other major visceral afferent input is from the solitary tract, which is formed by cranial nerves (VII, IX, and X). These carry the parasympathetic visceral sensory information as they enter the brain stem. The NTS has significant projections to the parabrachial nucleus and the A5 and A6 (also known as the locus coeruleus) noradrenergic nuclei in the pons, as well as the nucleus ambiguus. There is a substantial convergence of visceral and somatic afferents in the brain stem as well as in the spinal cord. Projections then go to multiple higher centers such as the hypothalamus.

From viscera to brain stem, afferent pathways related to visceral sensory processes are relatively straightforward to identify and track. After one reaches regions of the central nervous system above the brain stem, tracking specific pathways becomes much more difficult and the results less clear because of the complexity of the tracts involved. Although there are certainly feedback loops even at the level of the brain stem and below, interconnections among higher structures is much more complicated, to the point that the appropriateness of identifying a particular tract as afferent vs. efferent often becomes impossible (or meaningless). Thus, rather than trying to identify relevant pathways at this level, one often is able to only identify relevant structures.

Unlike most of the other structures at this level, there is a general somatotopic organization to visceral afferent pathways in the thalamus, especially in the ventral posterior lateral nucleus. Like the thalamus, the hypothalamus has many readily identifiable nuclei and substantial involvement in visceral function, but there is less clarity about how some of these nuclei connect to the visceral afferent pathways. In contrast to the thalamus which seems to serve mainly as an integrator of input of exteroceptive sensory information from the external environment (although this is a simplified generalization), the hypothalamus appears to be an integrator of visceral-autonomic-homeostatic (ie, interoceptive) inputs that come from many sources within the central nervous system as well as from the periphery. These inputs in the brain and periphery to the hypothalamus include the visceral sensory, olfactory, visual, limbic, and circumventricular (chemoreceptors and osmoreceptors) systems, and the functions involved include hormonal, reproductive, behavioral, immune, thermoregulatory, gustatory, and biorhythm, as well as autonomic.

Going back at least to the early 20th century, neuroanatomists have identified brain structures just below the cortex that appeared to be especially highly interconnected. Different descriptions include somewhat different structures, but the fornix, the stria terminalis, and the cingulate, dentate, and hippocampal gyri were commonly included. These are now collectively called the limbic system, although there is also doubt as to whether or not these particular structures are more closely linked functionally to each other than to other brain structures. These structures are of potential relevance to interoceptive processes because of their putative involvement in emotional-motivational behavior.

One structure that is sometimes considered to be part of the limbic system, and is strongly implicated in control of emotional function, is the amygdala. Afferent inputs reach the amygdala from the olfactory bulb, septal nuclei, thalamus, primary sensory cortex, medial prefrontal cortex, regions of the “association” cortex, cingulate cortex, and the subiculum (which in turn receives input from regions that include the hippocampus and the entorhinal cortex). Inputs mainly enter the amygdala via the lateral nucleus. There are
internal connections in the amygdala, which lead to output mainly from the central nucleus.

Although many subcortical structures are significantly involved in visceral sensory function, the cortex is essential, including the likelihood that that conscious awareness, including awareness of visceral function, requires a functional cerebral cortex. Four cortical regions are most strongly implicated in interoception, the somatosensory cortex, cingulate gyrus, frontal cortex, and insular cortex. It has been hypothesized that the more medial brain structures, including cortical regions, carry information related to internal bodily states (whereas the more lateral structures are involved in processes related to the organism’s interactions with its external environment).

The somatosensory cortex is divided anatomically into two regions, designated SI and SII. The SII area is smaller than SI and is near the lateral fissure, in close proximity to the insular cortex. The SII region appears to be particularly involved in visceral sensation.

The functions of the cingulate gyrus (also sometimes called the cingulate cortex) have been described as including activation of visceromotor and skeletomotor processing (32). The cingulate is often divided into two large parts, the more anterior, which has been implicated in affective function, and a more posterior part, which has been associated with more cognitive processes. A four-division anatomical-functional breakdown of the cingulate has also been described in which the infracallosal region (anterior, under the corpus callosum) mediates visceral functions. Anatomically, this region is connected to the medial orbitofrontal cortex, rostral insula, ventromedial temporal lobe, and amygdala.

The frontal cortex is usually considered to mediate the “highest” brain functions—thought, judgment, etc., but also including substantial involvement in emotional functioning. Thus, the frontal cortex is at least indirectly implicated in visceral sensory processing. The medial frontal area seems to be somewhat more directly implicated than the lateral.

The region of the cortex that seems to be most directly involved in visceral sensation is the insular cortex (33–35). It also known as the Island of Reil, or the central lobe or the fifth lobe of the brain. This region seems most essential, because its activation appears to be most directly related to distinct or discrete visceral sensory activation. An outline of the peripheral and central nervous system structures involved in visceral sensation appears in Table 1.

**TABLE 1. Anatomical Structures and Pathways Involved in Visceral Sensation, From the Periphery to the Cortex**

<table>
<thead>
<tr>
<th>Periphery</th>
<th>Visceral sensory pathways</th>
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<tr>
<td>Receptors—pain, physiological, specialized (chemo-, osmo-, and thermo-receptors)</td>
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<td>Fibers—sympathetic, parasympathetic</td>
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<td>Enteric nervous system</td>
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<td>Spinal cord</td>
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<td>Sympathetic, some parasympathetic (from pelvic nerves)</td>
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<td>Via laminae I, V, VII, and VIII</td>
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<td><strong>Brainstem</strong></td>
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<td>Tracts</td>
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<td>Major—spinothalamic, spinoreticular, spinomesencephalic</td>
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<td>Others—spinocervical, spinohypothalamic</td>
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<td><strong>Nuclei</strong></td>
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<td>Nucleus of the solitary tract—entry point of some parasympathetic fibers (e.g., vagus nerve)</td>
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<tr>
<td>Parabrachial nucleus</td>
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<tr>
<td>Adrenergic, especially A6 (also known as the locus coeruleus)</td>
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<td>Central gray</td>
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<td>From brainstem to cortex</td>
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<td>Thalamus</td>
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<td>Hypothalamus</td>
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<td>Cerebellum</td>
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<td>“Limbic system”</td>
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<td>Amygdala</td>
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<td><strong>Cortex</strong></td>
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<td>Somatosensory—SI, SII</td>
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<td>Cingulate—anterior, medial</td>
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<td>Frontal—medial orbitofrontal, lateral</td>
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<td>Insula</td>
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**Cardiovascular and Respiratory Interceptive Data**

Even though a sensory impulse need not reach conscious awareness in order to affect behavior, a major interest in interoception research has been the question, “Under what circumstances does a visceral event reach consciousness?” An issue closely related to this question is the distinction that has been made between a detection and a perception of a visceral event. In this context, the concept of detection has been used to refer to the organism’s response purely on the basis of the afferent physiological information, whereas the concept of perception refers to a response based on all of the information available to the organism, including such additional factors as learning and expectations (36). This is an important distinction, because some methods of studying interoceptive processes are more likely to be affected by perceptual factors other than detection than will others. Furthermore, perceptual factors beyond sensory input can compete with simple detection to affect responses. For example, it is commonly observed that correlations between actual physiological changes and verbal reports of symptoms or emotional experiences are not strong, probably in significant part because the verbal reports are affected by
other factors in addition to detection of sensations from the viscera. Last, it is clear that there are substantial individual differences among subjects in interoceptive ability and that some subjects for some specific types of sensations are quite accurate. Visceral organs produce afferent sensory impulses, including pain but not limited to it, that do sometimes reach consciousness.

The methods used in interoception research can affect results to a considerable extent. For example, in studies designed to investigate ability to detect heart beats, three general methods have been used. Questionnaires have been used extensively, especially in clinically oriented studies, but seem to be least directly related to detection per se and most affected by other perceptual factors. Tracking techniques, in which subjects are asked to count heart beats over a period of time, have been used to determine whether subjects can sense heart rate. Discrimination methods, in contrast, have been developed to assess subjects’ ability to recognize individual heart beats. Discrimination tasks appear to most nearly measure detection not influenced by other factors. The question, “What is being detected?” will be addressed below.

Beyond the issue of whether or not sensory impulses arise from the viscera generally, several more specific questions should be asked. 1) From which visceral organs do sensory afferent impulses originate? 2) What role do such impulses play in the function of the organ in question, for example, homeostatic processes? 3) Do these impulses contribute to complex motivational or emotional states such as thirst or fear, and/or do they contribute to cognitive processes? 4) Do these impulses reach conscious awareness? 5) Do these impulses affect behavior, and if so, in what ways? 6) What is the relationship between these interoceptive functions and the physiological functioning of the central nervous system? The first two questions listed here (1 and 2) relate mainly to physiology per se, and the next three (3 through 5) relate to physiological functions as they interact with behavior and consciousness. The last question (6) addresses the role of the central nervous system in mediating these functions and processes. In attempting to understand psychosomatic processes, answers to all of these questions, but especially questions 3 to 5, will be fundamental to the larger question noted at the beginning: “How does the body talk to the brain?”

The most extensively studied interoceptive process is awareness of cardiac action, both heart rate and individual heart beats. Variables related to subject characteristics (i.e., individual differences), methodological factors (independent variables), and outcome measures (dependent variables) have all been assessed. These three sets of variables will now be discussed in turn.

Although not all studies have found this, the bulk of the data support the observation that men perform cardiac interoception more accurately than women. (This has also been found for awareness of other functions such as gastrointestinal contractions.) This finding for cardiac interoception, however, might be due to a confounding factor—body composition involving percentage of body fat. At least one prior study found that, when leanness was controlled, both lean male and female subjects showed awareness of cardiac action and there was no difference in gender, whereas nonlean groups showed poorer ability to detect heart action. These data suggest that increased body fat content diminishes cardiac detectability. There are data inconsistent with finding as well, however.

Younger individuals show better cardiac detection than do older people. This could also be related to leanness and percentage of body fat. Another possible explanation is the change in adrenergic function commonly observed in association with aging. Still another possibility is that the age factor relates to fitness differences. More fit subjects are more aware of their heart action (at least for men), and younger individuals are typically more fit than older people. Again, percentage of body fat could contribute to this observation, given that more fit individuals are typically leaner.

Last, symptom proneness contributes to the individual difference factor. This can be reflected either as a tendency to report awareness of symptoms and/or the actual presence or absence of a diagnosable disorder or disease (for example, an anxiety disorder). Clearly, this is an important factor from the point of view of potential relevance of interoceptive functions to psychosomatic medicine.

Effects of several independent or methodological variables have been assessed in studies of cardiac interoception. It should be noted at the outset that test-retest and other forms of reliability and validity have not been adequately assessed in interoception research generally, including studies of cardiac interoception. Some, but not all, data indicate that individuals are least aware when in a standing posture, most when lying down, and intermediate when sitting (or lying at an angle, as on a tilt table) (37). This appears to be true because postural change produces cardiodynamic changes created by gravity. (This postural effect bears on the question of the mechanism by which awareness occurs. It is inconsistent with the hypothesis that awareness is due in significant part to sensations produced by the heart beating against the interior of the anterior chest wall, as has been suggested, a mecha-
Exercise substantially affects cardiac interoception. Increases in the inotropic and chronotropic effects of the heart produced by exercise substantially increases cardiac awareness. Results of studies that combined posture and exercise demonstrated that awareness appears to be more closely associated with measures of heart action related to the inotropic effect of the heart rather than with the chronotropic effect. In other words, it is the strength of the heart beat, not heart rate, that is the more important determinant of the sensory stimulus. The threshold for exercise-induced cardiac awareness is at a heart rate of approximately 100 beats per minute, the high end of the normal adult resting heart rate.

Emotional tone can affect cardiac awareness. Subjects rated high on state anxiety and emotional lability were found to be more sensitive on both tasks that involved detection of individual heart beats (while not differing in actual heart rate) and heart beat tracking tasks. In another study, subjects who showed greater variations in GSR (skin conductance, a putative measure of arousal and emotionality) could learn a heart beat discrimination task better than those with less variability.

In the research setting, training can be thought of in several ways. First is the prior experience that individuals have before any structured experimental protocol is initiated, and the second is any ongoing learning or benefit that subjects accrue during the study. Prior experience can be part of the research (ie, training before testing) or the uncontrolled experiences that occur as a part of daily activity (eg, people who engage in frequent vigorous exercise will have more exposure to high, and therefore probably sensible, inotropic and chronotropic effects on the heart). Training separate from testing has not been systematically studied in interoception research. Experience with the task as a form of training that occurs during research studies does improve results, although the effect is not great and is probably diminished by the conflicting effects of boredom in studies requiring many trials. Knowledge of results (feedback with verbal or other types of external stimuli signifying the correctness or incorrectness of the response) does improve performance.

It is unlikely that all of the paradigms and methods proposed to assess cardiac awareness measure the same thing. Even for tasks that claimed to be specific heart beat discrimination tasks, correlations between tasks were typically weak. In other words, the dependent or outcome measures can and do vary among studies.

In addition to the usual outcome measures such as accuracy of detection of individual heart beats, other dependent variables are of interest. Among these, some of the most interesting are the central nervous system changes observed during interoception. EEG and imaging studies have been reported (38).

The EEG studies have focused mainly on two brain regions, the somatosensory cortex and the frontal cortex. Results indicated that 1) cardiac action was apparent in the evoked potential in the anterior parietal somatosensory regions, 2) highly aware subjects showed stronger evoked potentials than less aware subjects, and 3) this representation was stronger in the right hemisphere than in the left. Evoked potential changes from the frontal cortical regions were also related to cardiac awareness and were more prominent in the right (ie, nondominant) hemisphere. In a number of studies with different methodologies, results of the studies of hemispheric localization of cardiac awareness, and of general central nervous system cardiac control (at least sympathetic control), are consistent in the documentation of involvement primarily of the right cerebral cortex.

A small number of imaging studies have started to appear that address the question related to cardiac interoception (39–41). Studies with ischemia-induced cardiac pain and without (ie, “silent ischemia”) have shown activation of regions generally consistent with basic science studies of brain structures involved in cardiac visceral input to the brain. Regions implicated include the insular cortex, frontal cortex, thalamus, cingulate gyrus, and somatosensory cortex.

Interoception of vascular and respiratory changes have both been studied, but the number of reports is small, and conclusions are not yet warranted. Studies of pathological conditions, especially those related to cardiac function (eg, imaging studies of cardiac ischemia and pain), are just beginning to appear. Again, conclusions would be premature.

The final question to be addressed in this section is, for cardiac interoceptive detection, “What is the stimulus that the subject is responding to?” How is the action of the heart sensed? The timing of the cardiac-generated stimulus as well as other factors appears to exclude the possibility that chemoreceptors, osmoreceptors, or thermoreceptors could be involved and implicates mechanoreceptors. The apparent effects of weight and percentage of body fat are consistent with this implication. Greater weight could have a dampening effect on mechanoreceptor stimulation, and greater body fat in particular could diminish sensitivity because body fat has few if any of the relevant receptors.

Where could the relevant receptors be located? They could be in the heart itself or elsewhere. Two possibilities for elsewhere need to be considered. The first
possibility is in the blood vessels, especially the vessels near the heart such as the aortic arch. The second is other tissues near the heart that could be affected by the mechanical action of the heart such as nonvisceral somatic touch or pressure receptors in the thorax, especially the inside of the anterior chest wall. As noted above, postural data suggest, but do not demonstrate conclusively, that stimulation of anterior chest wall receptors is not a sufficient explanation. The following tentative hypothesis seems to have the most support: mechanoreceptors in the heart or, more likely in the major arterial blood vessels coming off of the heart, respond to the change in pressure produced by the chronotropic but mainly inotropic effect of the individual heart beats. An outline of the subject (individual differences), methodological (independent), and outcome (dependent) variables appears in Table 2 (38).

Alimentary-Gastrointestinal Interoceptive Data

It is often said that nonpainful sensations are vague and emotionally colored, and anatomical localization often is diffuse. However, such sensations as those referable to the alimentary tract—for example, nausea, severe hunger, and overfed satiety—are typically very specific in sensory characteristics and intense, even though not painful. Painful stimuli in the gastrointestinal tract are also often vague when it comes to localization, but the pain itself—from such stimuli as chemical irritation, distention, torsion, traction, forceful contraction, inflammation, and ischemic changes and necrosis—can be excruciating and is certainly not vague. Distention, for example, is a robust source of gastrointestinal sensation that has been assessed in interoception studies. As is true in other systems such as the cardiovascular, in the alimentary system, descending modulation by the central nervous system is known to affect sensory processes. There has been longstanding interest in interoceptive processes in the gastrointestinal tract (42, 43).

Unlike studies of interoception in the cardiovascular system, which have focused mainly on normal subjects, studies of alimentary interoception has focused considerably on disorders. For example, symptom studies have found that approximately one third of people with noncardiac chest pain have demonstrable abnormalities of esophageal motility. When experimentally controlled rectal distention with anorectal manometry was used, it was reported that thresholds of awareness and symptom reports differed in people with IBS in comparison to normal controls, and that the patients with IBS not only had abnormal rectal sensitivity but also a more generalized increase in sensitivity throughout the gut. Typically, subjects showed changes in visceral sensory function in response to rapid, but not slow, distention. In research that has assessed awareness of both cardiac and gastrointestinal function, gastric and cardiac awareness were significantly positively correlated.

A broad view of the alimentary tract encompasses not just the esophagus to the rectum but the taste and olfactory receptors and processes such as hunger and thirst (44). Imaging studies of sensory awareness in the alimentary system include studies of these processes. For example, brain activation in response to salty taste (in right-handed normal subjects), measured with functional imaging techniques, was more apparent in regions in the right than in the left hemisphere and appeared mostly robustly in limbic and paralimbic regions. Viewing faces with the expression of disgust activated anterior insular cortex on the right and regions linked to a “limbic corticostriatal-thalamic circuit.”

Moving down the alimentary tract, somatosensory areas were activated by nonpainful esophageal stimulation, the insular region and premotor area were activated by more intense esophageal stimulation, and when the sensation became painful, anterior cingulate activation was seen. In other words, there was a gra-

<table>
<thead>
<tr>
<th>TABLE 2. Subject (Individual Differences), Methodological (Independent), and Outcome (Dependent) Variables Shown to be Relevant in Cardiac Interoception (Modified from Jones [—38]).</th>
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<td>Subject (individual difference) variables</td>
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<td>Age</td>
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<tr>
<td>Fitness</td>
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<tr>
<td>Gender (including control for body fat)</td>
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<tr>
<td>Symptom proneness (including diagnosis—anxiety, etc.)</td>
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<td>Weight and percentage of body fat</td>
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<td>Methodological (independent) variables</td>
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<tr>
<td>Emotional induction (arousal, stress, etc.)</td>
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<td>External stimuli</td>
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<td>Knowledge of results (feedback)</td>
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<td>Number of training trials</td>
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<td>What is the stimulus?—cardiovascular dynamics</td>
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<td>Somatic (and proprioceptive?) changes</td>
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</table>
Changes in awareness (other physiological changes can also be detected). The most robust changes occurred in the precentral gyrus, the postcentral gyrus, and the thalamus; this activation did not correlate with magnitude of distention. Another study, which involved normal subjects and individuals with IBS, assessed subjects both when painful rectal stimulation was occurring and when it was not occurring but was anticipated. For normal subjects, the anterior cingulate cortex was the region most activated by painful stimulation. The intensity of activation correlated positively with the pain intensity ratings in normal subjects but not in patients.

Drugs, Pain. Proprioception, Phantom Limbs and Organs, and Bodily Awareness

Changes in internal sensory states are obviously related to interoception. Five that will be briefly mentioned here are state-dependent and discriminative effects of drugs, visceral pain, proprioceptive functions, phantom limb or organ phenomena, and body schema or bodily awareness. These states are all potentially of direct relevance to psychosomatic processes.

Although it has been argued that organisms respond only to drug effects in the central nervous system, that is not completely correct. Although effects produced within the central nervous system are more robust, there are examples of effects restricted to the periphery as well. Epinephrine (adrenaline) does not cross the blood-brain barrier, yet studies have demonstrated that the peripheral effects of epinephrine can function robustly as discriminative stimuli. Another substance that does not cross the blood-brain barrier and produces purely peripheral anticholinergic effects can also be detected.

Epinephrine is an endogenous substance normally present in the body. Other endogenous substances and other physiological changes can also be detected. Changes in awareness ("symptoms") can occur in normal subjects when hypoglycemia is produced by intravenous insulin administration. Additionally, a number of studies have shown that state-dependent effects can be produced by direct electrical brain stimulation.

It has been hypothesized that there are two pain pathways from a functional point of view. One pathway ("epicritic") carries the impulses that involve the discriminative component of pain. The other pathway ("protopathic") carries impulses that involve the affective-motivational-emotional component. The discriminative pathway is phylogenetically newer, anatomically more lateral in the central nervous system, and more concerned with events in the external environment, whereas the affective-motivational-emotional pathway is older, more medial anatomically, and more concerned with bodily (visceral) functional states. Imaging studies have indicated that all types of pain stimuli typically activate the thalamus but that visceral and nonvisceral pain show differences in brain activation patterns. For example, activation of the primary somatosensory area occurs in conjunction with nonvisceral pain but is less likely to occur with visceral pain.

Proprioception and phantom limb phenomena are less directly related to interoceptive phenomena than are drug states and visceral pain. Nonetheless, they do relate to the schema of the body overall and its place in space and time. To the extent that awareness of the viscera, however vague it is, is part of the larger awareness of the body itself, these are related experiences. Furthermore, although not formally studied, it does seem that phantom sensory experiences of visceral organs can occur. And the hypothesized "somatic markers" of emotion must depend on bodily awareness for their very existence.

Finally, the concept of the body image map should be mentioned. These are maps within the brain, which are labile and not completely bound to the anatomical limits that movements and positions the body actually impose. They appear to be at least partly unconscious, and they incorporate the external world as well. They are maps of the body in relation to both the internal structure and function of the body itself as well as the immediate environment within which the body resides.

Interoceptive Data in Mental Disorders

Psychosomatic medicine, as a part of psychosomatics more broadly conceived, deals with pathological processes. Understanding dysfunctions of interoception—how visceral sensory processes can and do malfunction—is an essential part of psychosomatic medicine. Interoceptive malfunctions in gastrointestinal and cardiac illness have already been mentioned. In this section, the realm of mental disorders will be touched on, including anxiety disorders, depressive disorders, and somatoform disorders.

Natural panic attacks are highly associated with subjective reports of symptoms referable to the viscera, especially cardiac and respiratory, but also gastrointestinal. Panic attacks induced experimentally are associated with cardiovascular sympathetic activation and respiratory changes. Based primarily on results.
from imaging studies, one theory of the pathophysiology of panic disorder has implicated many of the brain regions relevant to visceral sensory processes—brain stem (nucleus of the solitary tract, parabrachial nucleus, periaqueductal gray, locus coeruleus), thalamus, amygdala, hypothalamus, “limbic lobe,” cingulate gyrus, and insular and medial prefrontal cortices (56).

Concerning panic, patients with full panic disorder, less severe panic, or other anxiety disorders reported more cardiac and gastrointestinal awareness than normal subjects. With a heart beat counting task, panic patients were more accurate than other patients, including those with specific phobics or infrequent panic attacks. In a study that also used the heart beat counting task, panic and generalized anxiety patients were more accurate than depressed people. Anxious individuals report more somatic, including visceral, symptoms than healthy individuals, but more data must be collected before it can be determined the extent to which this is a difference in detection per se.

In large part because of the frequent co-occurrence of anxiety in major depressive disorder, interoceptive function in depressive disorders would be of interest. Little research has so far been reported, however. Because of the defining characteristics of somatic symptoms in the somatoform disorders, they also would be of special interest. Again, however, few directly relevant studies have thus far appeared.

Visceral Awareness

Throughout this exposition, and throughout the field of interoception research generally, the issue of visceral awareness is paramount. As has already been said, it is not necessary that a visceral sensory impulse reach awareness to affect behavior. But it seems highly likely, nevertheless, that those impulses that do reach awareness have different effects than those that do not, because of the very fact that they do. The question of how both kinds of impulses affect behavior, thought, and/or emotion is a separate question that also demands understanding.

The question of the connection between awareness or consciousness and interoception has two essential aspects. One, as already noted, is the probability that visceral sensations that reach awareness have different effects on thought, emotion, and behavior than those that do not. The second is that consciousness of the “self” most likely depends to a substantial extent on awareness (however vague, ill-defined, and folded into a larger consciousness) of the body per se, including its visceral organs and functions. It has even been argued that all consciousness, including consciousness of self, arose out of the evolutionary development of sensory—including visceral sensory—processes. The body and subjective awareness of the body, including visceral awareness, instantiates the “self” and provides the intermediary by which the nervous system interacts with the external world.

Future Directions

Interoception is a “psychosomatic phenomenon par excellence,” connecting, as it does, body to brain to behavior and thought (and to the “rational mind”). Of particular note, although most interoception research has depended on awareness because it has depended on verbal reports, interoceptive processes undoubtedly can and do occur outside of awareness. Interoception even touches the realm of neurophilosophy, because awareness of the body is basic to consciousness of self. To close this exposition, issues related to methods of studying interoception, mechanisms by which interoception occurs, and pathophysiology of interoception will be summarized, with an eye to future directions for research.

Investigators must be clear, to themselves and to others, whether they are studying interoceptive detection or perception. To what extent are factors beyond “pure” detection affecting responses? Factors related to conditioning and learning, or emotion and motivation, or both must be determined. And potential effects of efferent motor behavior on sensory phenomena must be assessed. Functional imaging methods are likely to be especially useful in linking visceral afferent events to central nervous system events because these methods can bypass the need for verbal report or any dependency on awareness (although, of course, verbal report and related measures can be incorporated in these studies as well) (57).

Although increasing interest in visceral sensory mechanisms has occurred in the last two decades, much remains to be learned. Other than pain, little is yet understood of the location and functioning of interoceptors in the viscera. For example, where are the cardiac interoceptors? Are they actually in the blood vessels instead of the heart itself? Do some visceral organs have interceptors whereas others do not? Or do all organs have them but only some send impulses to “higher brain centers”? What is the neural basis of individual differences (58)? Might some people have a different set point, such as a different “emotional tone,” that includes differences in interoceptive sensitivity? Apropos of the James-Lange theory, what is the relevance of the visceral sensory impulses, and sensory impulses for the body more generally, to homeostatic control of the milieu interieur and emotion?

Turning to the central nervous system, there is
much more to be learned of the anatomy, physiology, and pharmacology of visceral sensation. Is the “closed-loop” concept correct, which says that the motor and sensory sides of visceral innervation—like that which often occurs in the rest of the body—functions largely as an integrated whole? At the level of “higher brain processes,” what roles do conditioning and other forms of learning and maturation play in interoception? Does operant conditioning affect the functions of visceral organs, and, if so, what role do sensory processes play? Although awareness is not necessary, does it sometimes occur. Under what circumstances? For what functions or “purpose”? Which brain regions are implicated when awareness occurs vs. when it does not?

A process as complex as interoception undoubtedly sometimes, under some circumstances, malfunctions. This is the part of the realm of psychosomatic medicine. Abnormal visceral pain is an important aspect but not the only one. Other abnormal visceral sensations, such as some occurrences of nausea or cardiac awareness during anxiety, are examples. Some organs seem more commonly involved than others, especially the heart and gastrointestinal tract. It has even been demonstrated that specifically identifiable brain regions are associated with pathological changes in immune function (59).

Some processes—stress and the stress response and some emotions (eg, fear, anger)—are thought of as often on the “border” of normal vs. abnormal functioning. Interoceptive awareness occurs very commonly in these circumstances. More must be understood of the relationships among these processes. Although studies of both normal and abnormal interoceptive processes have shown consistency in the brain regions involved (eg, pain [60]), generalizations such as observations about potential similarities and differences among interoceptive abnormalities in different pathological states such as cardiac ischemia, irritable bowel syndrome, and panic disorder would be premature.

In addition to the so-called medical disorders—eg, cardiac and gastrointestinal—that involve interoceptive changes, psychiatric or mental disorders apparently do as well. Most research has been done with the anxiety disorders, especially panic. The role of interoceptive changes in the somatoform disorders is ripe for study. Furthermore, despite the success of the syndromal approach to diagnosis of both medical and mental disorders, the study of the pathophysiology of individual bodily symptoms (which do not covary precisely with specific individual disorders) from the point of view of interoceptive dysfunction is called for. In summary, interoception fits well with the body-mind and behavior continuum—ie, a psychosomatic—perspective on both normal functioning and disease.

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