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I



AN INTRODUCTION TO INTEROCEPTION

How do you feel?

That's a familiar question that we hear every day. If I pause to examine my feelings now, at this moment, the very first observation I have is that I'm having lots of ongoing feelings. My feelings include several about my recent interactions with others, a few about my walk up the hill and my plans for the coming weekend, and recurrent feelings about my current goals, about writing this book, and about the ideas I want to share with you. I am also experiencing feelings that relate neither to the past nor the future, but rather to the immediate present. I have feelings about this room, about the lighting, and about the items I see nearby (my lunch!). I have feelings coming from different parts of my body, and I have affective or emotional feelings, mood feelings, which are constantly ongoing and which color everything. Emotional feelings extend across several timescales and occasionally become very strong, episodic, and maybe even overwhelming.

I'm sure you can describe your feelings similarly. We share a commonsense view of what feelings are. It is based in part on what our parents taught us. In the same way that they taught us what color belongs to the word "red" (regardless how it actually looks to you), they taught us what the word "hot" means by teaching us to associate the word "hot" with a particular sensation coming from our fingers, and they taught us what the word "angry" means by associating the word "angry" with the way they were behaving at the time, or the way you were behaving. Each one of us has exclusive access to our own subjectively experienced feelings, yet we humans share a common understanding of feelings that is based on language, culture, and empathy. At the core of our common understanding of feelings is a set of specific behaviors and facial expressions that are cross-cultural and biologically characteristic of our human species, which importantly are associated with specific feelings and emotions.

Nevertheless, we do not have a genuine understanding of what a "feeling" is or how we experience a feeling. In the dictionary, we find that the word "feel" in English has several different meanings. There are feelings of touch; so, I can say

that I feel the keys as I type, or I can say how rough or smooth an object feels. I regard these as discriminative tactile sensations; a feeling is something deeper and more complex. As the dictionary tells us, the word “feel” can also have an indirectly tangible reference; I can describe the “feel” of a piece of cloth in my hand or a wine in my mouth or the air outside. I can also say that I feel the temperature of objects I touch, as in, “I can feel that the cup is hot.” Notably, that usage can even be shortened by projection to the external object, as in, “the cup feels hot.”

Emotional feelings, though, are even less tangible and more ephemeral. If I tell you how I feel or ask how you feel, we are referring mainly to our subjective personal feelings. Our personal feelings are of two kinds. First, there are the feelings that come from our bodies—I can say that my arm hurts or that my feet feel cold. Second, there are affective feelings that relate our moods, dispositions, and emotions—I can say that I feel happy or I feel sad. Affective feelings are of course what most people relate when they describe their feelings. “I feel anxious,” or “I feel good today!”

Now when we say either of those expressions, we are referring not just to emotional feelings; we are referring also to how our bodies feel. Our descriptions of affective feelings in general seem to be associated with the body; we say that feelings come “from the heart” (as Aristotle taught), or we talk about “gut feelings” (which some equate with intuition). In fact, when we share our feelings, we don’t use only words; we use tone of voice (prosody), facial expressions, and body language. Our emotions are expressed by our bodies, and we feel that.

So it makes sense to regard feelings from the body as the most primal feelings. We feel them all of the time, and they underlie most of our emotional feelings, if not all. The most basic feelings from the body represent aspects of its physical condition. Do I feel hungry or thirsty? Am I warm enough, or do I feel a chill? Does the small skin wound on my arm that is still healing itch or burn? Or, does the chair feel comfortable—which actually means, are my muscles and joints complaining about my physical position? In addition, I can feel less direct aspects of my body’s physiological condition, such as, How much energy do I have? or, Am I overheated? or, Do I need a breath of fresh air?

Such feelings from the body that signal its condition are the basis for what some call “the material me,” or what was called *Gemeingefühl* in the German literature of the nineteenth century (which literally means “common sensation”). There is a marvelous review of that literature in a chapter written by the preeminent British neurophysiologist Charles S. Sherrington, entitled “Cutaneous Sensations,” in *Schäfer’s Textbook of Physiology* (1900); when I first read it, I couldn’t help imagining him seated at a long library table, writing in longhand under the pale light of tall windows and gas table lamps, as his thoughts flowed and, day by day, his synthesis slowly developed. Unfortunately, in his final analysis, he discarded the concept of common sensation. Yet my research showed that primates

have a sensory pathway to the forebrain that represents the physiological condition of the body, a sensory capacity for which I redefined the term *interoception*.

The word “interoception” was coined by Sherrington (who received the Nobel Prize in 1932 for his studies of the motor system and the spinal cord) to refer to sensations from the interior of the body, especially the viscera. He differentiated interoception conceptually from *exteroception* (sensory inputs activated from outside of the body), *proprioception* (sensory inputs that relate limb position), *teloreception* (sensory inputs activated from a distance, i.e., vision and audition), *chemoreception* (taste and smell), *thermoreception* (temperature), and *nociception* (sensory inputs activated specifically by physically damaging or threatening stimuli, which cause specific motoric reflexes that Sherrington measured; a term also coined by him). He categorized nociception and thermoreception together with the sense of touch as aspects of exteroception, because he regarded all three as discriminative cutaneous sensations. Sherrington’s codification underlies the conceptual organization of all modern neuroscience textbooks; they don’t include the concept of common sensation because Sherrington didn’t.

Like Sherrington, virtually all previous authors thought of sensations from the skin as exteroceptive sensory inputs activated from outside of the body, but my findings underlined the accumulated evidence indicating that most sensory receptors in the skin that have small-diameter fibers (or, axons) and cell bodies actually signal the condition of the tissue itself. The skin is the largest organ of the body, and it has very important functions for *homeostasis*, the continually ongoing process that maintains the health of the body (see chapter 2). For example, the skin is critical for water and electrolyte balance, thermoregulation, and vitamin D production. In the same manner, small-diameter sensory activity from muscle signals workload (energy use), metabolite concentrations, and vascular distension, in addition to physical conditions like mechanical distortion and temperature. As with the sensory input from the viscera, the small-diameter sensory inputs from skin and muscle (and from all other tissues of the body, including bone) provide the continuous flow of sensory information required for homeostatic control of ongoing changes in blood flow and respiration, that is, the control of smooth muscle. In contrast, the sensory fibers from skin that have large-diameter axons and cell bodies signal mechanical contact with external stimuli (pressure, velocity, stretch, vibration frequency), and those from muscle and joints signal changes in force, length, and position, all of which are important for guiding movements produced by skeletal (striated) muscle. Though not described in textbooks, this fundamental distinction provides the only sensible explanation for the presence of two completely separate anatomical pathways for ascending sensory activity, the *dorsal column–medial lemniscal* and the *spinothalamic pathways*, and for the presence of two morphologically separable regions in the sensory-processing portion of the spinal cord (i.e., the dorsal horn) that differentially process large- and small-diameter sensory input (described in chapters

2 and 3); in both cases, the first one serves exteroception and the second serves interoception. My research demonstrated that there is also a distinct *interoceptive cortex*, which contains the primary cortical representation for both thermoreception and nociception (see chapter 5); this finding substantiates the fundamental neurobiological distinctness of interoception. As explained in chapter 3, modern genetic analyses of the evolutionary origins of the vertebrate nervous system show that these two morphological/functional neural systems are produced by two distinct gene regulatory networks that have ancient sources.

Thus, one of the conceptual advances from my research is the enlargement of the term *interoception* to include small-diameter sensory input from the whole body—not only from viscera, muscle, joints, and teeth, but also from skin. This concept of interoception includes the idea of common sensation. And in this conceptual framework, nociception and thermoreception are aspects of interoception, not exteroception, because they report aspects of the physiological condition of the body conveyed by small-diameter sensory fibers and the spinothalamic pathway to the interoceptive cortex. The research described in this book demonstrates that feelings of pain and temperature are based on activity in body maps that occupy specific portions of interoceptive cortex.

Of course, the reason that thermoreception and nociception were so easily categorized as exteroceptive cutaneous sensations is that we have a spatial and intensive discriminative capacity in both modalities that closely resembles the discriminative capacity of cutaneous mechanoreception. We readily refer such thermal and noxious cutaneous sensations to a causative external stimulus, ignoring the fact that the sensations actually report the condition of the skin itself. That certainly confounds this fundamental conceptual shift. But all thermoreceptors and nearly all nociceptors in the skin can be activated either by an exogenous or an endogenous change in conditions; in contrast, cutaneous mechanoreceptors can be activated *only* by an externally applied force. For example, the skin can be rapidly cooled by a reduction in blood flow caused by autonomic vasoconstrictors, which the small-diameter thermoreceptors immediately signal; in fact, providing feedback for thermoregulation is their original and primary function. Similarly, nearly all peripheral receptors that are categorized as “nociceptors” can be activated by changing metabolic conditions in the skin, such as the pH changes and chemicals associated with inflammation (e.g., interleukin-1-beta) or with ectoparasites (e.g., mosquito bites). In contrast, the large-diameter mechanoreceptor sensory terminal that enwraps the base of a hair follicle is activated only when the hair is flicked sufficiently quickly by contact with an external object.

Nevertheless, our primate brains clearly enable interoceptive activity to be used for discriminative sensation. Furthermore, modern evidence indicates that some cutaneous nociceptors have sensory terminals in the exterior part of the skin, large-diameter fibers that are fast-conducting, and a central terminal branch that targets spinal interneurons which drive skeletal muscle reflexes; these cer-

tainly fit the Sherringtonian concept of a nociceptor. Another small subset signals graded sharpness, regardless whether it feels painful or not. Both of these receptors can be described as serving exteroception rather than interoception. However, these exceptional elements still share the basic morphological, chemical, and genetic properties that differentiate the interoceptive fibers, and they drive ascending spinothalamic axons that activate interoceptive cortex. In other words, they belong to the category of interoceptive fibers that represent the physiological condition of the body. (See box 3 for discussion of this issue.)

More generally, our perceptions of natural stimuli are always based on the central integration of activity across the various available sensory channels, and furthermore, as explained in this book, to my mind any sensation must be transformed to a feeling in order to be “felt,” or experienced in subjective awareness. The model of interoceptive integration described in chapters 5–7 can explain how all types of sensory and neural activity generate feelings that are used to guide behavior.



The idea that we can feel the condition of all of the tissues of our bodies might be intuitively clear to you because we are all familiar with these feelings. Everyone I have met or know of (other than certain patients) can describe the most basic feelings from her/his body, like whether she or he feels warm or cool, hungry or thirsty, or how much something hurts, and whether the source is skin, muscle, or joint tissue. These feelings depend on the small-diameter sensory fibers from all tissues of the body and the interoceptive sensory pathway in the brain.

There is a wealth of experimental evidence demonstrating the deep significance of bodily feelings for human performance. The following paragraphs highlight some of this evidence. (The citations for these findings are all provided in the bibliography at the end of this book.)

As individuals, we each have a different capacity for so-called bodily awareness. Bodily awareness has been called *interoceptive awareness* by investigators interested in the effects of cardiorespiratory or visceral sensory activity on human mood, emotion, and performance. The feeling of heartbeat awareness is a quantifiable capacity that is often used as a measure of the capacity of individuals for interoceptive awareness. Heartbeat awareness can be measured by asking a person to count the number of heartbeats she or he feels in objectively timed intervals of 30, 45, and 60 seconds, and comparing those numbers to real counts obtained from an electrocardiogram (ECG) recording or a finger pulse oximeter. Alternatively, one can use the ECG or pulse oximeter signal to drive a tone generator and produce a short series of single beeps that are either in time with the heartbeat or are out of time by being delayed half of one second. The participant is asked to determine whether the tones are in time or delayed across repeated trials. In the latter paradigm, a control for each participant’s attention can be

obtained by using a similar short series of tones, varying one and asking the participant to report whether they are all the same or not. [Cameron, 2001; Schandry, 1981; Wiens, 2005]

Heartbeat awareness varies widely across individuals; it is not an all-or-none characteristic. It is used as a generalized index for interoceptive awareness, although there are only two relevant reports, both of which found that heartbeat awareness correlates with gastric sensitivity (this issue certainly needs more work). It may be related to particular cardiodynamic parameters. An individual's heartbeat awareness score also correlates with that individual's self-reported sense of bodily awareness and with her or his sensitivity to pinch and ability to tolerate a maintained painful stimulus. Importantly, an individual's heartbeat awareness score also correlates with that individual's ratings of the intensity of her or his own emotional feelings, whether positive or negative. Better heartbeat perceivers are better at reading their own emotional feelings, and subjects who are better at reading their own feelings are better at reading others' emotional feelings. [Whitehead and Drescher, 1980; Herbert et al., 2012; Schandry et al., 1993; Herbert and Pollatos, 2012; Pollatos et al., 2007b, 2012]

Those observations fit with the idea that the cortical processes that enable us to feel the interoceptive feelings of the body's condition also provide the basis for our awareness of emotional, social, and all other feelings. As described in this book, there is now plenty of evidence for this concept (see chapters 2 and 7). The detailed physiological and functional imaging findings on heartbeat awareness provide direct insights into the fundamental role of interoception in human feelings, and they directly corroborate the identification of a particular portion of our brains, the *anterior insular cortex*, as an essential site for our awareness of feelings. The distinct sensory pathway to the interoceptive cortex in primates that my research identified provides the substrate not only for the affective feelings from the body that we humans experience, but also for the interoceptive foundation of emotion that psychologists and psychiatrists have long envisioned. [Critchley et al., 2004; Pollatos et al., 2007a, 2007b; Craig, 2002]

Better heartbeat perceivers function better not only on an emotional level but also cognitively. They make better decisions based on subtle environmental cues, they perform better in tasks of selective and divided attention, and they respond more quickly to intuitive choices. They also have a more accurate subjective sense of time, in the range of 8–20 seconds; that is, individuals with greater interoceptive awareness can provide a more accurate estimate of the passage of present time. That finding fulfills a prediction of the model of interoceptive integration described here (see chapter 7). Recent physiological and functional imaging evidence directly supports the integral role of interoceptive sensory processing in insular cortex for our subjective sense of time (see box 9). [Werner et al., 2009; Dunn et al., 2010, 2012; Meissner and Wittmann, 2011]

Importantly, better heartbeat perceivers expend less energy than poor heartbeat perceivers during a 15-minute free-exercise period on a stationary bicycle, despite reporting comparable feelings of fatigue; this finding has been interpreted to indicate that interoceptive awareness enables better self-regulation of ergometric behavior, or energy utilization. Similarly, the attainment of optimal behavioral performance by elite athletes or highly trained military warriors depends crucially on signals in interoceptive cortex. [Herbert et al., 2007; Paulus et al., 2010, 2012]

Optimal energy utilization is an inherent goal of the process of homeostasis. The balanced patterns of integrated homeostatic responses described in chapter 2 clearly indicate that efficient energy utilization is a key priority. Interoception directly supports homeostatic energy efficiency. For example, many of the small-diameter sensory receptors in muscle are activated by a unique combination of metabolites that effectively signals muscular work, and these receptors can readily be called *ergoreceptors*, or energy sensors. Further evidence indicates that these receptors are directly involved in energy self-regulation in an exercising human during exercise to exhaustion, and they are a main contributor to the subjective feeling of fatigue. Optimal energy utilization is crucial for the evolutionary success of all organisms, and it is a primary feature of homeostasis and interoception. The basic role of the sensors that report the physiological condition of all tissues and organs in the body is to enable the neural, endocrine, and behavioral functions that support the process of homeostasis to perform optimally and efficiently together, without wasting hard-won energy. [Kanosue et al., 2010; Light et al., 2008; Amann et al., 2011]

A very important question about interoceptive awareness may already be forming in the back of your mind, and I want to address it immediately. Interoceptive awareness confers many benefits, so a natural question is, can we increase interoceptive awareness with practice or training? The answer is yes. There is indeed evidence that an individual's capacity for interoceptive awareness can improve with training. There is also evidence that interoceptive or insular activation in the brain can be modified by biofeedback training using real-time functional magnetic resonance imaging (fMRI), which could be especially useful in clinical patients. [Schandry and Weitkunat, 1990; Caria et al., 2010; Domschke et al., 2010; Farb et al., 2013b]



Like musical or athletic abilities, both nature and nurture contribute to an individual's capacity for interoceptive awareness. We all had experiences while growing up that helped us learn to pay attention to our bodies. We learned as children to control our behavior so that it is acceptable. Those experiences also led us to differentiate between our mind and our bodies. In particular, our parents or

guardians and other adults encouraged us to pay attention to the feelings from our bodies, to develop our bodily awareness, in order to gain volitional control of bodily functions, especially urinating and excreting. As we all know, these are very hard tasks to learn as children, and as a result, each one of us grows up with the implicit understanding that body and mind are different. My body has functions that my mind cannot control. My body does not necessarily respond to my mind. I knew that it was not the appropriate time to urinate, but my body behaved autonomously. As you may recall, our bodies in fact contain a widespread network of fibers and nerve cells called the *autonomic nervous system* (ANS), which is a nonvolitional visceromotor system that controls the heart and all internal organs (see chapter 2). The word “autonomic” literally means that it functions independently; it has a mind of its own. So, as children, it is unavoidable and completely natural to learn to believe that our cognitive minds are distinct from our physical bodies.

The adult version of this childhood perspective is called *dualism*, and you can read a philosopher’s description of this concept in great detail at the Plato Web pages of Stanford University or at your library. If I understand correctly, the essential idea is that the mind consists of an ephemeral, intangible substance that is different in kind from the material body. The body doesn’t produce thoughts; thoughts belong to the domain of the thinking mind. This perspective is encapsulated in Descartes’ famous phrase, “I think, therefore I am.” The concept he formulated, called *res cogitans*, is the dualistic idea that there is a cognitive, rational, volitional entity that is different from the material, biological body, which includes the brain. Of course, Descartes’ views on the separateness of body and mind in the 1700s had the practical benefit of enabling scientific studies of the body and the brain, because these were simply mechanical vessels, and no longer contained the mind or soul, which was the province of the Church.

The concept of dualism is clearly inconsistent with the view that our thoughts and feelings are actually substantiated by our brains. The idea that mind is different from body, and the related idea that feelings from the body are different from emotional feelings and from thoughts, make it virtually impossible to identify what a feeling is. We have feelings that are clearly associated with our bodies, yet the feelings are registered or experienced in our minds. This conundrum is at the core of the issue that people who discuss consciousness call “the hard problem.” How is it that our minds experience feelings from our bodies, and conversely, how do the thoughts and feelings in our minds propel the behaviors of these bodies?

Once the mind is reestablished in the body and the brain, those questions dissolve into questions about the interrelationship of the body with the brain, about the network organization of the brain itself, and about homeostatic (interoceptive) integration. The ideas I describe, supported by insightful imaging results

reported by others, provide a framework for understanding how different networks in the brain with different functional roles can be integrated as “me” on the basis of feelings, and how bodily awareness can underpin the subjective awareness of all of the different aspects of “me.”



The significance of interoceptive awareness of feelings from the body for human awareness of emotional feelings is a central tenet of so-called embodiment theories of emotion. The affective feelings we share are not simply mood colors. Even though we humans have espoused cold reason and logical planning in Western civilization ever since the Age of Enlightenment in the eighteenth century, modern research shows that our emotions guide our decisions and our behaviors and that interoceptive signals and interoceptive awareness are crucial. Some authors regard emotions as episodes because they focus on measurements of strong emotions like rage or fear, but from an evolutionary neurobiological perspective, it makes more sense to regard emotion as ongoing, continually varying, and bivalent. From this perspective, all of our behaviors are emotional behaviors.

A major distinguishing feature of emotion theories is whether emphasis is placed on the body or on the mind, reflecting the inherent dualism in Western culture. Embodiment theories of emotion relate our emotions to the condition of our bodies, and they are remarkably consistent with the pathways in our brains that underlie our bodily feelings and our affective feelings. The embodiment theories of emotion emphasize the role of visceral sensation and autonomic activity in the body and brain as a causal source of emotional feelings. In other words, embodiment theories of emotion posit that our feelings are generated by autonomic activity and emotional behaviors, that our feelings are consequences or concomitant features that accompany autonomic activity and emotional behaviors. In the following paragraphs, I briefly highlight the ideas proposed by specific embodiment theorists whose writings contributed to my view of feelings. They incorporated cognitive appraisal to varying degrees. If you are interested in further reading on this subject, then I highly recommend these sources.

The earliest is Charles Darwin’s evolutionary theory of emotion (*The Expression of the Emotions in Man and Animals*, 1882). Darwin recognized the remarkable similarity in the facial expression of various emotional states across human cultures and across mammals, and he inferred an evolutionary origin for the expression of nearly all human emotions and feelings based on a wide variety of original and prior observations. He described patterns of subtle muscle movements in and around the face and related them to protective vascular adaptations in infants, to exaggerated behaviors in the insane, to observations of chimpanzee behavior he made himself at zoos (including the use of a mirror), and to the emo-

tional behaviors of aboriginal tribes around the world that he gathered through personal communications. He introduced the powerful and deep idea that our behavior patterns are heritable, that is, based on (genetic) factors that are expressed in the anatomical structure of our brains, and he gave many convincing examples. For instance, he described in detail the inheritance pattern of “peculiarities of blushing” in one family and an odd arm movement during sleep in another, behaviors that certainly had no volitional component. He also noted that humans born blind display the same facial expressions of emotion that normal humans do. Darwin made great use of the observations and ideas of others before him, such as Sir Charles Bell, Herbert Spencer, Duchenne de Boulogne, and Claude Bernard. Darwin’s penetrating insights and lucid expositions set the stage for the establishment of the field of ethology in this century by Nikko Tinbergen and Konrad Lorenz (who wrote the preface of the 1965 reprint of Darwin’s book), in which the heritable behavioral sequences that define social interaction in many varieties of animals have been categorized as either “fixed action patterns” or more flexible adaptive behaviors. The concept of emotion in mammals as an evolutionarily honed yet trainable system of adaptive behaviors that evolved as fast and flexible response patterns for particular environmental and social situations can be found in Darwin’s book.

At about the same time, William James published his seminal views on emotion (James 1884). He was a professor at Harvard who is often called the father of psychology, and you can find this article and many of his writings on the Web. If you’ve taken an introductory college course in psychology, you probably heard about the James–Lange theory of emotion, so named because a Danish psychologist, Carl Lange, independently made a similar suggestion. The main idea is that our emotional feelings are generated by the emotional behavioral and autonomic program that is initiated in the brain and body in response to some perception. So, you feel afraid when the bear is coming at you because your heart is racing and your pupils are dilated and you want to flee. This theory did not include an explanation for emotional feelings generated cognitively, for which it was sharply criticized. The concept that a specific pattern of autonomic activation precedes awareness of the consequent or concomitant emotional feeling comes from these early thinkers.

The James–Lange theory was directly challenged by Walter Cannon, the pioneering physiologist who defined homeostasis (see chapter 2); he held that the activation of the sympathetic nervous system was too monolithic and undifferentiated to distinguish the many fine gradations of human affective feelings. He used physiological measurements of various autonomic functions following an intravenous injection of adrenalin as prime evidence for his argument because he thought that the sympathetically activated release of adrenalin by the adrenal glands is a defining all-or-nothing concomitant of autonomic arousal that pro-

duces whole-body effects. Autonomic functions are now much better differentiated, and several well-executed studies using sophisticated measures have shown that alterations in cardiorespiratory activity do indeed distinguish different human emotional feelings and affect human perception of emotion. [Cannon, 1927; Ravinville et al., 2006; Harrison et al., 2010; Gray et al., 2007]

A modern successor to the James–Lange theory is known as the somatic marker hypothesis, described eloquently by the neurologist Antonio Damasio in the book *Descartes' Error* (1994), and later more clearly and expansively in a second book, *The Feeling of What Happens* (2000). His basic idea is that an autonomic activation pattern learned in response to a particular stimulus results in a reflexive sensory input from the body to the brain (the “somatic marker”) that distinguishes a particular feeling state and that this guides behavior, even precognitively (i.e., before conscious perception). Damasio’s descriptions of his team’s experimental and clinical observations brought the role of autonomic function again to the forefront of neuroscience research on emotion and highlighted particular regions of the brain. Damasio’s concept of a mental “as-if loop” that can model what certain future behaviors might “feel like” added an important predictive mechanism to the James–Lange model. In recent articles, he has reformulated his ideas to incorporate the notion that the upper brainstem engenders “core consciousness” in all mammals.

The fourth prior author I wish to highlight concerning embodiment theories is the modern psychologist James Laird, a professor at Clark University whose book, *Feelings: The Perception of Self* (2006), builds on the foregoing contributions. Laird provides an invaluable summary and explanation of literally hundreds of studies in the psychology literature that support the hypothesis that feelings do not cause behavior but rather are the consequence of behavior. These data make a very strong case for self-perception theory, an expanded update of James–Lange theory, and he contributes a very lucid theoretical description of an original hierarchical feedback control model that has considerable explanatory power. His ideas regarding the temporal relationship between feelings and actions are an important element of the discussion of sentience and awareness in chapter 9.

Finally, another important book that describes experimental support for these embodiment concepts and which I strongly recommend is *The Illusion of Conscious Will* (2003), by Daniel Wegner, a professor of psychology at Harvard University. The well-controlled experiments described in his book pick up where William James left off in his later studies of séances and Ouija boards. One of the most important ideas supported by the evidence in Wegner’s book is that we often emit or perform emotional behaviors without being aware of what we are doing. Conversely, observing someone emit a behavior or display a facial expression does not mean that person is having the feelings you infer.

The writings of these authors, along with the contributions of many additional prior and contemporary authors, support the following idea: our affective feelings derive from the brain networks that generate flexible and adaptable emotional behaviors, which evolution built by expanding upon the ancient homeostatic neural systems that automatically take care of the body. In other words, the affective feelings that you experience are interoceptive reflections of emotional motivations, which are expressed by activity throughout the peripheral and central autonomic systems of your body and your brain and which produce behavior that you “feel” as it happens. The findings described in this book are consistent with this idea.

The thought that your feelings do not propel your behavior is one of the fundamental ideas in this book. Another is the idea that the homeostatic principle of optimal energy utilization underlies the evolution of the human capacity for subjectively experienced feelings, for emotional awareness. To my mind, the evidence indicates that a feeling is an interoceptive construct that the brain uses to represent the overall energy costs and benefits of any actual or potential emotional behavior, that is, homeostatic valuation, in order to facilitate choices that guide behavior in the most energy-efficient manner. As I explain in the following chapters, I believe that feelings are the coinage of that valuation system. This idea may seem idiosyncratic and speculative to you now, but over the course of this book, I explain the findings and the reasoning that lead to this conclusion.



There is a common feature underlying all of the feelings we experience from our bodies and the affective feelings that are associated with our emotions, as well as all of the instances described above for which the English language allows use of the word “feeling.” A “feeling” is more than a sensation, it is a subjective experiential phenomenon, what I believe certain authors mean by the word “qualia.” Not only did my research suggest that feelings from the skin, muscle, and viscera share a common neural basis with affective feelings of emotional motivations, but the convergence between my observations and the burgeoning literature on the activation of the same cortical regions also suggested the deeper idea that whatever comes into awareness is a “feeling.” Being able to “feel” every thought, perception, emotion, motivation, intention, or potential behavior provides a powerful common currency for the evaluation and comparison of physical energy costs and benefits. In my view, optimization of energy utilization and acquisition in an organism in which the brain consumes 25% of the entire energy budget compelled the evolutionary development of a common valuation system for energy cost-benefit analysis that is capable of representing not only the homeostatic significance of any behavior but also the homeostatic significance of the potential behaviors inherent in any network pattern of neural activity. As you may already know, paleoanthropologists now recognize that the enlargement of the hominid

brain during evolution required an enormous increase in dietary energy, which was likely afforded by the availability of cooked meat and fish. Thus, optimal energy utilization in both the body *and* the brain was necessary, and in the brain that meant both physical and virtual utilization.

As a functional neuroanatomist, I believe that the brain in our bodies is what engenders our feelings, thoughts, and behaviors. There is no question in my mind that the neural structures, pathways, and systems that emerged in the human brain during 53 million years of primate evolution support our ephemeral inner beings and our ecological outer beings as members of a unique primate species. The brain is not a mystical place. It is evolutionarily and reproducibly well organized, and it provides the basis for the health, survival, and growth of each individual, for the cooperative advancement of our species, and for the progressive emergence of our civilizations. Your brain, in its natural setting in your body, provides the basis for your mind. The better we understand how our brains work, the more we will understand who and what we are. This belief system is known in philosophy as naturalistic materialism. For me, this is obvious. [O'Leary et al., 2013]

In order to understand how our brains work and how they produce the feelings that we humans experience, we need to know how they are organized structurally and functionally. We need to identify the patterns of connections between identifiable sets of neurons, and we need to understand the functional significance of different modes and patterns of activity. The brain is not color-coded, and its internal connections are not readily apparent. We need to use experimental methods to uncover its organization and function. By using the right methods, we can actually see the structural basis of its functional organization. The experimental tools of a functional neuroanatomist include a variety of histological staining and pathway tracing methods which enable recognition of neuroanatomical organization, as well as a variety of electrophysiological methods, which enable recognition of patterns of functional organization, both types of methods being applied across several different levels of physical scale. In order to understand how the human brain is organized, we need to apply these experimental methods in the closest extant experimental animal available, the macaque monkey, which does not possess the neural substrate that is responsible for self-awareness in our brains, consonant with the fact that it cannot recognize itself in a mirror. Then we must use correlative features to infer comparable patterns of organization between monkey and human. Today we have functional imaging methods, which provide such correlative data with stunning portrayals of the human brain at work but which need careful interpretation.

The purpose of this book is to provide a clear and accessible explanation of the ideas that emerged from my work on the lamina I projection map shown in figure 1. I have been developing this map for the last twenty-five years, and it is very much a work in progress. I have accumulated a wealth of evidence in the labora-

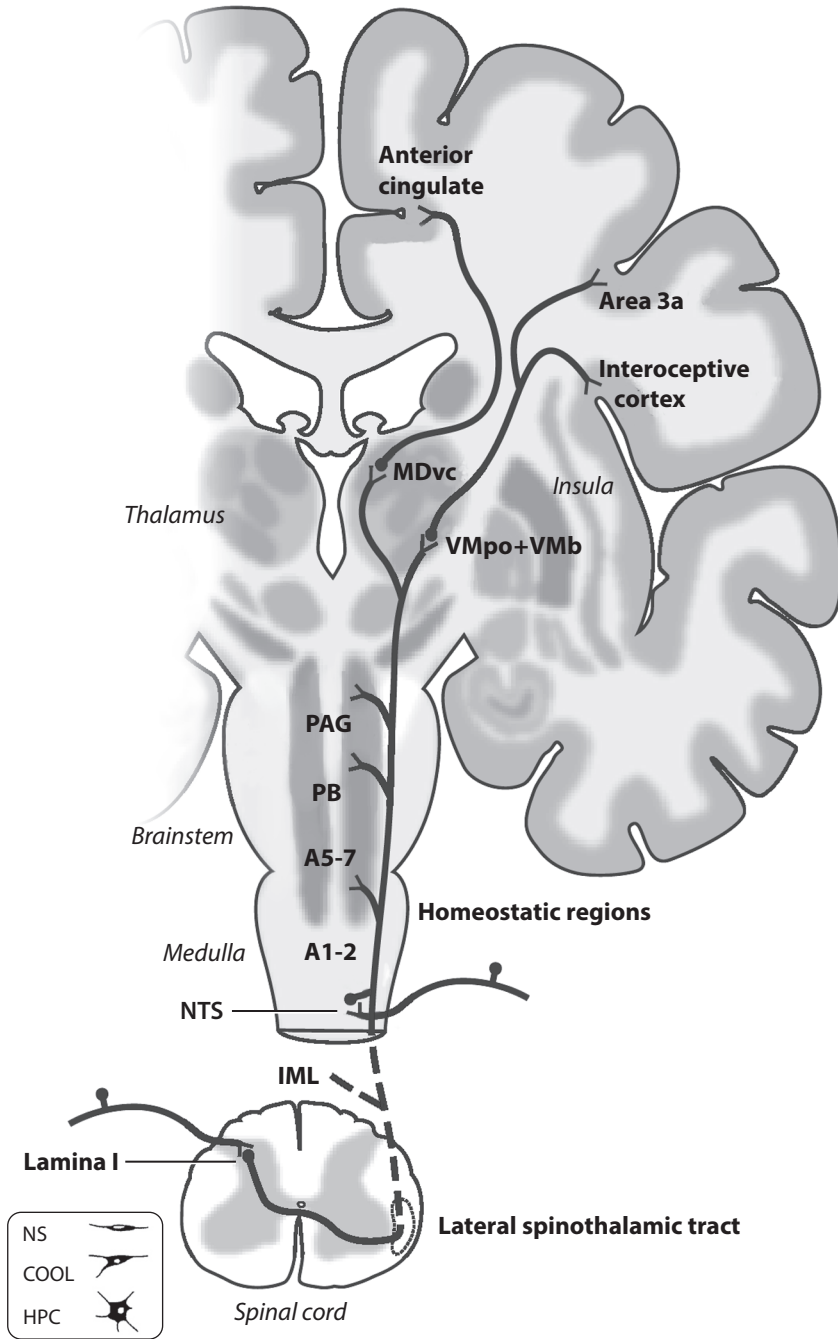


FIGURE 1. The central projection map for homeostatic sensory inputs in the monkey.

tory, some of which is still unpublished and which I continue to analyze and explore. The truth is, I have been distracted from writing the scientific reports describing those data because I haven't been able to stop thinking about the implications of the new ideas that emerge from this map. These ideas have fundamental significance. These ideas provide a plausible conceptual explanation for the instantiation of our subjective thoughts and feelings in our brains, and my goal now is to share these ideas and this explanation with you in these pages.

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