information processing, nor does it explain the neural mechanisms that support these computations. It mainly tells us about the level of brain organization that carries out these operations. For example, consider the search for the neurons that achieve knowledge about the color red, despite changes in the spectral content of the morning and evening light—a phenomenon known as color constancy. Instead of searching in sensory areas for neurons that respond selectively to red in this invariant way, one might look for neurons that guide the choice of ripe fruit. This does not obviate the computations required to recover the surface reflectance properties of the fruit's skin, despite variation in the spectral content of the illuminating light. The raw data for such computations are supplied by sensory neurons that lack color constancy and maintain temporal fidelity with changes in the environment. The knowledge state "red," however, is invariant to the illuminant and likely persistent. In animals that lack language, the knowledge state may not be dissociable from "ripe vegetation."

The second caveat is that we have not distinguished knowledge states that we are consciously aware of from those that we experience unconsciously. For example, as I make my way through the forest trying to find the creek that I hear burbling, my brain might consider locations of objects I pass that are graspable, attached to vegetation, and with color suggesting ripeness. I may be unaware of this consciously. Yet that evening in my search for food, I may return to this part of the forest, guided by these unconscious encounters. I may do this without knowing why, or the memory might pierce consciousness. All that has been said up to now could apply to conscious and nonconscious experience. We are now prepared to elucidate the difference.

Consciousness Can be Understood Through the Lens of Decision Making

Clearly, we are unaware of most of the operations that transpire in our brains, and this is true even for the processes that ultimately pierce consciousness. This is why Freud famously quipped that consciousness is overrated. Every thought that enters our awareness began as neural computation preceding the conscious awareness of that thought. Indeed, the sophistication of nonconscious mental processes, including those leading to "I've got it!" moments and the activities we perform while occupied by a phone call, involves decisions that transpire without conscious awareness.

It is difficult to study nonconscious processing because people deny experience of the process. Indeed, the term nonconscious experience seems like an oxymoron. The experimenter must find a way to prove that information processing has occurred despite the fact that the subject is unaware of it. In recent years, it has become possible to establish conditions whereby information is provided to a human subject that has a high likelihood of going unnoticed but is nonetheless able to influence behavior, thereby permitting scientific characterization of nonconscious mental processing (Chapter 59). This has encouraged neuroscientists to ask what it is about the neural activity that gives rise to the thoughts, perceptions, and movements that do reach conscious awareness. We will not review this vast topic here but instead share a pertinent insight: Viewed through the lens of decision-making, the problem of consciousness may be simpler than imagined.

Broadly speaking, two sets of phenomena fall under the heading consciousness. The first concerns levels of arousal. One is not conscious when one is asleep, under general anesthesia, comatose, or having a generalized seizure. One is fully conscious when awake, and there are levels of consciousness between these extremes. These states are associated with terms such as confusion, dissociation, stupor, and obtundation. Some alterations of consciousness are normal (eg, sleep), whereas others are induced by toxins (eg, alcohol), metabolic disturbances (eg, hypoglycemia), low oxygen, trauma (eg, concussion), or fever (eg, delirium).

The neuroscience underlying these states—and the transitions between them—is immensely important to medicine. We might classify this group of phenomena as neurology-consciousness. However, these topics are not what most people mean when they speak of the mystery of consciousness. This is partly because they are less mysterious but also because their characterization is more objective and the phenomena can be studied in animals. That said, there is much to be learned about the mechanisms responsible for sleep, awakening, anesthesia, and so forth. Much of the neuroscience is unfolding at a rapid pace (Chapter 44).

We will not say more about neurology-consciousness here, except to seed one useful insight. Imagine a mother and father sleeping comfortably in their bedroom as a storm ensues outdoors. There are also traffic sounds and even the occasional thunder. This scene goes on for some time, until the cry of a baby awakens the parents. This common occurrence tells us that the nonconscious brain is capable of processing sounds and deciding to become conscious. It decides, nonconsciously, that some sounds afford an opportunity for more sleep while others sound a call to nurture. This

decision is similar to the perceptual decisions considered earlier in this chapter. Both involve nonconscious processing of evidence. However, the commitment to awaken and parent is a decision to engage the environment consciously. This may be a touchstone between neurology-consciousness and the more intriguing consciousness that you are experiencing as you read these words (or so the authors hope).

When neuroscientists, psychologists, and philosophers ponder the mysteries of consciousness, they are referring to loftier themes than wakefulness. This loftier set of phenomena comprises awareness, imagery, volition, and agency. There is a subjective component to all conscious experience. The experience of conscious perception incorporates a sense that it is me that is beholding the content. It parallels the "me" in volition. It is not that my arm moved on its own; I made it move! We used the term deliberation earlier in this chapter to describe the thought process leading to a decision. Our use of the term was metaphorical. It describes a computation and a biological mechanism, but it does not require awareness. Actual deliberation implies conscious intention. We are aware of the steps of reasoning along the way. We could report, were we asked, about the evidence we relied upon—that is, the evidence we were consciously aware of during the decision and possibly some of the evidence we used nonconsciously were it accessible from memory to include in our report. Could the difference between conscious awareness of an item and nonconscious processing of that item be a mere matter of whether the brain has decided on the possibility of reporting? Could it be this simple?

Consider the following scenario. A psychologist concludes that a study participant has seen something nonconsciously because the item affected a subsequent behavior and the participant denies having seen it. Suppose the subsequent behavior involved reaching in the direction of the object. Based on what we know about decision-making, we would conclude that brain circuits like the ones discussed earlier received sufficient evidence to commit to the possibility of looking, reaching, and approaching, but there was insufficient evidence to commit to the possibility of reporting. Just as the brain entertains the possibility of looking, reaching, or grasping, it may also entertain the possibility of reporting. That is, reporting is also a *provisional affordance*.

Events afford the possibility of reporting, and this includes the nonconscious states of knowledge acquired through decision-making. Indeed, the event of having decided may be experienced consciously—the *aha* moment—by virtue of another decision to report. In the study scenario, the participant was not consciously aware of the item because her brain did

not commit to a provisional report. The evidence did not satisfy a decision criterion like the termination bounds in the perceptual decision-making task considered earlier in the chapter.

This account provides a plausible explanation of the failure of the participant to report that she saw the item, but the mere entertaining of the possibility of reporting does not seem to explain the phenomenology of the perceptual experience itself, at least not at first glance. This explanation demands more careful consideration of the character of the report. Just as we attach states of spatial knowledge to configurations of the hand for reaching and grasping, we must consider the knowledge state that accompanies the affordance of reporting. Whether by language or gesture (eg, pointing), the report is a provisional communication with another agent or oneself (eg, in the future). It presumes knowledge about the mind of the receiver.

Cognitive scientists use the term theory of mind to refer to this type of knowledge or mental capacity. It can be demonstrated by asking someone to reason about the motivation behind another agent's actions, and it can be studied in animals and preverbal children by examining their reactions to another child or puppet. In one study protocol, two children witness a desired toy placed in a left or right container (Figure 62–2). The test child then witnesses the toy's displacement to the other container while the other child is absent. When that child returns, the experimenter assesses the test child's expectation of which container the returning child will open to find the toy. Children under 3 years old do not exhibit theory of mind by this assay. They think the returning child will open the container that contains the toy, not the one it was in before the transfer. Whether animals other than humans have theory of mind is controversial. We suspect there are inchoate forms of this capacity in the animal kingdom and in children under 3. When adults perform tasks that depend on theory of mind, the right temporal-parietal junction and superior temporal sulcus are active.

Theory of mind—in concert with narrative—has profound consequences for the knowledge state associated with the reporting affordance. Imagine a woman looking at a power drill resting on a table. She experiences the location of the drill, relative to her eyes and hand, as well as its texture and shape. It has a graspable surface that is partly in her line of sight and partly occluded (eg, the back). These are the knowledge states that arise through provisional commitments to look at, reach for, and grasp the drill. They are likely to involve neural activity similar to what is illustrated in Figure 56–7, and they are the outcome of simple decisions. The drill brings to mind other affordances

associated with its utility as a tool, its potential to make noise, and the potential danger posed by the sharp bit at one end. This is an elaborate, potentially rich collection of knowledge, but it could all be experienced nonconsciously. For example, if the woman were preoccupied with some other task, such as a phone conversation with her friend, she might nonetheless make use of these knowledge states.

But suppose there is a man on the other side of the table and suppose the woman—her brain, that is—has also reached a provisional commitment to report to the man about the drill between them. Consider the change to her knowledge state. The drill now has a presence not only in her visual field, relative to her gaze, her hand, and her repertory of actions, but also in the man's field of vision and his possible actions. The parts of the drill that are not in plain sight to her are known to be in the line of sight of the man. Indeed, her capacity for "theory of mind" also supplies knowledge that other parts of the drill are seen only by her and that the man could be experiencing those parts just as she experiences the parts that are not in her direct line of sight that is, both preconsciously as occluded parts of the object and consciously as part of an object that could be seen directly from another vantage point. There is something about the drill that is at once private, public, and in the world—independent of either mind. The drill is there for the next person who enters the room, or an imagined person. The transformation of knowledge of the drill is from a collection of first-person experiences (eg, qualities and affordances) to a thing in the world that possesses an existence unto itself. It is conceivable that this state of knowledge is our conscious awareness of the world, or at least a part of it, for the knowledge state associated with a decision to report is further enriched by content of the report itself.

The report might be simple, like pointing to the location of a tool or a hiding spot, or it might involve narrative. In the case of the hiding spot, additional content might be conveyed to indicate that the enclosure affords safety from a predator or, alternatively, a predator's location. Many simple reports do not require narrative because items such as tools and enclosures persist and theory of mind presumes the affordance of a tool or a hiding place in another's mind, whereas events, which also afford the possibility of reporting, often require narrative because they are transient.

The knowledge state associated with narrative can incorporate history, simulation, prediction, etiology (eg, origin stories), purpose, and consequence. For the drill, narrative might enhance the knowledge state to include memory of the place of purchase, an episode in which it malfunctioned, and the mechanism of its

detachable bit. Narrative allows us to reason in more complex environments than the scenarios considered earlier (eg, the umbrella example and the probabilistic reasoning task; Figure 56–9). We could not reason about science, medical diagnosis, and jurisprudence without origin stories, simulation, hypotheses, prospection, and counterfactuals. The evolutionary advantage of this capacity is obvious (at least for the time being, until it leads us to make the earth uninhabitable).

To summarize, the conscious awareness of an item might arise when the nonconscious brain reaches a decision to report the item to another mind. The intention is provisional in that no overt report—verbal or gesture—need occur, just as no eye movement need ensue for the parietal cortex to engage the possible intention of foveating. Just as the provisional intention to foveate corresponds to preconscious knowledge of the location of an as yet unidentified object in the periphery, the possibility of reporting to another agent (or self), about whom we have theory of mind, corresponds to the knowledge of an item in a way that satisfies most aspects of conscious awareness.

Naturally, our journey from perceptual decision-making through affordances to consciousness is at best incomplete. For example, it does not yet provide a satisfying account of what a conscious experience feels like. But it is a start, as it supplies a coarse explanation of why sensory information acquired through the eyes is experienced differently from auditory or somatosensory experiences, and it provides insight into the private aspects of perceptual awareness as well as our experience of objects as things in the world, independent of what they afford to the perceiver. These last features follow from the consideration of another agent's mind.

The view of consciousness from the perspective of decision-making is, if nothing else, simplifying. There is no reason to search for a special area of the brain that bestows consciousness, or a special neuron type, or a special ingredient in the representation of information (eg, an oscillation or synchronization), or a special mechanism. The mechanism might look like any other kind of provisional commitment—that is, a decision that confers a state of knowing but does not entail conscious awareness. Of course, brain activity itself is not conscious, just as the brain activity supporting a possible hand posture is not the hand posture itself. In this sense, the mechanism of consciousness is only different from other affordances because it involves reporting instead of reaching, looking toward, eating, drinking, hiding from, walking through, and mating. All are likely to involve decision formation and threshold detection.

Thus, by studying the neuroscience of decision-making, we are also studying the neuroscience of consciousness. There is still much to be learned about the mechanisms of the simplest decisions described in the first part of the chapter. For example, we do not know what sets the bounds and how thresholds are implemented in brain circuits. Nevertheless, answers to these and other fundamental questions are in the crosshairs of modern neuroscience, and therefore, so is human consciousness.

Highlights

- 1. A decision is a commitment to a proposition, action, or plan—among options—based on evidence, prior knowledge, and expected outcomes. The commitment does not necessitate immediate action or any behavior, and it may be modified.
- Decision-making provides a window on the neuroscience of cognition. It models contingent behavior and mental operations that are free from the immediate demands of sensory processing and control of the body's musculature.
- 3. A decision is formed by applying a rule to the state of evidence bearing on the alternatives. A simple decision rule for choosing between two alternatives employs a criterion. If the evidence exceeds the criterion, then choose the alternative supported by the evidence; if not, choose the other alternative.
- 4. For certain perceptual decisions, the source of evidence and its neural representation are known.
- 5. The accuracy of many decisions is limited by considerations of the signal strength and its associated noise. For neural systems, this noise is attributed to the variable discharge of single neurons, hence the variable firing rate of small populations of neurons that represent the evidence.
- 6. Many decisions benefit from multiple samples of evidence, which are combined across time. Such decision processes take time and require neural representations that can hold and update the accumulated evidence (ie, the decision variable). Neurons in the prefrontal and parietal cortex, which are capable of holding and updating their firing rates, represent the evolving decision variable. These neurons are also involved in planning, attention, and working memory.
- 7. The speed–accuracy trade-off is controlled by setting a bound or threshold on the amount of evidence required to terminate a decision. It is

- an example of a policy that makes one decisionmaker different from another.
- 8. Many decisions are about propositions, items, or goals that differ in value to the organism. Such value-based decisions depend on stored associations between items and valence.
- The source of evidence for many decisions is memory and active interrogation of the environment information seeking. These operations come into play when animals forage and explore, and when a jazz musician improvises.
- 10. Decision-making invites us to consider knowledge not as an emergent property of neural representations but the result of directed, mostly nonconscious interrogation of evidence bearing on propositions, plans, and affordances. The intention is provisional in that no overt action need ensue. Just as the provisional intention to foveate corresponds to preconscious knowledge of the location of an as yet unidentified object in the periphery, the possibility of reporting to another agent (or self), about whom we have theory of mind, corresponds to the knowledge of an item in the ways we are aware of it consciously.
- 11. Viewed through the lens of decision-making, conscious awareness of an item might arise when the nonconscious brain reaches a decision to report to another mind. The affordance has the quality of narrative, much like silent speech or the idea preceding its expression in language. It also imbues objects with a presence in the environment inhabited by other minds, hence independent of the mind of the perceiver. It confers private and public content to aspects of the object as perceived.

Michael N. Shadlen Eric R. Kandel

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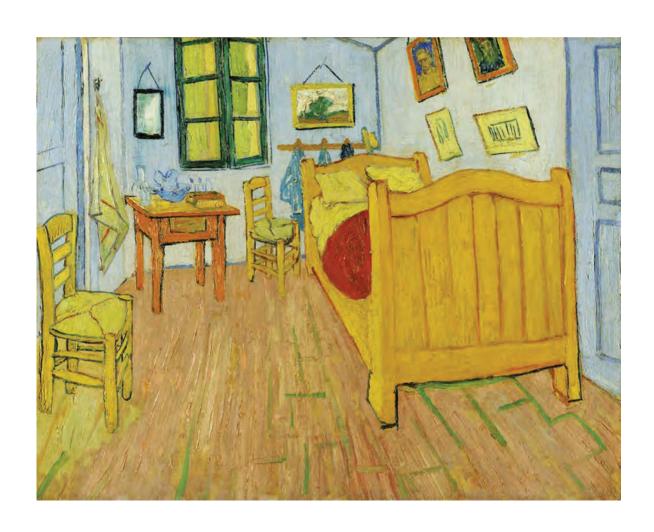
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Part IX



Preceding Page

Bedroom at Arles by Vincent Van Gogh. Van Gogh wrote to his friend and fellow painter, Gaugin, that he had felt "my vision was strangely tired. Well, I rested for two and a half days, and then I got back to work. But not yet daring to go outside, I did . . . a no. 30 canvas of my bedroom with the whitewood furniture that you know. Ah, well, it amused me enormously doing this bare interior. With a simplicity à la Seurat. In flat tints, but coarsely brushed in full impasto, the walls pale lilac, the floor in a broken and faded red, the chairs and the bed chrome yellow, the pillows and the sheet very pale lemon green, the blanket blood-red, the dressing-table orange, the washbasin blue, the window green. I had wished to express utter repose with all these very different tones, you see, among which the only white is the little note given by the mirror with a black frame (to cram in the fourth pair of complementaries as well)." Van Gogh had psychotic episodes, but there is still debate about the cause—among the theories considered have been bipolar disorder, temporal lobe epilepsy, syphilis, schizophrenia, and even toxicity from the foxglove plant (a remedy for mental illness at the time) in combination with lead poisoning from his oil paints and the consumption of absinthe. (Van Gogh Museum, Amsterdam.)

IX

Diseases of the Nervous System

He remembered that during his epileptic fits, or rather immediately preceding them, he had always experienced a moment or two when his whole heart, and mind, and body seemed to wake up to vigour and light; when he became filled with joy and hope, and all his anxieties seemed to be swept away forever; these moments were but presentiments, as it were of the one final second (it was never more than a second) in which the fit came upon him. That second, of course, was inexpressible. When his attack was over, and the prince reflected on his symptoms, he used to say to himself: "These moments, short as they are, when I feel such extreme consciousness of myself, and consequently more of life than at other times, are due only to the disease—to the sudden rupture of normal conditions. Therefore they are not really a higher kind of life, but a lower." This reasoning, however, seemed to end in a paradox, and lead to the further consideration: —"What matter though it be only disease, an abnormal tension of the brain, if when I recall and analyze the moment, it seems to have been one of harmony and beauty in the highest degree—an instant of deepest sensation, overflowing with unbounded joy and rapture, ecstatic devotion, and completest life?" Vague though this sounds, it was perfectly comprehensible to Muishkin, though he knew that it was but a feeble expression of his sensations.*

That, exactly, is the nature of the relationship between the mind and the brain? Dostoevsky's own experience of epilepsy profoundly influenced his writing, and in this passage, he probes some of the most profound questions about human experience. Are our thoughts and moods simply transient combinations of chemicals and electrical signals? Do we have any influence over them? If not, can we be held responsible for our actions? What if some of our peak experiences are just happy chemical accidents? Or, as Prince Muishkin wonders, what if some of our peaks are happy accidents of disease? What, then, would it mean to "get better"? Individuals with bipolar disorder, for example, can have a very difficult time relinquishing the expansive feelings and creative energies that can accompany mania.

Although these profound questions are the purview of philosophers rather than neuroscientists, few circumstances bring the mindbrain relationship into question as sharply as becoming victim to a neurological or psychiatric disorder. The range of these conditions

^{*}Dostoevsky F. *The Idiot*. Translated by Eva Martin. Project Gutenberg EBook, last updated May 13, 2017.

is very wide, from motor disturbances to epilepsy, schizophrenia, mood imbalances, cognitive disorders, neurodegeneration, and even aging. The more we learn, the more it becomes apparent that these diseases exert very broad effects that blur the boundaries between their classifications. So-called movement disorders such as Parkinson disease, for example, involve cognitive and affective changes; disorders of cognition such as autism or schizophrenia can have very physical manifestations.

Despite these somewhat fuzzy boundaries, each chapter in this section will examine the principles underlying each major class of disease from the perspective of neuroscience. The emphasis here is on molecular mechanisms, so far as they are currently understood. It is perhaps surprising that so many different disease conditions seem to converge on one physiological point: synaptic function. In autism and several psychiatric disorders, synaptic development goes awry; in epilepsy, abnormal ion channel activity disturbs the balance of synaptic input from excitatory and inhibitory neurons. Aging and neurodegenerative disorders bring about synaptic loss through gradual alterations in protein and RNA homeostasis that tax normal cellular functions.

This observation is offered to help give shape to the material you are about to encounter, but should not be used to oversimplify. Anyone tempted by reductionism would do well to engage with the works of great artists such as Dostoevsky and Van Gogh, who represent the complexities of human experience in all its anguish and glory.

Part Editor: Huda Y. Zoghbi

Part IX

Chapter 57	Diseases of the Peripheral Nerve and Motor Unit
Chapter 58	Seizures and Epilepsy
Chapter 59	Disorders of Conscious and Unconscious Mental Processes
Chapter 60	Disorders of Thought and Volition in Schizophrenia
Chapter 61	Disorders of Mood and Anxiety
Chapter 62	Disorders Affecting Social Cognition: Autism Spectrum Disorder
Chapter 63	Genetic Mechanisms in Neurodegenerative Diseases of the Nervous System
Chapter 64	The Aging Brain