FUNDAMENTALS OF COGNITIVE NEUROSCIENCE

A BEGINNER'S GUIDE

SECOND EDITION

NICOLE M. GAGE
BERNARD J. BAARS

ACADEMIC PRESS
An imprint of Elsevier

2018

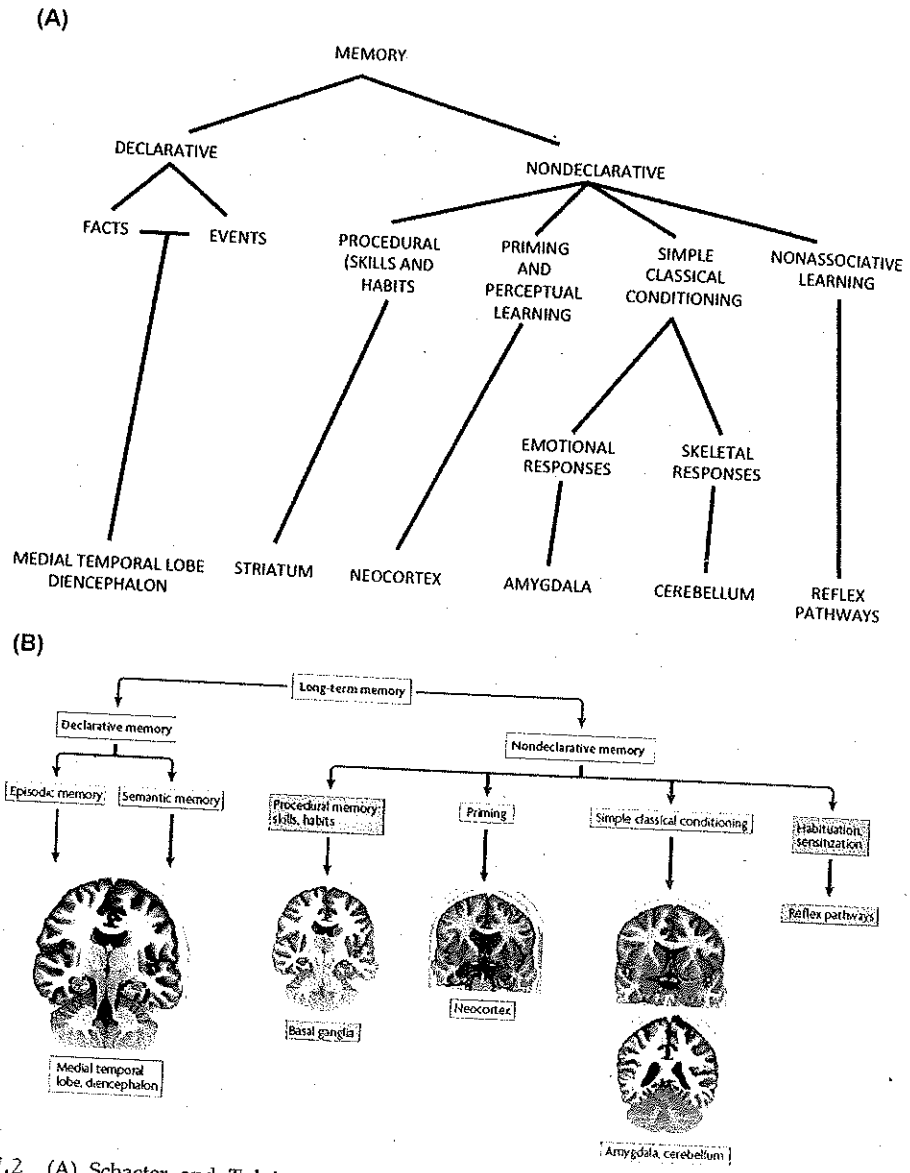

FIGURE 7.2 (A) Schacter and Tulving initially proposed this classification of memory types. Declarative memories have been studied in great detail and are believed to be explicit (conscious). Nondeclarative memory types are said to be unconscious or implicit, but this claim is still debated. We will focus mainly on semantic versus episodic memory, where a great deal of research has been done. (B) Brain regions hypothesized to subserve the memory classifications presented in (A). *(A) Source: Squire (2004) and (B) Source: Henke (2010).*

memory. You may not remember when you learned that Paris is the capital of France or when you understood a new idea about the human brain. In semantic memory, you do not need to remember the time and place when you learned it. All you need is a meaningful piece of information.

BOX 9.1 *(cont'd)*

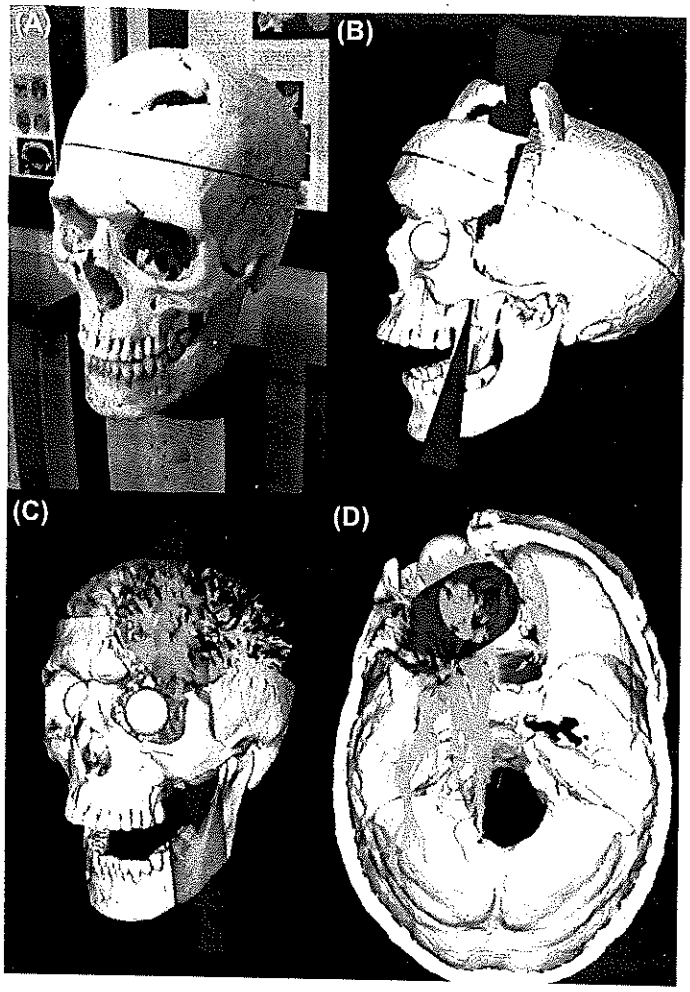

FIGURE 9.1 The reconstruction of the damage to Phineas Gage's head from the tamping iron. (A) The actual skull of Phineas Gage is on display at the Warren Anatomical Museum at Harvard Medical School. Note the damage done by the tamping iron at the top of the skull where the iron exited. (B) Computerized tomography (CT) scans were made of the skull and a reconstruction was made showing the hypothesized location of the tamping iron (shown in *red*) as it passed through the skull and brain. (C) A rendering of the tamping iron and the brain fibers that were likely damaged in the accident (shown in *green*). (D) A top view of the fibers that were likely damaged in the accident—in this view, the left hemisphere is shown on the left of the image, and the forehead and face areas are shown at the top of the image. *Source: van Horn et al. (2012).*

BOX 9.3

PROBLEMS FOR THE MIRROR NEURON THEORY OF ACTION UNDERSTANDING

Mirror neurons. This fascinating discovery by Rizzolatti et al. blazed into neuroscience glory in the 1990s and has fueled revised motor theories of mammalian cognition for monkey and man ever since.

What is a mirror neuron and why is it so captivating? Here is the description of the *mirror mechanism* in the scientists' own words:

> Mirror neurons are a distinct class of neurons that discharge both when individuals perform a given motor act and when individuals observe another person performing a motor act with a similar goal. Mirror neurons were first discovered in the ventral premotor cortex (PMv) of the macaque monkey (area F5) (1, 2, 3). Neurons with mirror properties have subsequently been found in many brain cortical areas of monkeys and other species, including humans.
>
> The discovery that a large number of cortical areas that are involved in the production of certain motor behaviours selectively respond to those behaviours irrespective of whether they are being performed or observed indicates that the mirror mechanism, far from being a specific characteristic of the premotor cortex, is a basic principle of brain functioning. This statement becomes less surprising once it is acknowledged that the brain acts, first and foremost, as a planning and control system for organisms whose main job is exploring their surrounding world and facing its challenges and that are able to catch positive opportunities and escape threats. ***(4), p. 757.***

According to Rizzolatti et al., during *action observation*, the mirror neurons encode not just the actions themselves—finger and hand movement, for example—but the *action goals*. That is, these neurons encode *the outcome of the action*. In humans, brain areas involved in the grasping-observation network of the mirror neuron system include inferior frontal gyrus, dorsal premotor cortex, and parietal and temporal lobe areas (Fig. 9.23).

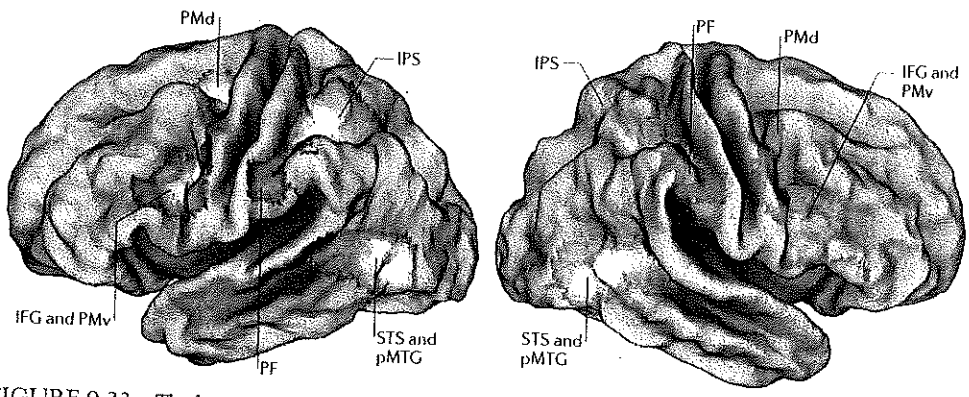

FIGURE 9.23 The human grasping-observation network. A metaanalysis of many investigations of the grasping-action observation function shows left (on the left side) and right (on the right side) hemisphere activation in the inferior frontal gyrus (IFG), ventral premotor cortex (PMv), the dorsal premotor cortex (PMd), the parietal area F (PF), intraparietal sulcus (IPS), superior temporal sulcus (STS), and posterior middle temporal gyrus (pMTG). *Source: Rizzolatti and Sinigaglia (2016).*

BOX 9.3 *(cont'd)*

While, as we stated above, the Mirror Neuron Theory of Action Understanding put forth by Rizzolatti et al. has sparked an enormous outflow of interest, replication studies, and new lines of research, it has also met with some pushback by scientists looking carefully at the observed data and their inferences.

One of these scientists, Greg Hickok, wrote a critical review article entitled *"Eight problems for the Mirror Neuron Theory of Action Understanding in Monkeys and Humans"* (2009). As the title states, Hickok reviews the literature and comes away with a strong case against the theory. In his words:

> The discovery of mirror neurons in macaque frontal cortex has sparked a resurgence of interest in motor/embodied theories of cognition. This critical review examines the evidence in support of one of these theories, namely that the mirror neurons provide the basis of action understanding. It is argued that there is no evidence from monkey data that directly tests this theory, and evidence from humans makes a strong case against the position. *(5), p. 1229.*

Hickok steps through those eight problems with the theory, carefully citing specific studies and assessing the findings with respect to the theory. What are those eight problems? Here they are briefly; we encourage you to read the entire review. It is an education.

Eight problems for the Mirror Neuron Theory of Action Understanding in Monkeys and Humans:

1. There is no evidence in monkeys that mirror neurons support action understanding
2. Action understanding can be achieved via nonmirror neuron mechanisms
3. M1 [primary motor cortex] contains mirror neurons
4. The relation between macaque mirror neurons and the "mirror system" in humans is either nonparallel or underdetermined.
5. Action understanding in human dissociates from neurophysiological indices of the human "mirror system."
6. Action understanding and action production dissociate
7. Damage to the inferior frontal gyrus is not correlated with action understanding deficits.
8. Generalization of the mirror system to speech recognition fails on empirical grounds.

Hickok's review is not only a good read but also an excellent example of a truly careful approach to science. The explosion of enthusiasm and support for the appealing mirror neurons and the action observation theory has distracted the field from understanding their actual function in cognition. The lack of sufficient scientific rigor in data analysis and interpretation has confounded the problem.

Again in Hickok's own words:

> Unfortunately, more than 10 years after their [mirror neurons] discovery, little progress has been made in understanding the function of mirror neurons. I submit that this is a direct result of an overemphasis on the action understanding theory, which has distracted the field away from investigating other possible (and potentially equally important) functions. *(5), p. 1238.*

References

(1) Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996) Action recognition in the premotor cortex. *Brain, 119,* 593–609.

Continued

BOX 9.3 *(cont'd)*

(2) Hickok, G. (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *J Cogn Neuroscience, 21*(7), 1229–1243.

(3) di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Exp. Brain Res, 91*, 176–180.

(4) Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996) Premotor cortex and the recognition of motor actions. *Cogn. Brain Res, 3*, 131–141.

(5) Rizzolatti, G., & Sinigaglia, C. (2016). The mirror mechanism: A basic principle of brain function. *Nature Reviews Neuroscience, 17*, 757–765.

4.5 Rule Adoption

To navigate our way through our complex daily lives, it is critical to develop ways to shortcut all the things that we need to plan for and carry out. Humans are wonderful rule adopters; we develop and learn strategies for streamlining our busy lives. Like a strategic plan or a schema, rules help us increase our efficiency. The Wisconsin Card Sorting test (shown in Fig. 9.24) is a good example of the mental flexibility humans have in acquiring rules and, importantly, in changing them when needed.

Neuroimaging studies of rule learning in PFC have shown that, in a manner similar to attentional and working memory demands, neural activity in the frontal regions increases with the complexity of the rule set to be learned or carried out (Fig. 9.25) (Bunge, 2004).

Neuroimaging studies have shed new light on the many and diverse operations carried out—or directed—by the PFC, from paying attention to a stimulus in your environment, to monitoring how it is changing, to keeping something in mind, to complex decision-making. Many of these processes are highly overlapping in time and neural regions, so we are still elucidating which frontal lobe areas contribute to these processes. Although we are still in the early stages of understanding just how and where executive processes are being done in the PFC, converging evidence from neuroimaging studies are beginning to present a clearer picture of PFC function.

5. DAMAGE TO THE EXECUTIVE BRAIN

We have discussed many functions of the frontal lobe, including voluntary attention, working memory, decision-making, and even your personality. What happens when this

humans implicate the amygdala and the activation of β-adrenergic stress hormone systems during and after the emotional experience and memory formation. In a now-classic study, Cahill and colleagues (Cahill, Prins, Weber, & McGaugh, 1994) investigated the memory for an emotionally arousing story and an emotionally neutral story in human subjects who were assigned randomly to one of two experimental groups: placebo—with no medication given, and propranolol—with a dose of propranolol hydrochloride given, which is a β-adrenergic receptor antagonist or β-blocker. Subjects in both groups viewed a slide show of either an *emotionally arousing story* or an *emotionally neutral story*. All subjects' memories for the stories' events was tested 1 week later. Findings showed that all subjects—in both the placebo and the propranolol groups—performed similarly, on a memory test 1 week later for the emotionally neutral story. However, for the emotionally arousing story, the subjects in the propranolol showed much poorer memory than the subjects in the placebo group.

Cahill and colleagues interpreted these findings with human subjects, along with previous work with animals, as supporting the hypothesis that the emotional memory storage is modulated by β-adrenergic systems and further that these systems are not implicated in storage of emotionally neutral information or memories. These early findings have been well supported by more recent studies; however, a follow-up investigation by Cahill and colleagues (Cahill, Uncapher, Kilpatrick, Alkire, & Turner, 2004) has shed new light on the role of the amygdala in emotional memory processing: in an fMRI study of human subjects viewing pictures that varied in their emotional arousing ratings from tranquil to highly arousing. The amygdala region was activated by the arousing pictures, as hypothesized, but the central finding of the study was a strong *sex* × *hemisphere* interaction. For men, the *right hemisphere amygdala* was more activated for the emotional pictures; however, for the women, the *left hemisphere amygdala* was more activated (Fig. 11.18). This result has been replicated and reproduced by other experimenters—providing important new data about sex differences in the brain bases of emotional processing.

Reliving happy memories, including feelings of emotional arousal, can be a pleasant experience. However, when frightening or horrifying memories are reexperienced, along with the negative emotions felt when they were encoded, they can produce a life-altering state of stress and trauma. This is what happens in cases of posttraumatic stress disorder, or PTSD, discussed later in this chapter.

7. REWARDS AND MOTIVATION

When a behavior or a situation is highly rewarding to us, we tend to repeat that behavior or strive to have that situation occur again. If you are a chocolate lover, you do not need to be convinced that a bite of a brownie still warm from the oven sends you craving for more! This is a simplified explanation for how *reward* and *motivation* work together to influence behavior—we experience a *rewarding event* and this experience puts into place the *motivation to repeat the reward*...and if this reward is not able to be repeated, it may also begin a process of *craving for that reward*.

Brain pathways for this reward-inducing experience include the ventral tegmental area (VTA), the NAc, and the PFC (Laviolette & van der Kooy, 2004) (Fig. 11.19). Dopamine (DA) neurons from the VTA project to the NAc and PFC: this is a main *dopaminergic reward*

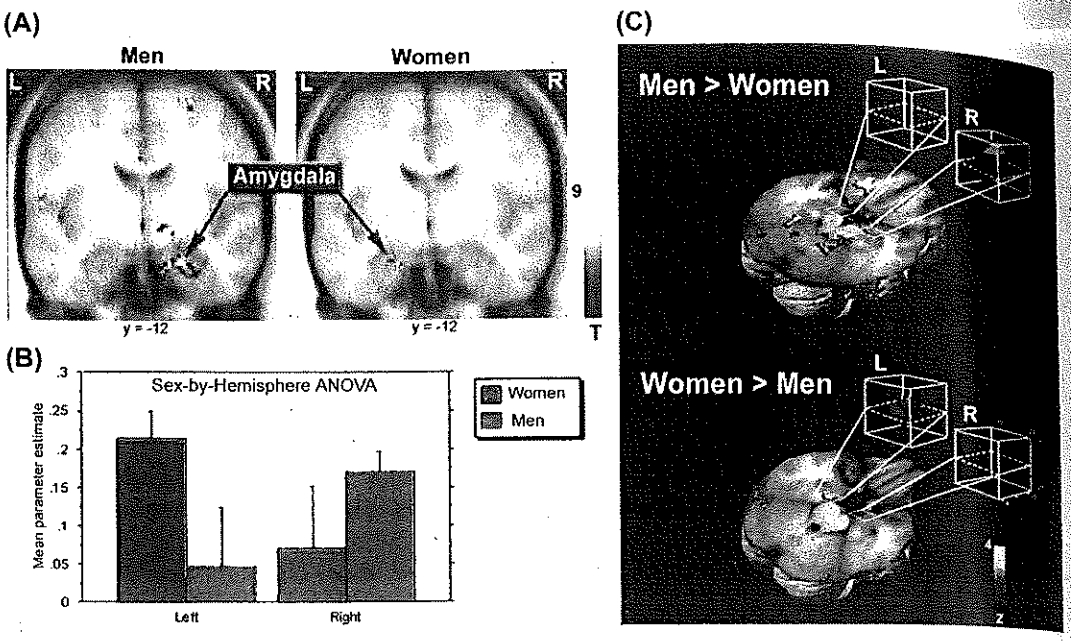

FIGURE 11.18 Cahill and colleagues investigated the activation of the amygdala in a functional magnetic resonance imaging (fMRI) study of human subjects viewing pictures that varied in their emotional arousing ratings from tranquil to highly arousing. The amygdala region was activated by the arousing pictures, as hypothesized, but the central finding of the study was a strong *sex* × *hemisphere* interaction. For men, the *right hemisphere amygdala* was more activated for the emotional pictures however, for the women, the *left hemisphere amygdala* was more activated. (A) A coronal view of the brain activity in the amygdala for the men in the study (left panel) and the women in the study (right panel). (B) Men and women showed a strong difference in amygdala activation. (C) Another view of the hemisphere asymmetry for men versus women in this study. This view shows coronal slices of the brain presented in a horizontal presentation. Shown in the small boxes is (top panel) the difference in activation for Men versus Women in the right amygdala and (bottom panel) the difference in activation for Women versus Men in the left amygdala. This result has been replicated and reproduced by other experimenters, providing important new data about sex differences in the brain bases of emotional processing. *Source: Cahill et al. (2004).*

signaling pathway. DA neurons from the VTA project to the PFC: this is the *mesocortical pathway*. They also project to the NAc: this is the *mesolimbic pathway*. Together, these two reward pathways are called the *mesocorticolimbic projection*. DA neurons' projections are shown in Fig. 11.20. DA neurons also innervate the amygdala and the hippocampus. GABA neurons can inhibit the DA projections. These DA and GABA pathways form a highly complex circuitry underlying our feelings of reward, motivation, and craving.

In addition to the naturally occurring rewarding experiences that produce DA, there are many other DA inducers: they include nicotine found in cigarettes, alcohol, and many drugs of abuse including cocaine. When these systems and pathways are functioning in a healthy way, they provide the brain bases for motivation and reward that influences our behavior in many positive ways. However, when these systems are altered or impaired, they can lead to addiction and mood disorders, discussed later in this chapter.