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Notes

Chapter 1

1. The full quote from the paper abstract was "we delineated 180 areas per hemisphere bounded by sharp changes in cortical architecture, function, connectivity, and/or topography."

2. Although neuroscientists more commonly use the term "area" to specify putatively well-delineated parts of the brain, I don't distinguish between the two in the book.

3. For his work on the structure of the nervous system, Ramon y Cajal was awarded the Nobel Prize in 1906.

4. Burdach actually described what is currently called the "basolateral amygdala." Other parts were added later by others.

5. When communicated by the media, neuroscience findings are almost exclusively phrased in highly modular terms. We've all heard headlines about the amygdala being the "fear center in the brain," the existence of a "reward center," as well as "spots" where memory, language, and so on take place. Whereas the media's tendency to oversimplify is perhaps unavoidable, neuroscientists are at fault, too.

6. For a related discussion, see Krakauer et al. (2017).

7. I am referring to the addiction study by Navqi et al. (2007); a study of faces by Kanwisher, McDermott, and Chun (1997); and an attention study described by Noudoost et al. (2010). The stimulation studies described by Noudoost et al. (2010) come closest to informing mechanisms.

8. The term "filler term" comes from Krakauer et al. (2017).

9. Although the quoted statement referred to "many regions," the point applies to most (if not all) brain regions.

10. Example inspired by Woodward (2013, 43).

11. Example borrowed from Striedter (2005), which was based on the work by Endler (1995).

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12. Quote by Newton and Descartes from Mazzocchi (2008, 10). Overall paragraph is based on Mazzocchi (2008).

Chapter 2

1. For a brief biography of Cécile Vogt, see M. Favero, S. Mele, and T. Metitieri, "Profile of Cécile Mugnier Vogt," in WiNEu, European Women in Neuroscience, Untold Stories: The Women Pioneers of Neuroscience in Europe, 2017, http://wineurope.eu/vogt-2/.

2. From "Korbinian Brodmann," *Whonamedit? A Dictionary of Medical Eponyms*, January 9, 2015, http://www.whonamedit.com/doctor.cfm/1264.html.

3. For a discussion of the number of regions and other historical aspects, see Šimic and Hof (2015), Finger (1994), and Amunts and Zilles (2015).

4. Galen's use of "thalamus" probably referred to one of the ventricles (Rikhye, Wimmer, and Halassa 2018).

5. A century later, Leopoldo Caldini claimed proof of this role based on lesion experiments on dogs, lambs, and goats (Finger 1994, 216): "I am satisfied with having provided proof, by means of experiments and (clinical) observations, that large or small lesions of the [striatum] are followed by paralysis, more or less severe and more or less extensive."

6. See Bear, Connors, and Paradiso (2020), from which the first few paragraphs of this section draw. The figure of 86 billion neurons comes from Herculano-Houzel (2009).

7. Thiebaut de Schotten et al. (2015) is a good reference for this and the next paragraph.

Chapter 3

1. Although the original study appeared in the prestigious journal *Brain*, it was largely ignored for decades. The 1973 study, cited in the next paragraph, was by Pöppel, Held, and Frost (1973).

2. The classic reference here is by Cowey (2004).

3. Technically, it should be "superior colliculi" (plural). Throughout the text, I avoid the Latin plural, which sounds heavy-handed (for the same reason we don't say in the United States "musea" but instead "museums"). So, I don't refer to amygdalae (plural for amygdala), for example.

4. Snyder, Killackey, and Diamond (1969) and Diamond and Hall (1969) tested the visual behavior of tree shrews and squirrels after complete removal of the striate cortex. See also Day-Brown et al. (2010).

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5. The classic reference is Dean, Redgrave, and Westby (1989), on which the subsequent paragraph was based. The idea that the superior colliculus is involved in defensive behaviors has not gained widespread attention. However, a growing body of findings is changing the treatment of this region as a simple sensorimotor interface. For evidence of its participation in defensive behaviors in primates, see DesJardin et al. (2013). For further discussion, see Pessoa, Medina, and Desfilis (2022).

6. In mammals, the hypothalamus also projects to intermediate layers of the superior colliculus; see Nieuwenhuys, ten Donkelaar, and Nicholson (1998), chap. 22, 1804.

7. Paragraph based directly on Dean, Redgrave, and Westby (1989, 146).

8. As newer methods become available, it now seems that a precise columnar arrangement in the PAG is an oversimplification. Instead, cells appear to integrate multiple inhibitory and excitatory inputs from distinct brain areas to select appropriate active or passive defensive behaviors (Tovote et al. 2016).

9. The connections are to the subpart of the substantia nigra called "compact" because of the dense packing of cell bodies there. For visual activation of the substantia nigra, see Comoli et al. (2003).

10. The "message is not in the molecule" is originally from chapter 5 of Thompson (2000).

11. This and next paragraphs draw directly from Thompson (2000, 140–141).

Chapter 4

1. The description in this paragraph is from Broca (1861). Online translation available at Classics in the History of Psychology, an internet resource developed by Christopher D. Green of York University, Toronto, http://psychclassics.yorku.ca/Broca/aphemie-e.htm.

2. The discussion in this and next two paragraphs builds heavily on Finger (1994, 38–40).

3. Text in this paragraph and next two paragraphs is based on Dunn and Kirsner (2003). Two key papers historically are Lashley (1952) and Teuber (1955). For an excellent modern discussion, see Young, Hilgetag, and Scannell (2000).

4. Discussion based on Plaut (1995). Patient PW was reported by Patterson and Marcel (1977) and patient CAV by Warrington (1981).

5. Yet nonmodular systems can also give rise to double dissociations when damaged; see Plaut (1995, 314).

6. Definitions by Shallice and Cooper (2011).

7. When regions A_1, A_2, etc. *jointly implement* a function F, the situation is conceptually quite different from the scenario being described. As developed in chapter 10,

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we can think of the set of regions $\{A_1, A_2, \ldots\}$ as a *network* of regions that, in combination, generates the function *F*. I thank Marco Viola for raising these issues.

8. The example in this paragraph was described by Passingham, Stephan, and Kötter (2002).

9. An excellent, short treatment is provided by Mayr (2004).

Chapter 5

1. See the excellent paper by Parvizi (2009); see also Finger (1994, 271).

2. The historical discussion of Walter Cannon's work is based on Carroll (2016, 17–21). Further material on Cannon borrows from Finger (1994).

3. Interestingly, Bard worked independently and only collaborated with Cannon on unrelated work on the innervation of the thyroid gland, which only led to negative results and were not published (Bard 1973).

4. Bard (1934) uses the term "consciousness" explicitly.

5. For discussion and references, see Pessoa (2013, 230–231).

6. See McEwen (1998); O'Connor, O'Halloran, and Shanahan (2000); and Brosschot, Gerin, and Thayer (2006), which is the source of the chances of developing cardiovascular disease at the end of the paragraph.

7. Paragraph copied from Feinstein et al. (2013, supplemental material). Patient SM's age quoted in the subsequent paragraph is reported by Feinstein et al. (2011).

8. For example, the central amygdala projects to the dopaminergic ventral tegmental area and adjacent substantia nigra pars compacta; the noradrenergic locus coeruleus; the serotonergic raphé nuclei; and the cholinergic basal forebrain nuclei.

9. See Paré and Quirk (2017) for an outstanding discussion of related issues.

10. The debate is still not settled, but it is perhaps safe to say that it's more nuanced today. Instead of focusing on "automatic" versus "nonautomatic" processing, many studies try to determine the conditions during which emotional perception is favored and the extent to which it is.

11. Modulation of visual cortex is believed to be, in part, related to amygdala projections to visual cortex. But many other circuits are likely involved (Pessoa 2013).

12. Again, see the excellent paper by Paré and Quirk (2017).

13. See Pessoa (2010, 2013). The study of saving versus spending behavior in rhesus monkeys, discussed in the subsequent paragraph, is by Grabenhorst, Hernádi, and Schultz (2012); the human functional MRI study is by Zangemeister, Grabenhorst, and Schultz (2016).

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14. As recounted by Thompson (1999, 5–6, 13).

15. Based on Olds and Milner (1954) and Olds (1958).

16. Midbrain cells that project to these diverse cortical regions are intermingled with each other (a cell that projects to the frontal cortex may be adjacent to one that projects to the temporal cortex). In addition, individual neurons often ramify, sending collateral axons to different cortical regions (say, a cell may project to both the prefrontal and parietal cortex). Overall, the projection system is rather diffuse.

17. This paragraph is close to verbatim from Schultz (2016, 24). Subsequent paragraph based on the same source.

Chapter 6

1. Macmillan (2002) covers the case of Gage extensively and argues strongly that most of what has been written about Gage is largely folklore, including changes in Gage's personality.

2. Surprisingly, the Wikipedia entry on Gage is rather carefully described and referenced; see "Phineas Gage," *Wikipedia*, M8n, citing Macmillan (2004), https://en.wikipedia.org/wiki/Phineas_Gage#M8.

3. The famous paper by James (1884) proposed what an emotion is; the quote on being "brought to consciousness" is from Lange ([1885] 1922, 75).

4. Quote by Vogt (2009, 12) is based on the original work by the neurosurgeons J. Bancaud and J. Talairach (1992).

5. See Finger (1994, 40). For example, in 1931, Otfried Foerster, one of the leaders in this area, said: "Strong faradic [electrical] stimulation produces a convulsion. . . ." (Foerster 1931, 310).

6. After years of searching for, but not finding, an English translation of Broca's monumental paper originally published in French, I sought to have it translated. With the support of the *Journal of Comparative Neurology* (a publication established in 1891, soon after Broca's work originally appeared), the paper was published in full and finally made available to English-speaking readers. See Broca (2015).

7. See Neafsey (1990, 155–156). This paper provides a good historical perspective of research on the autonomic nervous system.

8. See Vogt and Vogt (1926). The edited volume on the cingulate cortex by Vogt (2009) is an excellent source on this part of the brain.

9. See, for example, Etkin, Egner, and Kalisch (2011). The specific study is by Raczka et al. (2010).

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10. See Wager et al. (2013). Since this influential initial report, the research group has published extensively on this topic.

11. A long list of neuroscientists, including myself, have made this point throughout the past decades.

12. A good source is Saper (2002), from which I draw.

13. See Craig (2002, 2009); see also Damasio (1999).

14. Descending connections are mostly found in the posterior insula (Yasui et al., 1991); however, they likely exist in the anterior insula, too.

15. Description from Koenigs and Tranel (2006).

16. "Acquired sociopathy" is discussed by Eslinger and Damasio (1985) and nicely summarized in the entry "Psychopathy," *Wikipedia*, last modified January 4, 2022, 20:19 UTC, https://en.wikipedia.org/wiki/Psychopathy.

Chapter 7

1. See Finger (1994) for historical discussion.

2. For the quote, see the translation of Broca's 1878 paper in the *Journal of Comparative Neurology* (Broca 2015, 2553). See also the commentary by Pessoa and Hof (2015).

3. See Quiroga et al. (2005); see also A. Gosline, "Why Your Brain Has a 'Jennifer Aniston Cell,'" *New Scientist*, June 22, 2005, https://www.newscientist.com/article/dn7567-why-your-brain-has-a-jennifer-aniston-cell/.

4. See the work by Moran and Desimone (1985), which was further explored in detail in the next two decades.

5. The discussion in this paragraph is from Gazzaniga, Ivry, and Mangun (2009, 426).

6. The unusual study by the French neurologist in this paragraph is by Lhermitte (1983). The quote about a "healthy jab in the buttocks" is from Gazzaniga, Ivry, and Mangun (2009, 426).

7. Discussion of the Stroop task and the Wisconsin card sort task is based on Miller and Cohen (2001). Brenda Milner's landmark study was reported in Milner (1963).

8. This paragraph is closely based on Miller and Cohen (2001, 168), including the expression "rules of the game."

9. This is one of the central ideas of the work of Stephen Grossberg; see, for example, Grossberg (2021).

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Chapter 8

1. The term "intuition pumps" comes from Dennett (2013).

2. This ecosystem example is borrowed from Carroll (2017, 126).

3. This bacteria example is also borrowed from Carroll (2017, chap. 3).

4. See "Lotka-Volterra Equations," *Wikipedia*, accessed July 28, 2020, https://en.wikipedia.org/wiki/Lotka-Volterra_equations.

5. This paragraph is largely based on Juarrero (1999, 7). The term "emergence" appears to have first been proposed in the 1870s by George Henry Lewes in his book *Problems of Life and Mind* and taken up by Wilhelm Wundt in his book *Introduction to Psychology*.

6. This expression is from Deacon (2011, 166).

7. Paragraph draws from Levine et al. (2017).

8. See Bairey, Kelsic, and Kishony (2016). Just a few years ago, Levine et al. (2017, 61) pointed out that "higher-order interactions need to be demystified to become a regular part of how ecologists envision coexistence, and identifying their mechanistic basis is one way of doing so."

9. The problem of stability was central to celestial mechanics. For example, what types of trajectories do two bodies, such as the earth and the sun, exhibit? The so-called two-body problem was completely solved by Johann Bernoulli in 1734 (his brother Jacob is famous for his contributions in the field of probability, including the first version of the law of large numbers). For more than two bodies (for example, the moon, the earth, and the sun), the problem has vexed mathematicians for centuries. Remarkably, the motion of three bodies is generally nonrepeating, except in special cases. See "Three-Body Problem," *Wikipedia*, last modified January 3, 2022, 09:31 UTC, https://en.wikipedia.org/wiki/Three-body_problem, and J. Cartwright, "Physicists Discover a Whopping 13 New Solutions to Three-Body Problem," *Science*, March 8, 2013, http://www.sciencemag.org/news/2013/03/physicists-discover-whopping-13-new-solutions-three-body-problem.

10. More technically, until the 1960s, attractors were thought in terms of simple geometric subsets of the phase space (linked to the possible states of a system), like points, lines, surfaces, and simple regions of three-dimensional space (see "Attractor," *Wikipedia*, last modified October 24, 2021, 13:11 UTC, https://en.wikipedia.org/wiki/Attractor).

11. Von Bertalanffy (1950) stated that concepts like "system" and "wholeness," to which we could add "emergence" and "complexity," are vague and even somewhat mystical, and indeed many scientists displayed mistrust when faced with these concepts.

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12. See also the previously mentioned "Three-Body Problem," *Wikipedia*, and J. Cartwright, "Physicists Discover a Whopping 13 New Solutions to Three-Body Problem," as noted in the discussion of Newton's interest in planetary motion.

Chapter 9

1. An exception is in the case of some reptiles, which also have a simple form of cortex with three layers.

2. "No rat was ever an ancestor of any monkey" is quoted from Hodos and Campbell (1969, 345), from which the first two paragraphs of this section are based.

3. Sources for this paragraph include Bernardi (2012), Burghardt (2013), Mikhalevich, Powell, and Logan (2017).

4. Some of the key work is by J.-P. Ewert and summarized in Ewert (1987).

5. For further discussion and primary references, see Pessoa (2018a).

6. See Pessoa et al. (2019), where many of the themes discussed in this chapter are developed in considerable depth.

7. These parts include the anterior cingulate cortex and the temporal lobe.

8. A good discussion is by Salamone and Correa (2012), from which the following paragraph is based.

9. Active models include those by Pezzulo and Cisek (2016) and Pezzulo, Rigoli, and Friston (2015).

10. In his excellent book on brain evolution, Schneider (2014, 581) proposes something very similar: "As the neocortex has become the dominant source of inputs in the mammals, it has brought all the functions of neocortex into the striatal circuitry."

11. There are many excellent treatments of the evolution of the amygdala by comparative neuroanatomists. A recent, comprehensive work is by Medina et al. (2017).

12. The connections between the basolateral amygdala and ventral striatum are very substantial; however, there are pathways to the dorsal striatum, too (Amaral et al., 1992). The pathways discussed link the intra-telencephalic circuits of the pallial amygdala with the pallial-subpallial circuits of the basal ganglia and other regions of the base of the forebrain (such as the extended amygdala).

13. A comprehensive treatment is provided by Wagner (2014).

14. The analyses accounted for overall differences in amygdala size across species. For example, humans and gorillas are considerably larger than all other animals and thus would be expected to have a larger amygdala simply based on overall body and brain sizes. See Barger et al. (2012, 2014). Concerning the comparison of the cortex, see Rilling and Insel (1999); concerning frontal lobe, see Semendeferi et al. (2002).

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Chapter 10

1. The ideas in this chapter are developed more technically in Pessoa (2014, 2017b).

2. Another very influential paper was published soon after by Barabási and Albert (1999). These papers were followed by an enormous amount of research in the subsequent years.

3. Particularly useful here is the work by Kennedy and collaborators (e.g., Markov et al. 2013). For discussion of mouse and primate data, see Gămănuţ et al. (2018).

4. For an outstanding treatment of cortical-subcortical-midbrain systems, see Heimer et al. (2007); see also Pessoa et al. (2019).

5. These examples are from my lab's research; see Pessoa (2013).

6. See Bourdy and Barrot (2012). See also Nieuwenhuys, Voogd, and van Huijzen (2008) for the anatomy discussed in this section.

7. Concept developed in Pessoa (2017b).

Chapter 11

1. See "All Nobel Prizes," Nobel Prize Outreach AB 2022, *NobelPrize.org*, accessed January 8, 2022, https://www.nobelprize.org/prizes/lists/all-nobel-prizes/.

2. A good discussion is provided by Dunsmoor et al. (2015).

3. See Herry et al. (2006). For morphological changes in synapses, see Tovote et al. (2016).

4. See Herry et al. (2008) and Do-Monte et al. (2015).

5. This and the next paragraph based on Scoville and Milner (1957).

6. For the material from this and the next paragraphs, see discussions by Wikenheiser and Schoenbaum (2016), Eichenbaum et al. (2016), Jeffery (2018), and Barry and Maguire (2018). For the idea of the hippocampus and "memory map," see Buzsáki and Moser (2013).

7. Based on Maren, Phan, and Liberzon (2013); see also Maren (2011).

8. See Jones and Mishkin (1972). A good source for the material in this and the next paragraph is Schoenbaum et al. (2011).

9. Reviewed in Wikenheiser and Schoenbaum (2016).

10. See Fanselow and Lester (1988). The example of the gopher snake at the end of the paragraph is by Hirsch and Bolles (1980).

11. For an excellent recent perspective on escape behaviors, see Evans et al. (2019). See also Pessoa, Medina, and Desfilis (2022).

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Chapter 12

1. See "Homologies," *Understanding Evolution*, University of California Museum of Paleontology website, June 2020, https://evolution.berkeley.edu/evolibrary/article/0_0_0/lines_04.

2. Sentence borrowed from Murray, Wise, and Graham (2017, 35): "A structure adopts new functions during evolution, yet its ancestry can be traced to something more fundamental." Discussion of the hippocampus until the end of the paragraph also borrows from their excellent treatment.

3. See Striedter (2005). The Wikipedia page on just-so-stories is actually pretty decent; see "Just-So Story," *Wikipedia*, last modified December 13, 2021, 18:52 UTC, https://en.wikipedia.org/wiki/Just-so_story.

4. Text here builds directly from Paré and Quirk (2017).

5. "Cul-de-sac" expression inspired by Kim and Jung (2018).

6. See Allen et al. (2019).

7. See "MOND Theory," *Astronoo.com*, accessed January 5, 2022, http://www.astronoo.com/en/articles/mond-theory.html.

8. See Mordehai Milgrom, "The MOND Paradigm of Modified Dynamics," *Scholarpedia* 9, no. 6 (2014): 31410, http://www.scholarpedia.org/article/The_MOND_paradigm_of_modified_dynamics.

9. The zebrafish were studied during the larval stage; see Ahrens et al. (2012).

10. See Mannino and Bressler (2015). For "mutual causality," see Hausman (1984) and Frankel (1986).

11. Computational investigations in the past years have revealed a large number of families of periodic orbits; see Šuvakov and Dmitrašinović (2003). See also, as discussed in chapter 8, "Three-Body Problem," *Wikipedia*, last modified January 3, 2022, 09:31 UTC, https://en.wikipedia.org/wiki/Three-body_problem, and J. Cartwright, "Physicists Discover a Whopping 13 New Solutions to Three-Body Problem," *Science*, March 8, 2013.

12. "Process Philosophy," *Wikipedia*, accessed August 1, 2020, https://en.wikipedia.org/wiki/Process_philosophy. Interpretation presented here is using modern terms by Rescher (2000, 3).

13. The proximity of trajectories depends on the dimensionality of the system in question (which is usually unknown) and the dimensionality of the space where data are being considered (say, after dimensionality reduction). Naturally, points projected onto a lower-dimensional representation might be closer than in the

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original higher-dimensional space. For an excellent discussion of the concepts in this section, see Buonomano and Maass (2009).

14. We can arbitrarily consider "modern neuroscience" to start with Broca's clinical report (Broca 1861).

15. A good example here is quantum physics, which has immensely benefited from an intense (if at times strained) exchange between experimental physics, theoretical physics, and philosophy, for example.

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The Entangled Brain

How Perception, Cognition, and Emotion Are Woven Together

By: Luiz Pessoa

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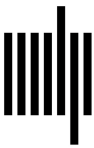

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