

Preface

Precisely one century before we finished this book, Orville and Wilbur Wright invented the airplane. You might wonder why a book about reaching and pointing begins with the Wright brothers, but we think that their experience offers several relevant lessons. One involves the concepts of reverse and forward engineering. For example, the earliest attempts at aircraft design emulated flying birds, an approach called **reverse engineering**. (Note: Words in boldface type appear in the glossary.) You can find many examples of this, but Leonardo da Vinci surely produced the most famous one. To practice reverse engineering, you take an existing system, try to understand how it works, and perhaps design something like it. If you are a neuroscientist or studying to be one, you should recognize reverse engineering; it is more or less what neuroscientists do. The Wright brothers, however, did not rely on reverse engineering—at least not at first. In fact, something more like the reverse of reverse engineering occurred. Instead of an analysis of bird flight leading to better aircraft design, aircraft design led to an improved understanding of bird flight. How? The accomplishments of the Wright brothers led to better theories of aerodynamics, and this body of theory led to the improved understanding of bird flight. So *lesson 1* from the Wright brothers is that sometimes engineering advances lead to a better understanding of biological systems.

Another lesson from the Wright brothers concerns the importance of models in understanding complex systems. The Wright brothers based their designs on mathematical models, in the form of equations. Their experience shows that models, even flawed ones, can sometimes lead to something important. For example, after more than two years of work with gliders, the Wright brothers realized that their aerodynamic models had problems. Years earlier, an aviation pioneer named Otto Lilienthal had developed those models to predict the amount of upward force, called lift, produced by wings of various designs. The Wright brothers used Lilienthal's equations, but they soon learned that wings designed in accord with his models produced only about a third of the predicted lift. Given the fact that Lilienthal had died years earlier in a glider crash, the Wrights might have been more skeptical of his theories, but—reasonably enough—they began with what they had. Through frustration and failure, they eventually realized that they needed to develop their own models,

and—in an astounding leap into modernity—they built a wind tunnel to test their theories. As a result, the Wright brothers developed better mathematical and physical models of airplane wings. *Lesson 2* from their experience, then, is that models can help in understanding the behavior of complex systems, but they need to be both tested and improved.

After the Wright brothers had solved the lift problem, their glider experienced continued difficulties with stability and control. Thus, *lesson 3* regards stability and control, problems with which the Wrights struggled for four years. Stability and control are general problems for moving systems, and your motor system is no exception. Temporarily stymied, Wilbur Wright returned to an examination of bird flight. That is, in a tight spot he resorted to reverse engineering. Wright noticed that bird wings warp during flight and, fiddling around with a flexible box, he saw how wing surfaces could warp in a similar way. Through such observations, the Wright brothers developed wing-warping controls to promote aircraft stability. *Lesson 4*: Combining reverse and forward engineering seems like a good idea.

After that breakthrough, the Wrights' glider no longer behaved erratically. Stability had been achieved, but problems remained with control. When, as pilots, the Wright brothers made maneuvers that should have turned the glider to the left, it often slid to the right instead. The addition of vertical tail fins alleviated that problem but generated new problems with stability. At that point, the Wright brothers must have begun to wonder whether stability and control were mutually exclusive. It is tempting in such situations to break down a complex system into its components and, by better understanding how each part works, hope to comprehend the overall system. This approach, called reductionism, has its place in understanding complex systems. However, the Wrights' biggest breakthrough came from enlarging the problem, not from reducing it. They recognized that it made no sense to study turning left or right in isolation from rolling the plane along its long axis; *they saw that airplanes turn by rolling*. If you want to turn an airplane to the right, you roll it so that its right wing rotates downward. This clockwise roll changes the direction of lift to the right, and the plane moves in that direction. *Lesson 5*, then, is that complex systems can be understood only at the systems level; reductionist methods help, but only in a limited way.

And the Rest Is History

In late 1903, Orville Wright took off on the first powered flight. He flew about 35 m, moving at less than 10 km/hour. The era of aeronautics had begun. (The era of really small seats and screaming infants followed shortly thereafter.) It is difficult in hindsight to appreciate the magnitude of the Wright brothers' breakthrough, but a few facts might help: Just 5 years later, Wilbur Wright flew his plane for 2 hours; 8 years later, a pilot flew across North America; 24 years after the first flight, a pilot flew an airplane from New York to Paris; and just 65 years after the Wright

brothers' plane first took off—within the lifetime of many people—the aerodynamic theories that they pioneered allowed three people to return safely from a voyage around the moon.

The Wrights' breakthrough resulted from three factors that can help you understand the neurobiology of reaching and pointing movements: combining reverse and forward engineering, joining theory in the form of mathematical modeling with empirical testing, and a systems-level approach. The Wright brothers' success depended on the combination of these factors. For example, most of their competitors had envisioned controlling aircraft through a system of rudders, by analogy with ships at sea. Unlike the Wright brothers, those engineers did not test their models in wind tunnels. If they had, they might have realized that a maritime analogy has little relevance to flying machines. Remember that airplanes turn by rolling. Rudders can control watercraft because a ship's buoyancy makes rolling largely irrelevant to turning (although too much roll can, of course, make for a bad day). *Lesson 6: Do not go out to sea in bad weather* (see Sebastian Junger, *A Perfect Storm: A True Story of Men Against the Sea*, Norton, New York, 1997).

How to Use this Book

This book draws on information from a broad range of academic disciplines. To help you follow the discussion of topics outside your field of study, five appendices provide brief “refreshers” on some fundamentals of biology, anatomy, mathematics, physics, and neurophysiology. (The best part is, no one will know if you consult the refreshers. We suggest that you deny—under oath, if necessary—consulting any of them.)

Because of the book's computational nature, we have made supplemental material available on the Internet. These “web documents” provide source code for most of the simulations, step-by-step derivations of certain mathematical formulations, and expanded explanations of particular concepts. The documents are currently available at the Universal Resource Locator (URL) www.bme.jhu.edu/~reza, the Reza Shadmehr home page. In the event that the URL changes, an Internet search for the text string “Reza Shadmehr Home Page” should lead you to these documents.

For cross references within the book, a link such as “see section 1.2.3” or (section 1.2.3) indicates that you might look for further explanation or background information under the third subheading of the second main heading in chapter 1. Figure 1.2 refers to the second figure in chapter 1. Box 1.2 corresponds to the second box in chapter 1. A glossary contains some brief definitions of technical terms and concepts, and you can find words that appear in the text in boldface type defined there.

Note that we do not aim to present a comprehensive summary of the motor system, motor learning, or even the scientific literature on reaching and pointing movements. Many of the topics taken up—and not a small number of those omitted—deserve book-length treatment. Nearly all of the major topics presented in this book are already, or someday will be,

the subject of full-length books. So this book leaves a lot out: the fields of oculomotor control, locomotion, speech, and movement disorders receive scant attention. Plastic change in motor maps, a subject often discussed in the context of motor learning, gets barely a mention. Obviously, we could not write—and you would not read—an encyclopedic dissertation on motor control and motor learning. Instead, this book presents an introduction to the computational neurobiology of reaching and pointing—with emphasis on motor learning in primates—based on an eclectic selection of topics. Chapter 1 explains why we have made those and other choices. A brief, annotated reading list and a selected (not comprehensive) list of citations appears at the end of most chapters.

We also draw your attention to another book, *Theoretical Neuroscience* by Peter Dayan and Larry Abbott (MIT Press, Cambridge, Mass., 2001). It is a useful complement to this one. *Theoretical Neuroscience* focuses on sensory processing, whereas this book addresses motor control and motor learning. We have, by and large, avoided duplication of the topics presented in *Theoretical Neuroscience*, especially background material such as the operations of neurons, et cetera.

The following acronyms and abbreviations are used throughout the book:

- CNS, central nervous system
- CPG, central pattern generator
- EMG, electromyographic (i.e., muscle) activity
- GABA, γ -aminobutyric acid
- ION, inferior olivary nucleus/nuclei
- PPC, posterior parietal cortex
- Abbreviated names of several cortical areas, illustrated in figure 6.3 and defined in its legend, including the primary motor cortex (M1), dorsal premotor cortex (PMd), ventral premotor cortex (PMv), and supplementary motor area (SMA).

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