

# Contents in Detail

Preface xv

<b>1</b>	<b>Introduction</b>	<b>1</b>
1.1	Why Motor Learning?	1
1.2	Why Now?	2
1.3	Why a Theoretical Study?	3
1.4	Why a Computational Theory?	3
1.5	Why Vertebrates, Why Primates, and Why a Two-Joint Arm?	4

## **I Evolution, Anatomy, and Physiology 7**

<b>2</b>	<b>Our Moving History: The Evolution of the Vertebrate CNS</b>	<b>9</b>
2.1	Birth of the Motor System	9
2.2	Components of the Motor System	10
2.3	A Brief History of the Motor System	12
2.4	First Steps: Inventing the Vertebrate Brain	15
2.5	More Recent Steps: Cerebellum and Motor Cortex	21
2.6	Summary	23
<b>3</b>	<b>Burdens of History: Control Problems That Reach from the Past</b>	<b>27</b>
3.1	Limbs	28
3.2	Muscles	32
3.3	Nerves	37
<b>4</b>	<b>What Motor Learning Is, What Motor Learning Does</b>	<b>39</b>
4.1	Motor Learning Undefined	39
4.2	Motor Learning over Generations: Links to Instincts and Reflexes	41
4.3	Learning New Skills and Maintaining Performance	46
4.4	Making Decisions Adaptively	51
4.5	Summary	58
<b>5</b>	<b>What Does the Motor Learning I: Spinal Cord and Brainstem</b>	<b>61</b>
5.1	Spinal Cord	61

5.2	Hindbrain	65
5.3	Cerebellum	68
5.4	Red Nucleus	71
5.5	Superior Colliculus	73
<b>6</b>	<b>What Does the Motor Learning II: Forebrain</b>	<b>75</b>
6.1	Basal Ganglia	75
6.2	Thalamus	80
6.3	Cortical Organization I: General Considerations	81
6.4	Cortical Organization II: Cortical Fields for Reaching and Pointing	85
<b>7</b>	<b>What Generates Force and Feedback</b>	<b>93</b>
7.1	Biological Versus Mechanical Actuators	93
7.2	Muscle Mechanisms	94
7.3	Motor Units	98
7.4	A Muscle Model	99
7.5	Converting Force to Torque	102
7.6	Muscle Afferents	108
7.7	Muscle Afferents in Action	112
<b>8</b>	<b>What Maintains Limb Stability</b>	<b>119</b>
8.1	Equilibrium Points from Antagonist Muscle Activity	120
8.2	Restoring Torques from Length–Tension Properties	121
8.3	Stiffness from Muscle Coactivation	123
8.4	Reaching Without Feedback in Monkeys	123
8.5	Equilibrium Points from Artificial Stimulation	126
8.6	Rapid Movements from Sequential Muscle Activation	127
8.7	Passive Properties Produce Stability	129
8.8	Reflexes Produce Stability	131
8.9	Reaching Without Feedback in Humans	135
8.10	Passive Properties and Reflexes Combined	136
<b>II</b>	<b>Computing Locations and Displacements</b>	<b>141</b>
<b>9</b>	<b>Computing End-Effector Location I: Theory</b>	<b>143</b>
9.1	Reaching and Pointing Require Sensory Feedback	143
9.2	Kinematics and Dynamics	144
9.3	Degrees of Freedom and Coordinate Frames	144
9.4	End Effectors and Adaptive Mapping	146
9.5	Predicting the Location of an End Effector in Visual Coordinates	147
9.6	Predicting End-Effector Location with Proprioception: Virtual Robotics	148
9.7	Predicting End-Effector Location with Proprioception: Computations	151
<b>10</b>	<b>Computing End-Effector Location II: Experiment</b>	<b>159</b>
10.1	Role of Proprioceptive Signals in End-Effector Localization	159
10.2	Introduction to Frontal and Parietal Neurophysiology	162

10.3	Encoding of Limb Configuration in the CNS	165
10.4	Errors in Reaching due to Lesions of the PPC	175
<b>11</b>	<b>Computing Target Location</b>	<b>179</b>
11.1	Computing Target and End-Effector Locations in a Common Frame	180
11.2	Computing Target Location in a Vision-Based Frame	183
11.3	Combining Retinal Location with Eye Orientation Through Gain Fields	188
<b>12</b>	<b>Computing Difference Vectors I: Fixation-Centered Coordinates</b>	<b>205</b>
12.1	Planning Reaching and Pointing with Difference Vectors	205
12.2	Shoulder-Centered Versus Fixation-Centered Coordinates	209
12.3	Planning in Fixation-Centered Coordinates: Experiment	212
12.4	Planning in Fixation-Centered Coordinates: Theory	216
12.5	Localizing an End Effector in Fixation-Centered Coordinates	221
12.6	Encoding End-Effector Location in Fixation-Centered Coordinates	222
12.7	Issues Concerning Fixation-Centered Coordinates	225
<b>13</b>	<b>Computing Difference Vectors II: Parietal and Frontal Cortex</b>	<b>229</b>
13.1	Computing a Movement Plan	229
13.2	Planning Potential Movements but Not Executing Them	237
13.3	Planning the Next Movement in a Sequence	241
<b>14</b>	<b>Planning Displacements and Forces</b>	<b>245</b>
14.1	Representing the Difference Vector in the Motor Areas of the Frontal Lobe	247
14.2	Population Vectors, Force Coding, and Coordinate Frames in M1	261
<b>III</b>	<b>Skills, Adaptation, and Trajectories</b>	<b>271</b>
<b>15</b>	<b>Aligning Vision and Proprioception I: Adaptation and Context</b>	<b>273</b>
15.1	Newts Cannot Adapt to Rotation of Their Eyes	275
15.2	Primates Adapt to Rotation of the Visual Field	276
15.3	Prism Adaptation Requires Modification of Both Location and Displacement Maps	279
15.4	Long-term Memories and Learning to Switch on Context	280
15.5	Prism Adaptation in Virtual Robotics	284
15.6	Consequences of Planning in Vision-Based Coordinates	286
15.7	Moving an End Effector Attached to the Hand	288
15.8	Internal Models of Kinematics	289
15.9	Estimate of Limb Location Is Influenced by the Likelihood of the Sensed Variables	291

<b>16</b>	<b>Aligning Vision and Proprioception II: Mechanisms and Generalization</b>	<b>295</b>
16.1	Neural Systems Involved in Adapting Alignments Between Proprioception and Vision	295
16.2	Generalization of Adaptation to Altered Visual Feedback	303
<b>17</b>	<b>Remapping, Predictive Updating, and Autopilot Control</b>	<b>319</b>
17.1	Remapping Target Location	319
17.2	Predictive Remapping of Target and End-Effector Location with Efference Copy	325
17.3	Remapping End-Effector Location	331
<b>18</b>	<b>Planning to Reach or Point I: Smoothness in Visual Coordinates</b>	<b>341</b>
18.1	Regularity in Reaching and Pointing	343
18.2	Description of Trajectory Smoothness: Minimum Jerk	350
<b>19</b>	<b>Planning to Reach or Point II: A Next-State Planner</b>	<b>353</b>
19.1	The Problem of Planning	353
19.2	Transforming a Displacement Vector into a Trajectory	354
19.3	The Next-State Planner	357
19.4	Minimizing the Effects of Signal-Dependent Noise	364
19.5	Online Correction of Self-Generated and Imposed Errors in Huntington's Disease	366
19.6	Transforming Plans into Trajectories: The Problem of Redundancy	371
<b>IV</b>	<b>Predictions, Decisions, and Flexibility</b>	<b>377</b>
<b>20</b>	<b>Predicting Force I: Internal Models of Dynamics</b>	<b>379</b>
20.1	Internal Models of Dynamics	380
20.2	Correlates of Adapting to Altered Dynamics	391
<b>21</b>	<b>Predicting Force II: Representation and Generalization</b>	<b>403</b>
21.1	The Coordinate System of the Internal Model of Dynamics	403
21.2	Computing an Internal Model with a Population Code	410
21.3	Estimating Generalization Functions from Trial-to-Trial Changes in Movement	416
21.4	A Not-So-Invariant Desired Trajectory	432
<b>22</b>	<b>Predicting Force III: Consolidating a Motor Skill</b>	<b>435</b>
22.1	Consolidation	435
22.2	A Role for Time and Sleep in Consolidation of Motor Memories	441
<b>23</b>	<b>Predicting Inputs and Correcting Errors I: Filtering and Teaching</b>	<b>447</b>
23.1	Cancellation of Predicted Signals by Adaptive Filtering	449
23.2	Predicting and Responding to a Stimulus	454
23.3	Similar Learning Mechanisms in Basal Ganglia and Cerebellum	462

23.4	A Training Signal for the Basal Ganglia	464
23.5	Why Does Huntington's Disease Result in Disorders in Reaching?	468
<b>24</b>	<b>Predicting Inputs and Correcting Errors II: Learning from Reflexes</b>	<b>473</b>
24.1	Climbing Fibers Encode a Signal That Represents Motor Error	475
24.2	Predictively Correcting Motor Commands	480
<b>25</b>	<b>Deciding Flexibly on Goals, Actions, and Sequences</b>	<b>495</b>
25.1	Deciding on a Target	496
25.2	Choosing Among Multiple Potential Targets of Movement	503
25.3	Deciding on Multiple Movements	504
25.4	Action Selection Based on Estimates of State	505
25.5	Moving to Places Other Than a Stimulus: Standard Mapping vs. Nonstandard Mapping	513
25.6	Summary	519
<b>V</b>	<b>Glossary and Appendixes</b>	<b>525</b>
	<b>Glossary</b>	<b>527</b>
	<b>Appendix A Biology Refresher</b>	<b>533</b>
	<b>Appendix B Anatomy Refresher</b>	<b>537</b>
	<b>Appendix C Mathematics Refresher</b>	<b>539</b>
	<b>Appendix D Physics Refresher</b>	<b>543</b>
	<b>Appendix E Neurophysiology Refresher</b>	<b>547</b>
Index		549