Table of Contents

Acknowledgments iii

List of Tables ix

List of Figures x

Abstract xv

Chapter 1: Introduction 1

Outline of the Thesis 4

Chapter 2: Biological Background 5

AIP 5

Visual versus Motor Cell Responses 7
Object Specific Activity 9
Size Selectivity 11
Position Selectivity 11
Temporal Characteristics 11
Summary of AIP Responses Properties 16

Inferior Premotor Cortex 16

Summary of F5 Responses 22

Chapter 3: Computational Building Blocks 24

Schema Theory 24

Opposition Space and Virtual Fingers 25

Chapter 4: A Region-Level View of the Reaching and Grasping Process 28

The Reaching/Grasping Task 28

Model Goals 29

Development of the Reaching/Grasping Model 30

Visual Processing (The How, What and Where of Objects in Space) 30

Interaction of the How/What Pathways 32
Adaptation of the Visual/Motor Mapping 34
High-Level Model of Visual Processing 35

Cortical Mechanisms for Object and Grasp Representation 37

The Dorsal System in Monkey 37
The Monkey Ventral System 39
High-Level Representation of the Grasping Program 39
Transformation from a Visual Representation to a Grasp 40
Expanded Model 41

Execution of the Grasp 43

Cortical Mechanisms of Low-Level Grasp Control 44
Model of Grasp Control 46

Interaction of AIP and F5 During Execution of the Grasp.....48
Remaining Computational Issues 50
Object/Grasp Mapping is Many-to-Many 51
Modulation of the Reach Program by the Grasp Program 53
Parameter Coding 53
The Full Region-Level Model 54
Further Biological Background.....54
The Complete Model.....56
Progression of Activity During Task.....57

Summary 59

Chapter 5: Low Level Details of the Grasping Model 61

μ-schemas: An Intermediate Computational Mechanism 61
The Columnar Structure.....63
Column Dynamics.....65

Connectivity of Regions.....68
Object Representations in PIP and IT 68
AIP.....71
Classes of Neurons in AIP 71
Projections from PIP.....71
Associations from IT.....73
Schema Cooperation/Competition Via the Basal Ganglia 74
F5 75
Representation of Grasp 75
Schema Priming by F6 and Cooperation/Competition Via the BG.....76
Task Specific Biasing of the Selected Grasp.....78
Interaction between F5 and AIP.....78
Phasing Via BG 81
Interaction of the AIP Active Memory and the BG Phasing Systems 84
Grasp Execution.....86
SI and SII.....86
MI 87
MI Activation.....89
Internal Timing Model of Current Hand Extension.....90
Full Execution Circuit.....91

Summary 93

Chapter 6: Model Simulation Results.....97

Introduction 97

Overview of Model Behavior.....98

Comparison to Observed Biological Data.....101
F5 Phasic Responses 101
AIP Phasic Responses.....101
AIP Visual/Motor Distinction 102
Population Analysis.....109

Population Analysis of Phasic Behavior....110
Population Analysis of Visual/Motor Properties....112

Model Predictions....115
Prediction #1: Object Coding in AIP....115
Population Analysis of Object-Related Responses....118
Prediction #2: When an Object Affords Multiple Grasps....121
Population Analysis Comparing Conditional and Non-conditional Tasks....129
Prediction #3: Object Size Coding....134
Prediction #4: Object Size Perturbation....139
Prediction #5: Object Parameter Coding....145

Object versus Grasp Coding in the Monkey AIP....148

Summary....150

Chapter 7: Linking PET Imaging in Humans to the Grasping Model....153

Synthetic PET Imaging....153
Computation of the Synthetic PET Measure....154
Synthetic PET Imaging for the Grasping Model....155
Conditional Task....156
Precision versus Side Opposition....157

Human Grasping Experiment....160
Materials and Methods....160
Subjects....160
Tasks....160
Performance Measures....161
Imaging....162
Image Analysis....162
Statistical Tests....162
Results....163
Behavioral Results....163
Imaging Studies....163

Comparison of PET and synthetic PET Results....167
Precision versus Side Opposition/Power Grasp....167
Conditional vs Non-Conditional Task....167

Summary....169

Chapter 8: Grasp Configuration Learning....172

Introduction....172

Neural Dynamics....173

Learning Dynamics....176

Reinforcement Prediction....179

Experimental Results....181

Summary....183

Chapter 9: Conclusions and Future Work 185
PET Imaging 187
Grasp Configuration Learning 188
Related and Future Work 188
Control of Wrist Orientation 188
Planning of Arm Movements 189
Coordination of Reach and Grasp 189
Learning of Motor Programs 190
Encoding of Grasp Programs in F5 191
Perception of Grasp 191

Appendix A: Model Implementation Details 193
Network Structure Description 193
Number and Distribution of Neurons 195
Network Wiring Rules 198
PIP -> AIP 198
IT -> AIP 198
AIP -> AIP 199
AIP -> F5 199
F5 -> AIP 200
F5 -> F5 200
F5 -> Mcx 200
F5 -> SII 201
SII -> F5 201
SI -> SII 202
SI -> Mcx 202
F5 <-> Area 46 202
AIP <-> BG 202
F5 <-> BG 202
F6 -> F5/AIP 203
F6/F2 -> BG 203
Protocols 203
Vanilla Protocol 203
Grasping in the Dark 203
Object Fixation 204
1 Object/2 Grasps (conditional case) 204
1 Object/2 Grasps (non-conditional case) 204

References 205

Index 212

List of Tables

Table 5.1: Description of AIP cell behavior 72

Table 5.2: F5 grasp descriptor.....76

Table 7.1: Significant regions of activity ($p < 0.001$): conditional - non-conditional (combined precision and power) 166

Table 7.2: Significant regions of activity ($p < 0.005$) : precision pinch - power grasp.....166

Table A.1: Description of grasp.....194

Table A.2: Description of objects.....194

Table A.3: Number of cells in each model layer 196

Table A.4: Distribution of F5 and AIP cells for two experiments.....197

List of Figures

Figure 2.1: Cortical regions in the macaque involved in reaching and grasping 6
Figure 2.2: The Sakata protocol 6
Figure 2.3: Behavior of a motor-type cell under different conditions 8
Figure 2.4: Cell that is active during lighted conditions 8
Figure 2.5: Visual/Motor cell 9
Figure 2.6: Dark enhancement cell 9
Figure 2.7: Object-specific activity 10
Figure 2.8: A cell that is selective for 'flat' objects. 11
Figure 2.9: Selective toward small objects, somewhat independent of object type 12
Figure 2.10: Activity independent of object size 12
Figure 2.11: Modulation of activity as object position changes 12
Figure 2.12: Small increase during key phase, with high activity during movement and hold phases 13
Figure 2.13: Same neuron as in Figure 2.12, except during movement in the dark condition 13
Figure 2.14: Ramp up of activity during key phase 13
Figure 2.15: Late onset of movement-related activity 13
Figure 2.16: Reduction during key phase and longer extent of activity 14
Figure 2.17: Increase, then decrease of activity during key phase 14
Figure 2.18: Suppression during key phase. Active during movement, hold, and release phases 15
Figure 2.19: Primarily a movement-related neuron 15
Figure 2.20: Visual and somatosensory receptive fields of an F4 neuron 17
Figure 2.21: Response of a single F4 neuron modulated by the region of peripersonal space that the monkey is reaching toward 18
Figure 2.22: An F5 neuron that codes for precision grip 19
Figure 2.23: F5 neuron responsive to precision grip 22
Figure 2.24: Another F5 cell that is responsive to the precision grip 22
Figure 3.1: The three primary oppositions and their corresponding virtual fingers 26
Figure 4.1: Experimental setup for the Gentilucci grasp adaptation task 35
Figure 4.2: A high-level model of cortical visual processing and its support of the reach/grasp motor program 36
Figure 4.3: The expanded seeing/reaching/grasping model 42

Figure 4.4: Motor cortex cell whose firing correlated with cutaneous stimulation of the lateral side of the index....46

Figure 4.5: The cortical regions involved in the low-level control of the grasping motor program....47

Figure 4.6: Interaction between AIP and F5 populations (circles) during execution of the preshape/grasp/hold program....48

Figure 4.7: AIP computes the set of affordances for an attended object....52

Figure 4.8: The complete model....57

Figure 5.1: Column architecture....64

Figure 5.2: Convention used for drawing columns....68

Figure 5.3: Illustration of PIP coding. Every object class is represented by a population of units....69

Figure 5.4: Example coding of three objects (pencil, stick, and a ball) in PIP and IT....70

Figure 5.5: Affordance mapping from PIP to AIP....73

Figure 5.6: Affordance mapping from IT to AIP....74

Figure 5.7: Cooperation and competition in AIP....75

Figure 5.8: Priming of the general grasping schema, and selection of a specific grasp to execute....77

Figure 5.9: F6 and F2 biasing of the grasp schema selection process....79

Figure 5.10: Interaction between AIP and F5 during execution of the reaching/grasping/holding task....80

Figure 5.11: F5 interaction with BG implementing the cascade of activity in F5 as execution of the motor program progresses....81

Figure 5.12: BG phasing when an F5 unit is active during both the extension and flexion phases of the reach/grasp/hold program....83

Figure 5.13: Abstract representation of the interaction between the AIP active memory and the BG phasing loops....84

Figure 5.14: Representation of hand state information in the somatosensory cortices (SI and SII)....87

Figure 5.15: Three classes of MI columns....89

Figure 5.16: Internal model of grasp extension state....90

Figure 5.17: The low-level circuit involving F5 extension columns....92

Figure 5.18: Low-level circuit involving flexion columns....93

Figure 5.19: Implementation of the hold phase of the motor program....94

Figure 5.20: Low-level circuit for the release phase of movement....95

Figure 6.1: F5 activity during execution of a precision grasp....99

Figure 6.2: F5/AIP interaction during execution of the grasp....102

Figure 6.3: A set of F5 cells with a variety of temporal properties....103
Figure 6.4: Variety of AIP cells....104
Figure 6.5: A pure motor-related AIP cell....106
Figure 6.6: A pure visual AIP unit....107
Figure 6.7: A visually-modulated AIP unit....108
Figure 6.8: Population analysis of F5 phasic behavior during a precision grasp....111
Figure 6.9: Normalized AIP responses over the entire population....113
Figure 6.10: Visual/Motor coding in AIP....114
Figure 6.11: Two objects that map to the identical grasp....116
Figure 6.12: Two visual AIP cells that show significant object-specific modulation....116
Figure 6.13: Two visual-related (with some motor) AIP cells....116
Figure 6.14: Two motor-related (set phase) AIP cells....117
Figure 6.15: Two motor-related AIP cells that are not modulated by the type of object....118
Figure 6.16: Comparison of population responses towards two different objects (but identical grasps)....119
Figure 6.17: Visual-related AIP receive object-specific inputs; motor-related cells receive recurrent inputs from F5....120
Figure 6.18: A single object mapping to two possible grasps....121
Figure 6.19: Two F5 units in response to the four conditions....122
Figure 6.20: A pair of set/extension cells in F5....123
Figure 6.21: A pair of extension-related F5 cells....124
Figure 6.22: F5 flexion and hold units....125
Figure 6.23: A pair of release phase F5 units....126
Figure 6.24: A pair of set-related F5 units....127
Figure 6.25: A visual/motor AIP cell (more motor-related)....128
Figure 6.26: A visual/motor AIP cell (primarily visual)....129
Figure 6.27: A primarily motor-related AIP cell....130
Figure 6.28: A pure motor-related AIP cell....131
Figure 6.29: Comparison of set-related F5 responses towards two different grasps....132
Figure 6.30: Comparison of set-related AIP responses towards two different grasps....133
Figure 6.31: Cylinders of different widths map to a precision grasp of varying aperture size....134
Figure 6.32: Thumb and index finger temporal behavior as a function of cylinder size....134
Figure 6.33: F5 cell responses during precision grasps of different apertures....135

Figure 6.34: Visual-related AIP cell that demonstrates object size specificity....136
Figure 6.35: Motor-related AIP cell....137
Figure 6.36: Visual-related AIP cell that demonstrates little modulation due to object size....138
Figure 6.37: Visual/motor AIP cell that is inhibited during the hold phase of movement for mid-range cylinders....138
Figure 6.38: F5 movement-related cell (A) and a hold-related (B) cell during the perturbation experiment....140
Figure 6.39: F5 cell responses (of cells with preferred aperture between 20 and 25mm only) during execution of the hold phase of a 20mm precision grasp....142
Figure 6.40: AIP visual cell that is active for all four conditions....142
Figure 6.41: AIP motor-related cell that is most active during the movement phase of 30mm aperture grasps....143
Figure 6.42: AIP visual/motor cell that is active in all conditions....143
Figure 6.43: AIP motor-related cell....144
Figure 6.44: AIP (primarily) visual cell....144
Figure 6.45: Four boxes of different dimensions....145
Figure 6.46: Comparison of AIP visual responses....146
Figure 6.47: F5 population responses for two objects of the same width....147
Figure 6.48: Response of a single monkey AIP cell to four objects....149
Figure 6.49: Response of a primarily visual-related AIP cell....150
Figure 6.50: Response of a visual/motor AIP cell....151
Figure 7.1: Neural elements involved in computing the synaptic activity for a simulated brain region....155
Figure 7.2: Functional interactions of F2, F5, and AIP....157
Figure 7.3: Predictions of relative synaptic activity changes....158
Figure 7.4: Positive and negative synapse contributions to the synaptic activity measure....159
Figure 7.5: Apparatus used in PET experiment....161
Figure 7.6: Reaction times for both the release of the switch and the depression of the next switch....165
Figure 7.7: Updated functional model....168
Figure 7.8: Significant activity ($p < 0.005$) for conditional - non-conditional tasks....170
Figure 7.9: Significant activity ($p < 0.01$) for precision pinch - power grasp....171
Figure 8.1: Schematic view of the architecture for the grasp configuration learning model....174
Figure 8.2: Responses of several feature detector units....182

Figure 8.3: Responses of four additional feature detector units.....182