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6. AUTHORS Stephen Grossberg and Daniel Bullock				
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13. ABSTRACT (Maximum 200 words) The reported projects developed mathematical models to explain how self-organizing neural circuits that operate under continuous or intermittent sensory guidance achieve flexible and accurate control of human movement. Neural models were developed for the control of visually guided arm/hand movements, saccadic eye movements, and limb gait transitions. These circuits generate movement trajectories, adapt movement execution on the fly to unforeseen contingencies, and improve accuracy over time by learning to act in anticipation of predictable contingencies. The circuits meet behavioral, neurobiological, and design constraints. Thus, the proposed circuits have operating characteristics that match those documented for human performance and learning, such as voluntary control of speed and amplitude, transfer of learning, and learned recovery from damage to parts of a circuit. The circuits also exhibit stability, robustness, short-term flexibility, and long-term adaptability. The circuits also provide an integrative explanation of many neuroanatomical, neurophysiological, and biophysical observations. By satisfying all three sets of criteria, these model circuits illustrate fundamental behavioral and neural science principles, and provide prototypes of high-competence adaptive systems that can be developed for many technological applications in adaptive robotics, especially active vision and sensor-guided manipulation. All circuits were published with a complete mathematical specification as a system of ODEs.				
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Final Report on Contract ONR N00014-92-J-1309

Self-Organizing Neural Circuits for Sensory-Guided Motor Control

Co-PIs: Daniel Bullock & Stephen Grossberg

Overview. The goal of this project was to understand how the flexibility and accuracy of human movement are achieved by self-organizing neural circuits that operate under continuous or intermittent sensory guidance. To that end, we studied separate neural circuits that function as movement generators for visually guided arm movements, and for visually guided saccadic eye movements. In each case, the goal was to specify mathematical models of circuit operations that enable movements to be generated, to be adapted on the fly to novel contingencies, and to be adapted over several learning trials to recurring contingencies. Each model was developed to satisfy multiple constraints. These constraints were of three types. First were behavioral constraints. The proposed circuits had to have operating characteristics that matched the operating characteristics of measured human performance and learning, such as the ability to recover from damage to one part of a circuit. Second were design constraints. The proposed circuits had to exhibit stability, robustness, short-term flexibility, and long-term adaptability as fundamental properties. Third were neurobiological constraints. The proposed circuits had to be consistent with, and provide an integrative explanation of, many neuroanatomical, neurophysiological, and biophysical observations. Circuit models that satisfy all three sets of criteria make contributions to fundamental behavioral and neural sciences, while also constituting prototypes of high-competence adaptive systems that can be developed for many technological applications in adaptive robotics. To ensure that the latter goal was facilitated, all circuit models were published with a complete mathematical specification, typically a system of ordinary differential equations. We now summarize the major results.

1. The Vector Integration To Endpoint (**VITE**) model for generation of voluntary point-to-point reaching movements. Relevant reference numbers (see attached publication list): 1, 3, 21, 22, **23**, 29, 30, **36**, 43, 78. Boldface marks recent major publications.

The initial version of this neural circuit model was developed in 1985-86 as a central pattern generator (CPG) for voluntary point-to-point movements of the arm. Such voluntary movements can be started and stopped, or slowed down and sped up, at will. Normally such movements exhibit smooth, bell-shaped velocity profiles that start at zero velocity and return to zero velocity after passing through a single peak velocity whose value scales with movement distance. The VITE circuit model explains the origin of these smooth, unimodal velocity profiles. The model also incorporates a mechanism for voluntary scaling of movement speed, and thus movement duration. Thus the model describes a way that one component of what has been called the will can be realized as a mechanism for starting, stopping, and modulating the execution of movement plans. The VITE model has served as a basis for developing a more comprehensive theory of trajectory generation for point-to-point and more complex movements. The model's name, VITE, pronounced VEET, is an acronym inspired by the French word, *vite*, for

“quickly”, because the circuit allows continuous variation of movement speed while overall velocity profile shape and movement vector are preserved.

The VITE model has recently been elaborated to explain how arm movements of variable speed can be planned and made under conditions of unexpected load, including the presence of obstacles (Bullock, Cisek & Grossberg, 1998; Cisek, Grossberg & Bullock, 1998). Also modeled were reciprocal links between the cortical VITE circuit and the spinal cord. This work shows how sensory feedback can improve force regulation under a variety of scenarios that arise during movement under load and during relaxation. This more mature model can simulate and explain the movement-related activation profiles of 6 well-established cell types in motor and parietal cortex during a variety of movement tasks. The model also allows strong predictions to be made regarding the form of the movement-related activation profiles that should be observed under novel experimental protocols. No other extant model can make predictions regarding such a range of cell types in sensory-motor cortex, because other models have failed to specify the closed loop through which cortical trajectory generation and sensory feedback work together.

From a control theoretic or robotics perspective, the latest circuit includes a speed-scalable trajectory generator in series with a PID controller. However, the model improves upon such a standard in-series control design in several ways, as detailed in Bullock, Cisek & Grossberg (1998). Briefly, routing the feedback to the trajectory generator as well as to the PID nodes allows the system to adjust the desired trajectory to loading conditions and thus to avoid the high energy costs and instability that would be entailed by attempting to move too large a load too rapidly.

2. The Factorization of Length and Tension (FLETE) model for independent control of joint position and joint stiffness by an opponent muscle system. Relevant recent reference numbers: 16, 17, 24, 25, 26, 43, 47, 86.

Muscles are wonderful actuators, with excellent mass distribution properties, high force to weight ratios, and intrinsic damping. Understanding how they are controlled in a goal-directed way benefits basic science, medical science, and robotics science. The initial version of the FLETE model for muscle control was developed to explain how circuits in the spinal cord allow higher brain circuits to use opposing muscle pairs to simultaneously control joint angle and joint stiffness (Bullock and Grossberg, 1991). This is a fundamental property because it allows animals to freely retune themselves along a continuum from rigid to fully compliant systems. The FLETE model explains how this retuning is mediated by the inhibitory and excitatory interactions among distinct cell types associated with control of opposing muscles. The FLETE theory explains how these interactions work to maintain an appropriate balance of forces across the joint despite a number of intrinsic non-linearities in the system. This circuit model highlights the fact that many non-linearities can be compensated by the opponent spinal circuit even in the absence of any feedback from kinesthetic and force sensors embedded in muscles and joints. Thus, although it delineates the distinct benefits of several types of sensory feedback, the model also helps explain how animals are able to continue to make fairly accurate single-joint movements even when deprived of all sources of sensory feedback.

The model thus explicates how careful circuit design (by evolution) has led to great robustness to loss of normal sources of feedback. Further development of the model has shown how to understand the spinal circuits of mammals as a cumulative solution to a set of inherent challenges associated with the use of muscle-like actuation. As such, the model provides insight into the degrees of freedom and design principles that will need to be used by roboticists when it finally becomes possible to manufacture and deploy muscle-like actuators. A 1998 study (#86) showed how the FLETE circuit parameters can be self-organized.

Among the central theses of the FLETE model is that the Renshaw cells play several critical roles in addition to those proposed by physiologists who attempted to characterize their role without undertaking a systems-level, mathematical analysis. In particular, the FLETE theory describes three functions that can be simultaneously served by Renshaw cells. They help stabilize the stretch reflex by upper-bounding its gain. They compensate for non-linearities introduced by the size principle of motoneuron recruitment, which is a fundamental principle about how cells with multiple scales cooperate to achieve smooth force generation in all muscle-like actuation systems. Third, Renshaw cells provide a node that works as a hook or port into the spinal servo circuit. Through this port, signals from the higher nervous system can rapidly switch the system between two distinct modes: a postural mode and a rapid/forceful movement mode.

In a 1997 study (# 43) we developed a model of general-purpose adaptive control of such mode switching. This work combined VITE, FLETE and a cerebellar circuit into a unified model for adaptive improvement of the performance of voluntary arm movements. Many movements involve force generation by multiple muscles acting at one or several joints. In most advanced vertebrates, and in all mammals, proper coordination of force generation by multiple muscles is a learned skill that is partly mediated by the cerebellum. A key goal of our work on a composite VITE-FLETE-Cerebellum model has been to understand exactly how cerebellar learning can greatly improve upon the performance that is possible from the combination of a kinematic CPG circuit (VITE) with a feedback-guided force-generation circuit (FLETE). This project led to several results of great interest for robotics. It shows how joint receptors can act in concert with kinematic error and force receptors to achieve the independent control of limb position and stiffness in systems using both mono-articular and bi-articular muscles. It also shows how the cerebellum can learn to use the Renshaw cell spinal circuit to switch the spinal servo between a postural mode and a rapid movement or high force mode in a task-appropriate way. The result is a self-organizing system with a highly stable default mode and the ability to use learning to safely switch to a higher performance mode whenever conditions warrant.

3. The Direction to Rotations Effector Control Transform ("DIRECT") model for inverse kinematic control of an arm with redundant degrees of freedom. Relevant references: 5, 6, 28, 29, 44, 45, 69, 75, 76, 77.

The initial version of the DIRECT model was developed in 1992-93 to propose a solution for a fundamental general problem that is often called the Motor Equivalence Problem:

How can an animal or robot learn to use the mechanical degrees of freedom of its body to accurately control spatially directed movements of its end-effectors, with or without visual feedback? For example, how can a primate learn to coordinate movements of back, shoulder, upper arm, lower arm, wrist, and fingers in order to make a straight-line hand movement in 3-D space, in a desired direction or to a desired endpoint? In addition, how can such a system use a novel tool, or adapt to novel constraints on moving joints, on the fly, without making movement errors? This is an ill-posed problem, because there are more degrees of freedom to control than spatial dimensions. It is a difficult problem because the motion component imparted to the hand by motion at any contributing joint depends on the angles of all the other joints, i.e., on the current posture or joint configuration. Also, the functional relations depend on limb segment sizes, which can grow continuously after birth. The model's solution is to use exploratory movements of the arm to incrementally discover and learn a posture-dependent mapping from directions in 3-D space to directions (rotation vectors) in the higher dimensional space defined by the angles of the contributing joints. Once this mapping has formed within an adaptive neural network, it can be used on the fly to automatically recruit the joint rotations needed to produce arbitrarily directed motions from arbitrary initial postures. This is done directly and in real time via a neural network, without recourse to any explicit representation of the geometry of the system. Moreover, the same learned mapping can be used to control a tool held in the hand without additional learning. Simulation studies have demonstrated the superiority of the DIRECT model to alternative pseudoinverse control solutions. In particular, DIRECT remains well-behaved near singularities (Fiala, 1995), and the inverse mapping can be implemented in a way (Cameron, 1996) that is very economical from the perspective of computational degrees of freedom (number of cells in the intermediate layer of the network that computes the pseudoinverse transformation). Several applications in robotics have been explored by the laboratory of Professor Juan Lopez Coronado in Spain (e.g., # 77).

DIRECT model principles have been incorporated into the DIVA model of speech production. The DIVA model has been developed by Professor Frank Guenther and his students (Guenther, 1992 etc.). It explains how the speech articulators can be efficiently recruited to produce desired sounds from arbitrary initial postures of the speech apparatus. In both the speech and limb motor control applications, the DIRECT/DIVA models reproduce the Motor Equivalence property that humans exhibit: the ability to automatically recruit alternative motor means when blockages or unusual initial conditions make more typical means unavailable. Note that this is accomplished in a continuous way by virtue of correct control circuit design, not by preprogramming a response to all anticipated contingencies.

The DIRECT model led us to propose new methods for analyzing neurophysiological data to better characterize the coordinate systems used to represent movement commands in the cerebral cortex. The initial mathematical analysis (Ajemian, Bullock & Grossberg, 1998) has shown how an analysis of movement vector field structure can differentiate between coordinate systems that would be difficult to distinguish without this method. The results support earlier VITE hypotheses about the role of motor coordinates, and motor cortex, in trajectory generation.

4. Adaptive timing models of the cerebellum. Principal references: 16, 17, 18, 19, 21, 26, 27, 43, 45, 47, 53, 62, 70.

Experimentalists have used the conditioned eye blink in mammals such as rabbits to localize our general ability to adaptively time anticipatory behaviors. Adaptively timed release of learned behavior has been localized in the cerebellar cortex. But the neural mechanisms of adaptive timing in the cerebellar cortex remained controversial. Our work on this problem developed in several stages from earlier work by Grossberg, with his colleagues John Merrill and Nestor Schmajuk, on similar adaptive timing mechanisms in the hippocampus. Hippocampal and cerebellar circuits cooperate to maintain motivated attention upon targets of interest for a task-appropriate duration, while adaptively timed movements are elicited towards them. Our 1996 J. Neuroscience article with John Fiala is perhaps the first article to link a specific biochemical mechanism of adaptively timed learning to the anatomy, neurophysiology, and behavior that it controls. In particular, we proposed a critical role for the metabotropic glutamate receptor system in adaptively timed learning. Two experimental articles published last year in *Nature* provided strong confirmatory support for our prediction.

When this result is combined with other observations regarding the computational properties of the cerebellar cortex, a theory emerges of a neural machine that performs arbitrary self-programming of movement production systems. It transforms and combs streaming context data to discover leading indicators of the need to perform control actions so as to minimize a cost function. Then it takes those actions at the optimal time within an interval of 90ms to 4 s post-indicator. This explains why the cerebellum is so critical to the successful adaptation of land animals to a full range of environmental niches, each requiring a different motor repertoire. The closest technological equivalent to the cerebellum would be a self-organizing production system, but such systems typically lack the critical adaptive timing competence that enables cerebellar production systems to exert real time control of motor systems with unique and variable dynamics in environments that impose variable timing constraints.

5. The VITEWRITE model of cursive handwriting production. Relevant references: 6, 22, 23, 24, 28, 30, 31, 55, 79.

This project designed a neural controller, based on the VITE model, for generating handwriting at variable speeds, sizes, and styles. The VITEWRITE model is a hierarchically organized architecture that addresses a number of key issues concerning the skilled performance of sequential actions: What is a motor program? How can a complex movement be flexibly performed at will with variable speed, size, and style without requiring new learning? How does the brain control a redundant manipulator that possesses more degrees of freedom than the space in which it moves? How can smooth curvilinear movements be organized by such a redundant manipulator? In particular, how is the timed launching of different groups, or synergies, of muscles achieved so that the desired directions, distances, and curvatures of movement are achieved? How do

volitional "acts of will" that vary the speed and size of movements change distances and curvatures of movement without changing global movement form through time?

The VITEWRITE model introduces a new concept of how a "motor program" can control sequential movements. This motor program is not explicitly represented in the model. Rather it is an emergent property of feedback between a working memory representation of desired movement directions and a VITE trajectory generator. The VITEWRITE model shows how the use of a redundant manipulator can simplify motor planning by enabling temporally unimodal commands to move different motor synergies. It also suggests how an outflow representation of movement speed can be used to trigger the next synergy to be performed, even while some synergies are in mid-flight.

The VITEWRITE model illustrates a new approach to applications that call for on-the-fly scaling and composition of trajectories. It has also served as a basis for the study of handwriting in Parkinson's patients (Contreras-Vidal et al., 1997). Such patients often exhibit small-sized handwriting, or micrographia, and a full understanding of its genesis through biology-based models like VITEWRITE should lead to improved understanding of the basal ganglia and to the development of improved therapeutic interventions.

6. The viaVITE model for performance of viapoint movements under guidance by a working memory that stores novel target sequences. Relevant references: 15, 21, 22, 23, 30, 31, 78, 79.

Much of human movement sequencing is controlled from working memory, which can store novel sequences that are used once and then discarded. An experimental task that has probed this ability is the viapoint movement task. Viapoint (VP) movements are movements to a desired point that are constrained to pass through an intermediate point. Studies have shown that VP movements possess properties, such as smooth curvature around the VP, that are not explicable by treating VP movements as strict concatenations of simpler point-to-point (PTP) movements. Such properties have led some theorists to propose whole-trajectory optimization models, which imply that the entire trajectory is pre-computed before movement initiation. We conducted new experiments to systematically compare VP with PTP trajectories. Analyses revealed a statistically significant early directional deviation in VP movements but no associated curvature change. An explanation of this effect is offered by extending the Vector-Integration-To-Endpoint (VITE) model (Bullock and Grossberg, 1988). The model explains the observed trajectories of VP and PTP movements as emergent properties of a dynamical system that does not pre-compute entire trajectories before movement initiation. The new model includes a working memory and a stage sensitive to time-to-contact information. These cooperate to control serial performance. The structural and functional relationships proposed in the model are consistent with available data on forebrain physiology and anatomy. In particular, the model suggests that the basic double-inhibitory circuit of the dorsal basal ganglia may be the minimal circuit solution to general problems inherent in the preparation and serial release of movement sequences.

7. An oscillatory VITE model for legato articulation in piano performance. Relevant references: 22, 23, 78.

This project investigates the neural mechanisms of rhythmic performance by modeling psychophysical data about piano performance. The brain contains many oscillatory movement generators. Locomotor generators in the spinal cord exist for multi-limb coordination. However, the cortical system for discrete voluntary movements is also sometimes engaged for oscillatory movements. Good examples are rhythmic foot tapping or rhythmic clapping, in which active movement may be restricted to the ankle or wrist joint. Such rhythmic tapping, or its covert "mental" residual, appears to be used as a timing device in a wide range of skills. Such timing may be most readily studied by examining musical performance. One aspect of musical performance where such timing is quite subtle is in *legato* articulation, where the temporal overlap between successive actions is under continuous control.

The key overlap times (KOTs) required for *legato* articulation varies markedly with tempo. For scales/arpeggios performed at inter-onset intervals (IOIs) of 100-1000 ms., prior reports show an increasing but non-linear functional dependence of KOT on IOI. Because the major non-linearity appears in the long IOI (slow tempo) region, the dependence of KOT on IOI is not attributable to gross biomechanical factors, such as finger inertias. Simulations show that the dependence can arise from a neural circuit in which a predictive central process and a slow sensory feedback process cooperate to control articulation. An oscillating neural network is first constructed as an extension of the vector-integration-to-endpoint (VITE) model for voluntary control of movement. The resulting circuit exhibits volition-controlled oscillation rates. It also affords predictive control by continuously computing an internal estimate of the remaining "time-to-contact" (TTC) with a targeted integration level, reaching of which triggers the oscillator's next half cycle. At fixed successive threshold values of this estimate of time remaining in the current half cycle, the performer first launches keystroke $n+1$ and then lifts keystroke n . As tempo slows, the time required to pass between threshold crossings elongates, and KOT increases. However, if performers used only such a central process to control articulation, they would not show the bend seen in the slow tempo region of the KOT vs. IOI function. The bend emerges if performers lift keystroke n whenever they cross the second internal threshold or receive sensory feedback from stroke $n+1$, whichever comes earlier. Empirical estimates of sensory feedback delay times are consistent with this interpretation.

8. Signal processing for navigation: Incorporation of motor information in processing of visual optic flow. Relevant references: 32, 71.

A key problem in sensory-motor control in mobile systems is how to remove components of sensory inputs that represent reafference, i.e., the feed-back effects of self-motion. An animal or robot that cannot distinguish between inputs caused by external motions and inputs caused by self-motion will have severe performance limitations because it will react inappropriately to many motion signals that arise during self-motion. For successful navigation, two key variables that need to be reliably extracted from optic flow

are heading direction and time to contact between looming objects and the body. For both variables, self-motion can lead to mis-estimates if it is not appropriately compensated. Following a strategy similar to that used in the DIRECT model, we have developed a model that is capable of self-organizing estimates of heading and time-to-contact by using an action-perception cycle during which reliable correlations emerge between self-generated motions and resultant optic flow patterns. This adaptive system successfully learns these estimates in the absence of any explicit knowledge of sensor geometry, motion signal gains, or the proximal motoric effects of self-motion commands. Thus, the same system architecture can be used to control different platforms that utilize different motors and sensors.

9. A neural model of multimodal adaptive saccadic eye movement control by superior colliculus. Relevant references: 1, 52, 53, 74, 76, 80, 81, 85.

A critical question for the efficient acquisition of visual information is how the eyes can be rapidly moved to foveate the most salient targets at any time. A still more general question concerns how distributed learning enables multiple sources of information to be used to make context-sensitive behavioral choices that are appropriate at that moment. The case of saccadic, or ballistic, eye movements nicely illustrates the new concepts, organizational principles, and neural mechanisms that are needed to explain such a competence. It is known that multiple brain learning sites are needed to calibrate the accuracy of saccadic eye movements. This is true because saccades can be made reactively to visual cues, attentively to visual or auditory cues, or planned in response to memory cues using visual, parietal, and prefrontal cortex, as well as superior colliculus, cerebellum, and reticular formation. The organization of these sites has been probed by a variety of saccadic adaptation paradigms, in which incomplete and asymmetric transfer of learning occurs between different tasks. A neural model of saccadic system organization, notably its distributed learning sites, has been developed to explain these data. In addition, it is known that multiple modalities send converging signals to the superior colliculus to determine which target will be selected for attentional focusing and movement. A neural model of how these multiple inputs from visual cortex, parietal cortex, and prefrontal cortex are fused through multi-modal learning into a self-consistent map for movement selection has also been developed. This model has been used to quantitatively simulate neurophysiological data about the dynamics of burst and buildup cells in the deeper layers of the superior colliculus during a variety of movement tasks. Finally, a model of how the saccadic system converts these signals from distributed decisions into properly calibrated movements has also been developed. This model explains the functional role of the cell types in the saccade generator in the reticular formation that are used to generate saccadic eye movements, and simulates heretofore unexplained neurophysiological and behavioral data about saccades.

The first study in this series analysed how the saccadic movement system can select a target when visual, auditory, and planned movement commands differ. In particular, visual information is received in retinotopic coordinates, and auditory information in head-center coordinates. Both types of information need to be transformed into motor error coordinates in order to make a saccade with the correct direction and length. In

addition, the brain needs to be able to decide whether to reactively look at targets which are defined by momentary sensory cues, or to look towards targets which are part of an action plan. The model suggests how visual and planned target positions become aligned through learning with visually reactive target positions to select a movement command. For this to occur, the retinotopic visual target representation is easily converted into a map of motor error coordinates. The auditory and planned head-centered representations of target position are transformed into this motor error map through multimodal learning. This multimodal fusion of information occurs in the deeper layers of the superior colliculus. The model shows how competition among these multiple sources of information can focus attention upon, and thereby select, the most salient target at any time. The mechanisms that focus attention upon salient targets also help to stabilize multimodal map learning through time. These mechanisms are variants of Adaptive Resonance Theory, or ART, circuits. Hence the model is called the SACCART model. In summary, the model suggests how multimodal learning, attention, and movement selection can be achieved by a single circuit. The model hereby provides a new framework for multimodal fusion of information that is coded in different coordinate systems by a system that can stabilize its own learning while attentively selecting the most salient piece of information at any time.

This map learning process enables the model to quantitatively simulate challenging recent neurophysiological and motor psychophysical data about saccadic movements. In particular, recent data about superior colliculus reveal a spreading wave of activation across buildup cells. The peak activity of this wave tends to occur at the map location that codes the current gaze error. In contrast, the map location of peak activity remains constant in a separate population of burst cells, whose activity levels decay with residual gaze error. The SACCART model quantitatively simulates neurophysiological data about burst and buildup cells, during a variety of movement tasks, as a manifestation of the mechanisms that transform head-centered target representations into motor error coordinates. The model also simulates neurophysiological data about multimodal enhancement and suppression of matched and mismatched target information in the superior colliculus, and predicts a role for known NMDA receptors in the multimodal movement map learning process.

10. A neural model of the saccade generator in the reticular formation. Relevant references: 1, 52, 53, 74, 76, 80, 81, 85.

How are the commands that are generated in the motor error map of the superior colliculus used to move the eye. In particular, how is this SPATIAL information converted into a properly calibrated TEMPORAL code for the production of a saccade? From the early 1970's there has been a long succession of local circuit models of the saccade generator in the brainstem, starting with the classical negative feedback model of Robinson (1975). All of these models have failed to explain key saccadic data and have made hypotheses that have not been supported by subsequent experiments. A new FOVEATE model shows how Feedback Opponent VECtor ARchiTECTure mechanisms can explain a much larger data set while using only well-known cell types in the reticular formation as a basis for the model circuit. The critical new idea is how to yoke together a

disinhibitory feedforward circuit with a negative feedback circuit. This yoking of circuits leads to a self-resetting trajectory controller that has many desirable properties. From the robotics perspective, the model suggests how to robustly coordinate horizontal and vertical movement controllers for active vision systems. In particular, the model can generate smooth, synchronous, straight trajectories despite different component motion amplitudes. It also provides a good interface for inputs from both reactive and goal-directed generators of visual tracking movements.

11. A neural model explains how distributed learning achieves task-appropriate adaptation of eye movement control. Relevant references: 1, 52, 53, 74, 76, 80, 81, 85.

Many parts of the brain compute possible targets for eye movements, and multiple brain learning sites are needed to calibrate the accuracy of these movements. This is true because saccades can be made reactively to visual cues, attentively to visual or auditory cues, or planned in response to memory cues. Different parts of the brain are used to compute these different types of information, including visual, parietal, and prefrontal cortex, as well as superior colliculus, reticular formation, and the cerebellum. A key problem for the saccadic eye movement system--indeed for any distributed learning system--is how to guarantee that different combinations of brain regions can all generate correctly calibrated movement commands. This requires a suitably designed distributed learning system.

The organization of these multiple learning sites has been probed by displacing a visual target during a saccade. Multiple task conditions have been devised to probe different aspects of the learning system, including electric, step, overlap, scanning, and memory paradigms. Psychophysical experiments have demonstrated different patterns of incomplete and asymmetric transfer of learning between pairs of these paradigms. A neural model of the saccadic system was developed to explain how these distributed learning sites are organized to correctly calibrate saccades during multiple saccadic conditions, and thereby to explain the learning transfer data, as well as data about saccadic coordinate changes.

This model shows how a combination of map learning in the superior colliculus and the prefrontal cortex, and gain learning across multiple pathways in the cerebellum can achieve the desired results. In particular, the reactive pathway includes the superior colliculus, the attentive pathway includes the posterior parietal cortex, and the planned pathway includes the prefrontal cortex and the frontal eye fields. This model provides a prototypical example of how distributed learning can allow a system with multiple bases for movement generation to maintain and recover accuracy despite significant changes in internal parameters, including damage to one or another central movement generator. Multiple bases for movement generation are a necessity in any freely moving system that must pursue goals while also reacting to unscheduled opportunities or challenges.

12. Neural control of interlimb oscillations: Human bimanual coordination, and biped and quadruped gait control and bifurcations. References: 37, 38, 39, 40, 73, 80, 82.

The previous projects have analysed phasic movements of the arms and eyes, as well as a role for rhythmic control of sequential movements. The present projects were devoted to modeling the central pattern generators whereby humans and animals can accomplish oscillatory movements. These results clarify how both phasic and oscillatory movements can be controlled by the same limb. It was shown how the ubiquitous on-center off-surround feedback circuits that exist throughout the brain could be specialized for this task. In particular, the excitatory neurons in these circuits operate on a faster time scale than their inhibitory circuits. A descending GO signal command – as in the VITE model – activates movement gaits and triggers gait transitions as its amplitude increases. A single model central pattern generator can elicit both in-phase and anti-phase oscillatory movements at different GO amplitudes. All the gaits and their transitions are emergent properties of this central pattern generator.

Simulations of human bimanual coordination tasks show how: anti-phase oscillatory movements of the two hands at low frequencies switch to in-phase oscillations at high frequencies; in-phase oscillations occur at both low and high frequencies; phase fluctuations occur at the anti-phase in-phase transition; a "seagull effect" of larger errors occurs at intermediate phases; and oscillations slip toward in-phase and anti-phase when driven at intermediate phases.

Simulations of quadruped vertebrate gaits include the amble, the walk, all three pairwise gaits (trot, pace, and gallop), and the pronk. Rapid gait transitions have been simulated in the order – walk, trot, pace, and gallop – that occurs in the cat, along with the observed increase in oscillation frequency. Precise control of quadruped gait switching uses GO-dependent modulation of inhibitory interactions, which generates a different functional anatomy at different arousal levels, a design property that has been demonstrated even for invertebrates. The primary human gaits (the walk and the run) and elephant gaits (the amble and the walk) are simulated, without such modulation, by oscillations with the same phase relationships but different waveform shapes at different GO signal levels, much as the duty cycles of the feet are longer in the walk than in the run. Relevant neural data from spinal cord, globus pallidus, and motor cortex, among other structures, are also clarified.

Summary

Human competence will remain the model for intelligent robotics into the indefinite future. Limitations of current robotic deployments can only be overcome if robots acquire the adaptivity, robustness, and flexibility needed to allow them to compose goal-directed behavior on the fly. Our studies have been explicating the neural circuit architectures that make humans able to quickly compose adequate actions adapted to novel momentary requirements, and then to perfect their execution of those actions when conditions allow their repeated use. This amounts to experience-guided self-programming or "self-organization" – the only truly general and practical alternative to the impossible task of attempting to pre-program a response to every possible

contingency. The same self-organizing abilities allow recovery after damage, so machines based on these ideas will also be self-repairing.

As a result of using mathematics to explicate the neural circuit bases of human sensory-motor flexibility, we have been able to construct and simulate several of the most comprehensive neural system models ever seen. These models have consistently raised the bar in the field of computational neuroscience, and we expect them (and their descendents) to serve as prototypes for many robotic designs going forward. Although many of the central circuits are already being applied, this process will further accelerate when technology begins to catch up with biology in key areas, such as miniature embedded sensors and practical muscle-like actuation.

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