A Hierarchical Model of Synergistic Motor Control

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Abstract—Experimental studies of motor control in humans and other animals suggest that complex movements are constructed from a relatively small set of motor primitives representing preferential coordinated activation patterns in groups of muscles. These have been termed synergies. We have previously presented a neurodynamical model of how motor primitives with the observed characteristics of synergies might be encoded in cortico-spinal and spinal neural networks. The model showed that a small basis set of synergies could be used to combinatorially generate linear trajectories in all directions from all points within the posture space of a two-joint, two degree-of-freedom arm. We now present an extension of that model, where useful combinations of these low-level synergies are encoded into higher-level primitives termed hypersynergies, such that the activation of a single hypersynergy with appropriate control parameters allows the generation of an extensive repertoire of movements over large parts of posture space. This repertoire is “exploited” by a cortical motor control system implemented through interacting neural maps. We argue that this system can generate complex movements with relatively simple neural control mechanisms.

I. INTRODUCTION

The neural basis of motor control has been a topic of intensive study for many decades, but many issues in the area remain unresolved. Prominent among these is the so-called degrees of freedom problem [1], which refers to the fact that the bodies of complex animals such as mammals and arthropods are highly redundant in terms of the degrees of freedom needed to perform specific movements. This creates a very difficult control problem, and many studies have sought to understand how this is solved by the nervous system. One important insight to emerge from these studies is that, rather than using explicit top-down trajectory-tracking, animals build many complex movements through the combination of motor synergies: preconfigured patterns of coordinated activity across groups of muscles [2], [3], [4], [5], [6], [7]. A small number of synergies can be used as basis functions in weighted linear combinations to form a large repertoire of movements which can be elicited simply by triggering the appropriate synergy combination rather than by explicit trajectory control [4], [3], [7], [8]. So far, motor synergies have been found only analytically through decomposition of experimentally recorded muscle activation patterns during multiple movements [3], [7], [8], and their physical basis in the neural system remains an open issue [9], [10]. However, the presence of synergies is consistent with the fundamental principles of modularity and emergent coordination that characterize all complex systems [11], [12], [13], and this dynamical “embodied” view of motor control has found both theoretical and experimental support [14], [15]. Indeed, it has been suggested that a hierarchy of synergies might underlie all cognitive function, including cortical functions associated with higher cognition [16], [17]. The presence of a synergy hierarchy is also indicated by experimental data showing that patterns of neural activity in cortical motor regions (motor cortex (M1), premotor cortex (PM) and the supplementary motor area (SMA)) encode complex movements such as sequences [18] and complex canonical movements such as bringing the hand to the mouth [19].

Motivated by experimental data, we recently proposed an abstract neurodynamical model for the encoding of motor synergies in spinal and cortico-spinal neural networks. Using a simple multi-layer system of attractor neural networks driving a 2-joint, 6-muscle arm, the model showed that a small basis set of synergies could be derived through a principled search procedure such that combinations of these synergies allowed movement in every permissible direction from every available posture [20], [21]. In this paper, we extend this model to the next hierarchical level by configuring a small set of canonical synergy combinations termed hypersynergies, such that a single hypersynergy can produce movement in all directions from many postures simply through variation of parameters. This greatly simplifies the control strategy for generating a specific movement, requiring only: 1) Selection of a broadly applicable hypersynergy (or sequence of hypersynergies); and 2) Selection of a few gain parameters (or parameter sequences). We hypothesize that animals use this strategy to learn and produce non-rhythmic automatic movements such as reaching, kicking, etc.

The rest of this paper is organized as follows: Section II explains the motivation for the hierarchical synergistic model and provides some background on other work. Section III describes the model and its use. Section IV provides simulation results and a discussion of these results, followed by a summary and conclusion in Section V.

II. BACKGROUND AND MOTIVATION

Researchers in the area of motor control have proposed three main types of control models: Cerebellar adaptive control models [22], [23], [24], basal ganglia-based reinforcement learning models [25], [26], [27], [28], [29], [30], and modular control models [31].

Among the earliest models involving the cerebellum were the classical models of Marr and Albus [22], [23] who
proposed that the cerebellum is a pattern recognition system that recognizes contexts for specific movements. Based on this, Ito (1993) hypothesized that the cerebellum provides a model of the body and the physical environment allowing for accurate movement control despite errors in sensory feedback.

The actor-critic architecture for the reinforcement learning of control tasks was proposed in the early 80’s by Barto and colleagues [30]. Based on the knowledge that the neurotransmitter dopamine mediates reinforcement learning through the basal ganglia in humans and other mammals [32], [33], several researchers have proposed actor-critic models of the basal ganglia [25], [28].

Optimal control has also been used as the basis for models of motor coordination and control. Todorov and Jordan proposed a model in which the desired trajectory is not enforced, but feedback is used intelligently by correcting only those errors that interfere with task goals [34]. Other models based on optimal control have used an iterative Linear-Quadratic-Gaussian (LQG) formalism as a model for control of a redundant biomechanical system represented by the motor system [35], [36].

A very different approach to motor coordination arises from the nonlinear dynamics and complex systems framework. An important insight derived from the study of complex systems is their extensive use of modularity and multi-scale self-organization. General processes, once discovered, are organized into functional modules and generate complex patterns at multiple scales through their interaction. This allows the systematic generation of unbounded complexity while maintaining the possibility of useful control.

More recently, Schaal and colleagues have developed a concrete mathematical framework using dynamical motor primitives (DMPs), and applied it very successfully to the control of high degree-of-freedom robots engaged in complex tasks [37], [38], [39], [40].

One of the benefits of a synergistic approach is that a large number of complex responses can be configured by the combination of a small set of synergies. These complex actions are triggered as a whole by a simple command input rather than being generated continuously through a detailed control signal. The synergies also provide a very stable internal memory for the system and are not disturbed by variations in the system. One of the most important properties of the synergies is that their stability also makes the response more robust to noise and other perturbations. It has been postulated that the synergistic, dynamical model studied in the motor system can be applied to the brain as a whole leading to the development of a complex dynamical view of all mental functions [17], [16]. This framework allows for the explanation of complex behaviors in animals from an evolutionary and developmental perspective.

From this viewpoint, all mental functions in animals are seen as emerging through the interaction of functional modules, i.e., synergies, configured at multiple levels through evolution, development and learning. The modularity in the sensorimotor control during motor adaptation processes has been studied by researchers [41]. The synergies in peripheral systems – the spinal cord, the brainstem, sensory receptors and the musculoskeletal system – are relatively inflexible and hard-coded, and are configured primarily through evolution and early development. Feature detectors in the visual cortex or central pattern generators in the spinal system are the examples of peripheral synergies. Core synergies are present in the neocortex, thalamus, hippocampus, cerebellum and basal ganglia. These synergies are flexible, diverse and subject to extensive modulation by the limbic system and other regions of the cortex. Though the basic substrate of the core synergies is configured by evolution and development, they are subjected to constant reconfiguration by information flow and synaptic plasticity.

Two levels of synergies namely the peripheral and the core synergies are developed in this work.

III. System Model

The overall architecture of the system model, shown in Figure 1, comprises five major components:

1) The Arm Model: This is a 2-jointed, 2-degree of freedom manipulator activated by three agonist-antagonist muscle pairs: One pair each for the individual joints – shoulder and elbow, respectively – and the third spanning both. The muscles are modeled using the Hill model. The angular range of movements for the two joints is constrained to $-75^\circ \leq \theta_1 \leq 75^\circ$ and $0^\circ \leq \theta_2 \leq 165^\circ$, respectively. The position of the shoulder joint is fixed, so the arm has a limited region it can reach. Given the fixed shoulder position and rigid arm members, every point of the reachable space corresponds to a unique posture for the arm, so the set of all postures – termed the posture space – is an arm-centric representation of the reachable space.
This arm model has been used extensively in research on motor control [42], [43], [20], [21].

2) The Spinal Circuits: These are pairs of symmetrically connected recurrent neural networks that form a central pattern generator (CPG) sending motor signals to each muscle pair. Each element of the pair includes an alpha motor unit that directly innervates the muscle, two inhibitory units and a stretch receptor providing feedback from the ipsilateral muscle. The pair have inhibitory cross connectivity, setting up the agonist-antagonist relationship between the muscle pair.

3) The Synergy Group Network (SGN): This is the main network encoding the motor primitives, or synergies, similar to those observed experimentally in [4], [3], [7], [8]. This has been described in detail in our previous work [20], [21], but, in view of its importance, it is briefly described here as well. Figure 2 shows the architecture of the SGN, which is a hierarchical, modular recurrent neural network. The network is organized into a set of synergy groups, each comprising a set of mutually interacting recurrent neural modules with delays. Each synergy group is, therefore, a recurrent modular network. Each module has \( n_m \) units of which \( n^I_m \) are internal and \( n^O_m \) output units. Each module embeds one of \( n_A \) canonical attractors. Each attractor has the same number of active units across all \( n_m \) neurons in the module, but distinct output neurons are activated by each attractor, and the weights from these neurons to the spinal networks are set so that the attractors provide different levels of activation to the target muscle(s). The interactions among modules also embeds a specific pattern of mutual delays between the triggering of attractors in the modules, and an inherent activity-limiting mechanism (e.g., sodium-dependent potassium channels) de-activates each attractor after a limited time. The net result is that, upon being triggered, an SGN produces a specific spatiotemporal pattern of pulses that projects to the target muscles with a controlled gain. This represents a single synergy evoked with different strength as seen in experimental data [4], [3], [7], [8]. For simplicity, we assume that all the synergy groups have 6 modules and projects to all 6 muscles with a one-to-one muscle map, but more complex connectivity patterns can be configured in the model.

Triggering a particular synergy from a specific posture leads to movement in a specific direction, with the length of the movement determined by the amplitude with which the synergy is triggered. At any given time, each synergy group can be in an enabled or inhibited state, depending on signals from the selector network described below. Thus, the input received by each muscle from the SGN is the combination of outputs from all enabled synergy groups.

The SGN, spinal circuits and the arm model have all been described in detail in our previous work to which the reader is referred [20], [21].

4) The Selector Network: This is a single layer attractor neural network, with recurrently connected neurons partitioned into three subsets: 1) An input set that receives input from higher layers; 2) An output set that sends enabling signals to synergy groups; and 3) A hidden reservoir of units that give the network sufficient size to store several different attractors. Due to this architecture, each attractor stored in the selector network enables a subset of synergy groups, and represents a hypersynergy, or a higher-level synergy. Using an attractor network rather than a feed-forward map given the system the ability to clamp a hypersynergy for extended time periods, and adds noise rejection and error correction capabilities.

5) The Spatiotemporal Control System (STCS): This is the higher level system mapping current postural state and desired movement to the synergy-based muscle control system represented by the first four components. This, along with the selector network, are the main focus of this paper, and details of the STCS are given below.

The main task of the STCS is to generate two things: 1) The hypersynergy to be triggered; and 2) The amplitudes to be applied to each synergy within the hypersynergy, i.e., to each enabled synergy group. A relative delay between synergies has also been found in some experiments [4], [3], but this is not a universal observation [7], [8], and the current model does not explicitly control delay.

A. Configuration of the Synergies

Experimental work showing the muscle synergies are quite similar across individuals [7], [44], [45] raises the possibility that they may be at least partially have evolutionary and/or developmental origins. To simulate this at the phenomenological level, we configure a small number of synergies through
explicit heuristic search in configuration space as described in [20], [21]. This is based on two fundamental principles:

1) Maximum Coverage: As a set, the configured synergies should cover movement in all directions from all points in the field of movement.

2) Minimum Redundancy: Pairwise, the synergies in the set should be significantly different from each other.

In addition to this, we also impose a requirement that, for the same amplitude gain, the movement generated by each basis synergy should be of similar length and minimal curvature.

The search process uses 49 regularly spaced points in the movement space, and the region centered on each point is divided into eight equal radial zones of 45 degrees each. A set of synergies is said to span posture \( k \) if they reach at least 3 zones at the posture with at least none intervening zone between each of the three. Extremal postures can be spanned by covering fewer zones. The maximum coverage requirement is met by a set of synergies that span all 49 posture, and comprises a synergy basis set because movements in all directions can be produced from any posture, in principle, by combining subsets of these synergies with amplitude. If the synergies are also distinct in their directional patterns, that the basis set is termed minimal.

Figure 3 shows movement fields for four synergies from a basis set of seven found by the search and used in this work.

![Movement direction fields for four of the seven synergies in the synergy basis set](image)

**B. Hypersynergies**

The set of peripheral synergies described in the previous section forms the lowest level of motor primitives in the system, and are assumed to be configured in animals through evolution. These motor primitives, each of which is a coordinated pattern of activity across various muscle groups, implicitly encode a repertoire of simple movements that are innately available. More complex movements are then generated by the composition and modulation of selected subsets of these primitives.

We hypothesize that, during early development, animals configure a few canonical combinations of the basic motor primitives, which we term hypersynergies. A large set of finely controlled movements of the limb can be generated by the modulated triggering of a single hypersynergy. This is supported by experimental evidence in frogs [46], cats [44] and humans [41]. Hypersynergies for individual limbs can then be combined in even higher level synergies to coordinate across limbs, culminating in synergies involving neural assemblies in the neocortex, basal ganglia and cerebellum [17], [47], [27], [26].

In the current model, hypersynergies are instantiated as attractors in a recurrent neural network called the selector system. As with the lowest-level synergies, the goal in the selector system is to instantiate the smallest set of hypersynergies that covers all movements from all initial positions. Given the fact that each basis synergy can only allow movement in one direction from a specific posture, and using the same definition of coverage, it is clear that coverage of any posture will require a set of at least three basis synergies with well-separated directions, which is a potential 3-unit hypersynergy. Typically, a given posture may be covered by multiple 3-unit hypersynergies, as shown in Figure 4. Amplitude modulation of the three synergies in any of these hypersynergies will allow movement in any direction from that posture, and each 3-unit hypersynergy will cover many neighboring postures because of the smoothness inherent in the system. The set of amplitudes corresponding to movement in a particular direction from a given posture form a continuous subspace in amplitude space, termed the unconstrained manifold for that direction.

The hypersynergy configuration process attempts to find a small number of 3-unit hypersynergies that cover the entire movement space from all postures (possibly with some redundancy). An important factor in finding these hypersynergies is to look for those with the most smoothly varying amplitude control manifolds over large neighborhoods of posture space. Once this set of hypersynergies is configured, a higher level system learns to control movement through it as described in the next section.

The primary advantage in choosing a small number of 3-unit hypersynergies is that it greatly simplifies the learning of movement control. Instead of producing specific time-varying inputs for each muscle, the controller only needs to do two things given the current posture and desired movement direction:

1) Trigger an appropriate hypersynergy.

2) Activate the right combination of modulation parameters for that hypersynergy.
The network is distributed in two layers – a hidden layer and an output layer. The internal neurons called selector neurons, and only have recurrent connections within the network. The output layer is termed projection neurons which, in addition to recurrent connections, also send enabling outputs to individual synergy groups of the SGN.

Each attractor pattern stored in the selector system corresponds to a particular combination of synergies. The attractor patterns are embedded into the selector network via recurrent weights specified via Hebbian learning. The activation of selector neuron $j$ at time $t$ is given by:

$$v^S_j(t) = (1-r^S)v^S_j(t-1)+r^S\left(\sum_k w^S_jk y^S_k(t-1)+I_j(t)\right)$$  

where $y^S_k$ is its output of selector neuron $k$, $I_j$ is the external input to neuron $j$, and $r^S$ is an inertial parameter.

The output of a neuron $y^S_j(t)$ is determined by a competitive process, with only the $K$ most excited neurons allowed to fire provided their activation also exceed a minimal threshold. The synergy map acts as a robust switchboard for triggering specific hypersynergies. It comprises a pool of generic pointer modules, each with $n^m$ coding units and one pointer unit. Each of these units can be seen as a group of neurons. The coding units for each pointer module $k$ receive input from the cortical networks encoding the current sensorimotor state of the arm – in this case, the current posture and the desired direction of movement – and send excitation to the pointer unit for the module. The pointer units of all modules act as a winner-take-all (WTA) network, so that only the pointer unit for the module with the most highly activated coding units can fire. Each pointer unit sends sparse excitatory connections to a small set of internal and projection units in the selector network, so that its firing triggers a particular pattern of neural activity in the selector network and, therefore, enables a specific set of synergy groups in the SGN, i.e., a hypersynergy. Thus, before training, the selector system can be seen as a pool or reservoir of triggers for a large population of potential hypersynergies. We hypothesize that developmental learning explores this pool through motor “babbling”, i.e., generation of movements via random (though possibly stimulus-biased) triggering of synergy combinations at different gains, and reinforcement of combinations through reinforcement. The result is that a small, near-minimal but sufficient set of hypersynergies become embedded as attractors in the selector network and linked to specific pointer modules triggered by appropriate sensorimotor states. The architecture of the pointer modules provides significant robustness in the selection of hypersynergies. Qualitatively, the synergy map could be seen as corresponding to the functionality usually associated with the basal ganglia [48], [48], [29], and the selector network as part of the cortical structures receiving afferent from the basal ganglia via the thalamus.

For the simulations reported in this paper, we selected a set of five hypersynergies through explicit search and embedded them in the selector system. The selector network weights were set using a covariance learning rule:

$$w^S_{jk} = \sum_{q=1}^{N^S}(y^S_{jq} - \bar{y}^S_j)(y^S_{kq} - \bar{y}^S_k)$$

where $w^S_{jk}$ is the synaptic weight from selector neuron $k$ to selector neuron $j$, $y^S_{jq}$ is the output of neuron $j$ for attractor pattern $q$, $\bar{y}^S_j$ is the mean activity of neuron $j$ over all the
attractor patterns stored in the selector network, and $N^S$ is the number of attractor patterns (i.e., hypersynergies) stored.

C. Learning Higher Level Control

![Diagram of the sensorimotor system]

The system described so far represents the low-level part of the motor system, providing an embodied substrate from which higher-level signals can evoke movements. The generation of appropriate movements requires an ongoing process of sensorimotor transformation, whereby the system generates goal-directed movements based on sensory information in the context of internal drives (e.g., a glass of water in the context of thirst). This is done through a control interface that links sensory and motivational signals to actions, i.e., a sensorimotor transformation. This is a complex, parallel distributed information processing task wherein sensory and internal driving signals need to be converted to an intermediate representation so that the motor commands can be generated. Studies indicate that the parietal cortex, which lies above the occipital lobe and behind the frontal lobe, is involved in sensorimotor transformation. Studies have also shown that parietal cortex not only combines various sensory signals but also encodes motor actions, combining both to form an internal state of both the world and the body [49], [50], [51], [52], [53], [54].

Drawing inspiration from these studies, we have developed a neural model that closely resembles the structure and the function of this association cortex. This model consists of three interacting neural maps [55], [56]:

1) The sensorimotor map (SMM), which maps sensor signals and motor commands to hypersynergies and amplitude gains. The motor command is represented as a desired direction of movement – presumably based on sensory and motivational information – and put in context by somatosensory input encoding the current posture.

2) The synergy map (SM), which indexes the hypersynergies as described in the previous section.

3) The amplitude map (AM), which encodes amplitude gains for the currently selected hypersynergy to generate the desired movement. The amplitude map has separate sub-maps for each hypersynergy.

Figure 6 shows the architecture of the system. Given the current arm posture and the desired direction of movement and generating two outputs: 1) A triggering signal to the appropriate hypersynergy; and 2) a set of $k$ gain amplitudes for the selected hypersynergy, where $k$ is the number of synergies comprising the hypersynergy. Assuming that $k = 3$ for all hypersynergies, the amplitude map for each hypersynergy is a conceptually 3-dimensional layer of neural units, each representing a particular amplitude combination with equal pitch in all dimensions. The output from the amplitude map is sent to the Synergy Group Network (SGN).

The internal connectivity of both the SMM and AM has a locally excitatory globally inhibitory (LEGI) structure, which leads to the formation of activity bump attractors [49], [56] in response to external input. In the SMM, the bump represents the current sensorimotor state. Excitatory projections from the SMM to the synergy map trigger an appropriate hypersynergy and place a state-dependent bias on the amplitude map, causing the amplitude map bump to move to a location corresponding to movement in the desired direction. The weights from the SMM to the amplitude map are learned through a babbling process similar to that used for the synergy map, and are reciprocal, so that activity patterns across the two maps essentially form a single self-stabilizing attractor. Details of the sensorimotor system and learning process will be described in other reports.

IV. Evaluating Hypersynergies

![Graphs of directional tuning histograms]

The system of networks with synergies and hypersynergies can be seen as a versatile, embodied system ready to be exploited by the sensorimotor control system described in the previous section. Our goal in the present paper was mainly to describe the low-level system and to evaluate whether it provides a suitable substrate on which sensorimotor control can build usefully through developmental and reinforcement learning. Since the hypersynergies provide the point of control for it, the lower-level system can be evaluated best by testing whether the hypersynergies meet their desired goal.
of providing omni-directional movement choices from large regions of movement space.

To test the performance of hypersynergies each one was tested with 1000 random amplitudes from every one of 12 positions. The directions of the resulting movements were binned into 24 radial bins and plotted with logarithmic scaling to show them more clearly. Figure 7 shows the results for two hypersynergies. The following conclusions can be drawn from these (and other similar) figures:

1) Each hypersynergy provides the opportunity to move in all directions from large parts of the movement space.
2) The distribution of directions across amplitude space is highly uneven, so that some directions are much easier to move in than others.
3) The directional biases for the two hypersynergies are oriented differently.
4) The hypersynergies show different, though overlapping, regions of maximum coverage. Importantly, the covered region for each hypersynergy appears to be broad and simple in shape, though this can be evaluated in detail only by sampling many more postures.

It is worth remembering that the data shown in 7 is for a "naive" system, i.e., one where the mappings from the high-level sensorimotor representation to the amplitude and synergy maps has not yet been learned. Thus, the movements associated with each hypersynergy represent its "raw potential", and are analogous to those that might be produced by a child in the early stages of babbling, where hypersynergies have been configured (though perhaps not finalized) but their use in controlled situations has not. In particular, the strong directional bias seen for all hypersynergies from all initial positions are analogous to the strongly stereotypical movements produced by infants and young children. A goal of sensorimotor developmental learning in the model will be to mitigate this bias by learned equalization across all directions. However, it should be noted that, in many cases, directional biases can have functional value in themselves. For example, a bias in favor of movement towards self is behaviorally important, and the goal of learning might be to select for it rather than equalizing it away.

V. CONCLUSION

In this paper, we have built upon our previous neurodynamical model of low-level motor primitives, showing how they can be configured into an even smaller number of highly versatile primitives, or hypersynergies, at the next level, which then allows sensorimotor control mechanisms in the cortex and basal ganglia to learn complex movements using a very simple control scheme. Our simulations showed that the hypersynergies configured in the system had the properties of broad coverage and diversity needed to provide the substrate for a successful motor control system.

REFERENCES


