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The uncontrolled manifold: a brief history of ideas, insights, and mistakes

GREGOR SCHÖNER[1]

[1] Institute for Neural Computation, Faculty of Computer Science, Ruhr-University Bochum, Germany

Correspondence to: Gregor Schöner.
email: gregor.schoener@ini.rub.de
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ABBREVIATIONS

OFC	Optimal feedback control
ORT	Orthogonal complement
UCM	Uncontrolled manifold theory

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ABSTRACT
This paper outlines a history of ideas around the notion of an "uncontrolled manifold" (UCM) from a rather personal perspective. While the UCM methods of analysis and experimental findings based on those methods have been reviewed many times, my history of ideas provides some background information, insights from negative results, and account of a few mistakes we made. I added a section on the much less well known attempts to theoretically understand the UCM structure of variance.

KEYWORDS: Motor learning | Motor synergy | Coordination | Neural control strategies | Variance analysis

THE IDEA OF AN UNCONTROLLED MANIFOLD (UCM)

In the scientific study of motor control, a long-standing tension between two strategies has persisted (see, e.g. [1]). In one strategy, simplified movement tasks are used to enable neural analysis and computational modeling. For instance, Evarts [2] trained monkeys to flex a single joint while recording from motor cortex. This enabled him to establish that neural activity varies when the exerted force varies. Similarly, much behavioral work entails movement of the hand in a plane, often restricted to one or two joint movement (e.g. [3]). Motor adaptation has been extensively studied by imposing external force-fields on the hand in simplified configurations [4]. Most computational modeling of motor control is aligned with this strategy as it strongly simplifies the system to be modeled [5].

The other strategy is to look at naturalistic movement tasks that approximate movement generation in the real world, involving many joints, muscles, and time courses of movement. For instance, Lacquaniti [6] asked participants to perform free "scribbling" motion of the hand in three-dimensional space without restricting which degrees of freedom to use or prescribing the timing of such movements (reviewed in [6]). Georgopoulos and collaborators trained monkeys to perform pointing movements with their unrestricted arm and were able to relate activity of neural populations in motor cortex to the hand's movement direction in space [7]. Bernstein's reflections on human movement generation came from the observation of workers in real-world manual tasks [8]. This strategy has been successful because regularities of human movement were discovered that simplify the, a priori, highly complex problem of motor control.

The tension becomes very concrete when we look at how the capacity to generate voluntary movements develops during infancy [9]. Infants do not follow task instructions, so we can only observe natural movements involving whatever degrees of freedom an infant activates. The movements observed are highly variable, making them difficult to align in time in order to average across trials or participants. In spite of these difficulties, development may provide key insights into how movement is generated.

I became aware of this challenge when I began visiting Esther Thelen's laboratory at Indiana University from my then home base in Marseille, France, in the mid-1990s. This beginning collaboration was actually directed at cognitive development, or, more precisely, at the close relationship between cognitive and motor development. Esther Thelen and Linda Smith had developed a line of thinking summarized in two books that had just come out [10,11]. I had been studying movement preparation and motor decision making with my students Klaus Kopecz [12] and Wolfram Erlhagen [13] laying the foundations of what became known as Dynamic Field Theory [14]. We used this framework to conceptually sharpen the Thelen-Smith approach around the problem of infant motor decision making [15].

While at Esther Thelen's lab, I participated in the lab meetings that were often about motor development, in particular, about the onset of reaching in infants. It was amazing to see how hard these babies were working to get their hand to a target which they were clearly focused on. Different infants used quite different strategies and followed different individual routes to successful reaching. I spent quite a bit of time thinking about these observations. For a number of years, I had tried to design an overall dynamical systems framework for movement generation that emphasized stability as a concept [16]. How would one think about the infant's hand paths and trajectories in these terms? Would they go from rather unstable trajectories to stable trajectories as they learn to reach? Stable in which sense: stable against variation in timing? Stable against variation of the hand's path in space? Stable against variation in the joint angle's trajectories? Or stable against variation in the patterns of muscle activation?

I became aware that stability, resistance to change, may evolve differently for these different kinds of variables: At some point in development, the infants might be able to generate adequately defined timing signals, but not control the spatial position of the hand in space or the level of activation of muscles adequately.

In a general review paper that I wrote in 1995, I gave a verbal account of these different levels of control with stability as a pervasive concept applying at all levels. To illustrate how stability may be structured, I made a very crude little model to articulate the idea that the human movement system might endow particular variables with stability, while keeping other variables less controlled (Figure 1). Rather than thinking about muscles, joints, and spatial positions, I used two different spatial components of the hand's position in a plane to illustrate the idea. This made it easier to make a drawing and to do the computations. In this toy model, the hypothesis is that the position of the hand is "controlled" to lie on a straight line. Where exactly along the line the hand is positioned is not supposed to matter, "is not controlled". The point of that section of the review article was really to clarify what "controlled" means: driven by neural processes to resist change.

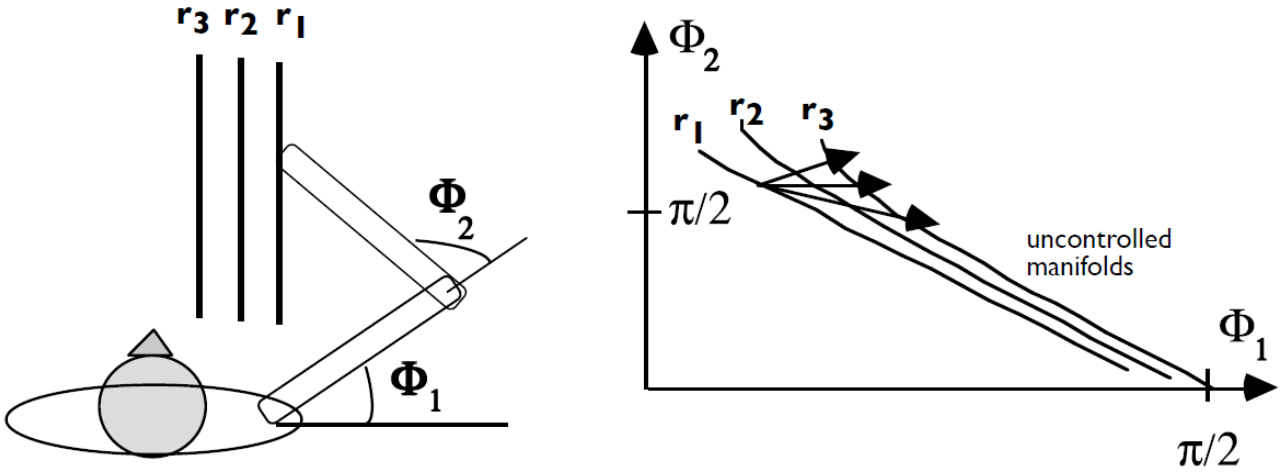

Figure 1. Left: A hypothetical toy example in which a two-joint arm moving in a plane is tasked to move the end-effector onto different vertical lines, r1, r2, or r3, no matter where along those lines the end-effector falls. Right: Continuously many combinations of the two joint angles are consistent with the end-effector lying on a particular vertical line. For each end-effector position on one of those lines r1, r2, or r3, these combinations span "uncontrolled manifolds", here one-dimensional curves in the space of two joint angles. To move the end-effector from one line to another, continuously many joint angle changes are possible illustrated here by the three example directions of change (arrows).

A straight line in the space of hand positions can be translated into a curved line in the two-dimensional joint space. Any point on that curved line represents a joint configuration that is an acceptable solution to the task. This is what I then called the "uncontrolled manifold" (UCM). "Manifold", because that is what the curved lines technically are. In general, manifolds are smoothly curved, continuous sets of a given local dimensionality that can be embedded in a higher-dimensional. "Uncontrolled" because there would be no resistance to moving the hand within the manifold, only to moving the hand away from the manifold.

I tried out this way of thinking by talking to people in Esther's lab and to my friends in motor control. I recall a visit to Mark Latash's lab at PennState around that time during which we continued a long history of conversations begun before I had moved to Marseille. In his characteristic action-oriented manner, he designed a simple set-up to test the literal idea of Figure 1. The participant (me) had to perform fast pointing movements toward different lines drawn onto a table. It would only matter that the finger lands on the line, not exactly where along the line the finger would land.

That did not work. The variance of the finger's end-point formed pretty much a circle on the tabletop. As crude as this was, it provided, at least in hindsight, an insightful negative result that has since been reproduced in many different contexts: One cannot just arbitrarily impose a task variable (the finger's position on the line) and expect variance to be organized around it. Humans generically control all components of their hand's spatial position, even when that is not explicitly requested. They cannot release a spatial component from control just by instruction. (Our shooting example below hints that such release is possible upon learning another task.) If this kind of thinking was to be useful, one would need to discover relevant task variables around which variance is organized.

MAKING THE IDEA OPERATIONAL: SIT-TO-STAND IN TWO DIMENSIONS

So, this notion of an uncontrolled manifold remained a theoretical idea and had not yet become a discovery. The empirical breakthrough came when John Scholz took the initiative to join me in Marseille for a sabbatical. We had previously collaborated on the coordination of rhythmic movement when we were both associated with Scott Kelso's lab and had stayed friends ever since. In Marseille,

I ran a theory and robotics group, so I did not have a movement analysis laboratory and could not run any experiments. A local movement group generously gave us access to their movement measurement system and allowed us to build a simple set-up (to my shame, I can't recall the names of these generous colleagues). Before going to the sit-to-stand experiment, a few comments about the choice of task and configuration.

We thought that whole body movements in a plane would be a simple enough setting to enable analysis and measurement. The task variable would be the position of the body in space, expressed as center of mass or as the position of some marker on the body. Those are meaningful task variables. The center of mass is important for mechanical stability: It must be positioned over the support area of the feet. Stabilizing the head's position in space is relevant for many other tasks. The exact joint configuration achieving that center of mass position would not matter: There would be an uncontrolled manifold of joint configurations that could achieve the same center of mass position. Restricting the analysis to a plane would make measurement, computation, and illustration easier. The sit-to-stand transition as the movement task made sense too: In the sit-to-stand transition, mechanical stability is challenged, so controlling the body's center of mass would be important.

We did not try quiet stance as a task, a seemingly even simpler motor behavior. This was because we could not imagine that something like an uncontrolled manifold could be relevant for that behavior. After all, the "inverted pendulum" account prevalent in the literature postulates that posture is controlled from the ankle. And the ankle joint is largely orthogonal to the uncontrolled manifold of the center of mass: flexing the ankle very effectively moves the center of mass, rather than leaving it invariant (but see below).

We thought we could manipulate the task by taking away the balance constraint: Have participants stand in ski boots on a pair of skis that were attached to the ground. Now participants could lean forward or backward as much as their fitness allowed, with no risk to their balance. We sacrificed an old pair of skis of mine for that purpose and ran a few participants (including me) with that. The ski did not seem to have any effect. Participants did not exploit the freedom to lean, another negative result (not well documented, alas) that would be consistent with the idea that participants cannot simply release variables from control by imposing task conditions.

So, we replaced that condition with having participants wearing the ski-boots, but not being attached to the skis. This manipulation restricted ankle motion. We added another condition that would emphasize the balance constraint: Participants had to stand on a narrow base of support. Neither manipulation mattered much, as documented in our 1999 paper [17]. These negative outcomes again support the view that the structure of variance is a robust property of the motor control system and cannot be altered on the fly.

This first study found reliable "UCM effects" for the center of mass, both in its vertical and its horizontal position: More variability of joint configurations that left the center of mass position invariant than of joint configurations that affect the center of mass position (Figure 2). For the head's position in space the same effect was observed, but in the second half of the movement the effect was inverted for the vertical position of the head. Here variance that moved the head vertically was compressed over variance that moved the head horizontally or not at all. This reflects the singularity of the body's configuration for vertical head position as the body reaches the fully upright position. A fully upright body has only a single joint configuration to lift the head to its highest point. As that point is approached, the range of possible joint angles decreases.

So here we finally had a discovery! The UCM analysis of variance uncovered structure in the variance in high-dimensional joint configurations that made functional sense.

THE UCM ANALYSIS OF VARIANCE

It was a fortunate decision to use a movement, sit-to-stand, rather than a non-movement, posture, to first operationalize the ideas. This droves us to develop all methodological steps needed in an UCM analysis of variance. This entails, in particular, normalizing movement time to temporally align different trials of the same movement, so that variance across trials could be analyzed separately at each moment in normalized time. The UCM analysis is essentially a quasi-postural analysis. At each point in time, deviations of the joint configuration observed in each individual trial from the mean configuration is projected onto the subspace of joint configurations that leave the hypothesized task variable invariant (the null space, a linear approximation of the UCM). The orthogonal complement of this projection (ORT) is computed by subtracting this UCM component from the original joint vector. Variance in these subspaces can be computed as a sum of squares. This must be normalized correctly to assess the variance per degree of freedom.

This analysis requires a theoretical model that connects joint space to a hypothesized task variable. Such models can be linearized to analyze variance which is assumed to be small enough for the linear approximation to be valid. The Jacobian characterizes this linearization, and its null-space is a linear approximation of the UCM. Its orthogonal complement, the range space, is the subspace in which the task variable varies maximally. The models for the sit-to-stand task are simply the kinematic equations that link joint configurations to center-of-mass or head position.

The null hypothesis is that variance in all directions of joint space is equal. The UCM hypothesis is that variance is larger in those directions in joint space in which a hypothesized task variable is invariant. That is the null space of the corresponding Jacobian. For the sit-to-stand data, the UCM hypothesis was confirmed in a set of separate tests of different task variables. These included the horizontal and the vertical spatial position of the center of mass, as well as the horizontal and vertical spatial position of the head.

In this first UCM analysis of variance we made a conceptual mistake: We used segment angles (angles of individual body segments relative to the gravitational vertical) to characterize each joint. Segment angles are not independent of each other. Leaning

forward by flexing the ankle, for instance, changes all other segment angles even if the joints themselves remain perfectly invariant. Because segment angles trivially co-vary, UCM effects could potentially being uninformative. I cannot recall how we came to make that mistake. We discovered this soon (but only after publication) as we moved to three-dimensional configurations in which segment angles are not practical. We then re-did our earlier analysis using joint angles and found identical results. Segment and joint angles are related by a linear transformation with determinant one that does not necessarily keep distances between joint configurations invariants. In practice, the variation is small, however. The problem of using segment angles becomes much more of an issue when one is looking at pairwise correlations between segment vs between joint angles [19,20].

Only years later we returned to the even simpler whole-body task of upright stance [21]. The UCM analysis of variance used data from Fay Horak's lab. To our amazement, these data revealed a very clear UCM effect! All joints had similar amounts of variance. The ankle did not stand out. And most of the variance was in directions in joint space that kept the body's position in space invariant. The "inverted pendulum" hypothesis needed to be reassessed (see below).

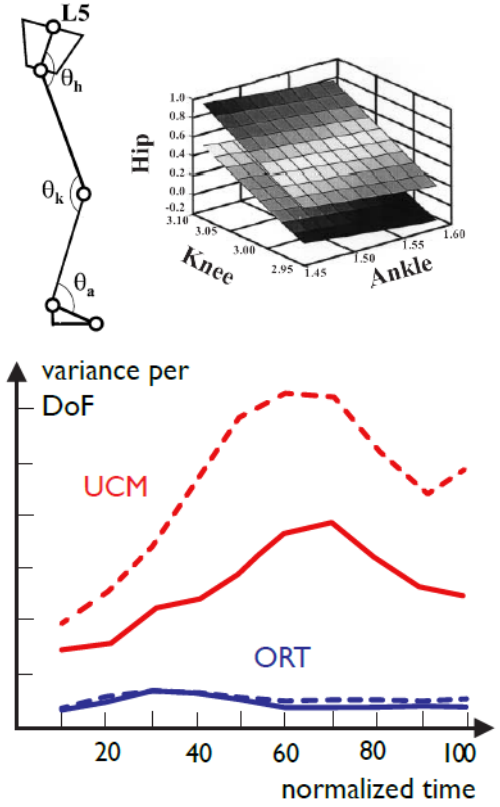

Figure 2. This illustrates the UCM analysis of the sit-to-stand transition from the paper Scholz, Reisman, Schöner [18] in which we actually used joint rather than segment angles. Top left: Only three joints were used in this study. Top right: The UCM null spaces for different horizontal positions of L5 (a point on the pelvis) form planes within which the ankle, knee, and hip joint may co-vary leaving the L5 horizontal position invariant. Bottom: The variance per degree of freedom within the UCM (top two lines) and orthogonal to the UCM (bottom two lines). Solid line: normal support; dashed lines: narrow support. Note how narrow support amplified the UCM, but not the ORT variance.

THE UCM IN THREE DIMENSIONS

John Scholz spent the second half of his sabbatical in Mark Latash's lab at PennState. There they elaborated a shooting task that would end up showing a UCM effect for a naturalistic 3D movement of the arm [22]. Again, the simpler task, pointing the finger at an object in 3D was done only after this more complex task [23]. We initially thought that UCM structure of variance in regular pointing could be considered trivial: If the task is to bring the fingertip to touch a specific point in 3D, then variance affecting that position would have to be low. In that later pointing experiment we removed the potential for such an external constraint on variance by having participants pointing into the center of a ring, so that the finger would not rest on a support surface in the final position. We found strong UCM effects not only near that final postural state, but well before the finger had reached the ring.

Shooting did not seem to have the same potential problem, as there is no contact on shooting. One could think of shooting as pointing with a pointer of variable length. Controlling the laser pointers many of us used in the past (or still today?) when giving presentations is a form of shooting. There are only two task variables: Given a particular location of the gun in space, two angles control its orientation such that it points at the target. The third orientation angle that controls rotation around the long axis of the gun does not matter.

In the study, participants moved a laser gun from their lap to a shooting position and pulled the trigger in one smooth motion, emulating something like "shooting from the hip" (Figure 3). We wanted to avoid a separate postural task in which participants would point the gun and then stabilize its aim by using visual corrections. During the shooting movement, participants could use the seven degrees of freedom of the arm (scapular motion was minimized by constraining the shoulder's position in space). These joint angles needed to be estimated in a way that correctly takes into account anatomical constraints so that these do not induce spurious structure into the variance data. "Stick-figure" estimates, for instance, would not work. At the time, these estimation techniques were not yet standard, so we invested into developing algorithms for that. Formalizing the kinematic model of shooting was also not entirely trivial.

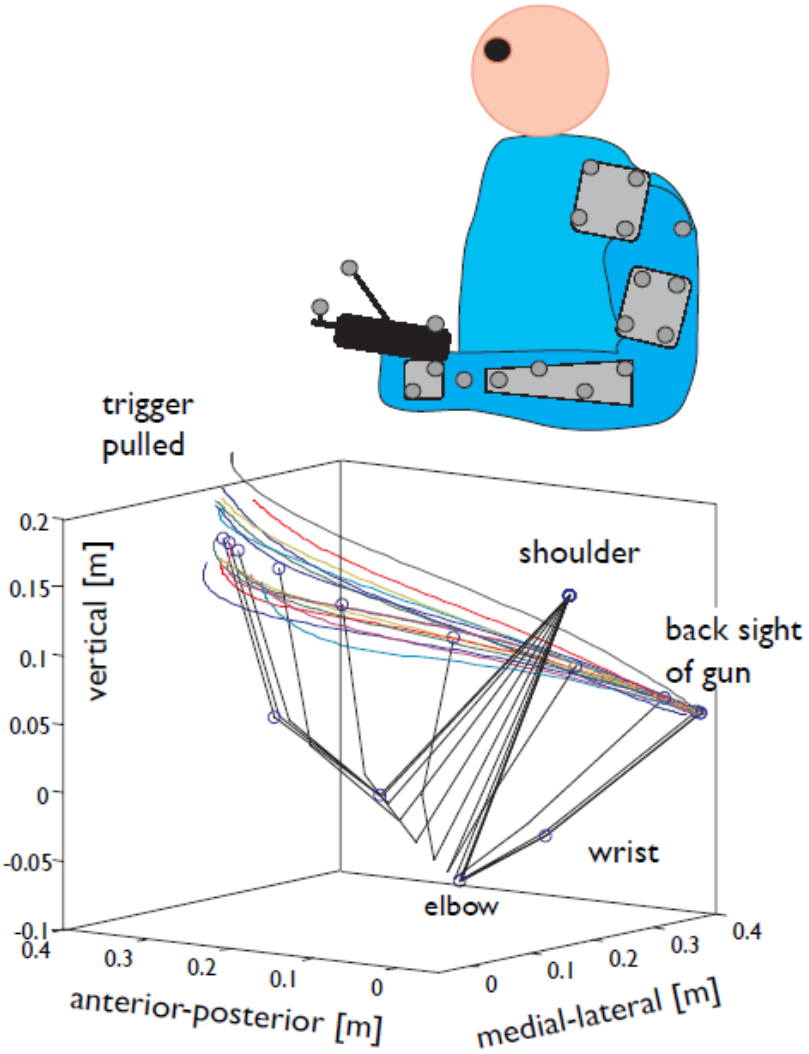

Figure 3. In the shooting study (Scholz, Schöner, Latash) [22], participants were free to use their arms with all seven degrees of freedom (top), while the shoulder remained approximately fixed in space. The laser gun was attached to the hand and carried markers that enabled us to compute its 3D orientation. Bottom: A view of key landmarks on the arm over time. You are looking at the arm from the back transparently through the body, with the shoulder closest to the viewer. The initial position is on the right, the final position in which the trigger is pulled is on the top left. The differently colored lines are trajectories of the back sight of the gun in different trials. Note how the shooting occurs from different final spatial positions of the gun.

I used the product of exponentials formalism to address both tasks because I found that approach mathematically elegant and easy to link to data [24]. This method has not become mainstream in human motor control, although some roboticists use it. I first simplified the upper arm by assuming that the rotation axis of the elbow joint is orthogonal to the extended arm. This made all the rotation matrices much simpler and facilitated the analytical inversion of the kinematic equations that is needed to estimate the joint angles. The computations filled a good 100 handwritten pages and were then transformed into Matlab code to analyze the data. After all was done and we had obtained outstanding UCM results, John Scholz, in his inimitable drive for precision, insisted that I correct the model to account for the actual orientation of the rotation axis of the elbow joint that slightly deviates from orthogonal. All equations got a lot more complicated, many more pages of formulas, more equations typed into Matlab. The results were pretty much the same! This drove home

a lesson, obvious in hindsight: The UCM analysis of variance is a very qualitative analysis: It simply says that there is more variance in the many directions in joint space in which the few task variables do not vary. Here, the UCM was a five-dimensional space, the ORT space was two-dimensional. When the UCM space is slightly rotated within the original seven-dimensional space, its alignment with the cloud of data points from different trials does not change much.

We obtained beautiful UCM signatures for the two orientation angles of the gun that are critical to the task. The UCM structure of variance was observed not only at the end of the movement, when the trigger is pulled, but throughout the movement of "drawing" the gun (Figure 4). By contrast, the spatial position of the gun as the task variable led to a UCM effect only early during the movement, but not close to point at which the trigger is pulled. In fact, the spatial position of the gun at the moment of shooting varied considerably across trials (see final position marked "trigger pulled" in Figure 3). The gun's orientation was adjusted to point toward the target from whatever final spatial position the gun achieved. This contrasts with the clear UCM signatures we later found throughout the movement when the task was to point the fingertip at a target position in 3D [23].

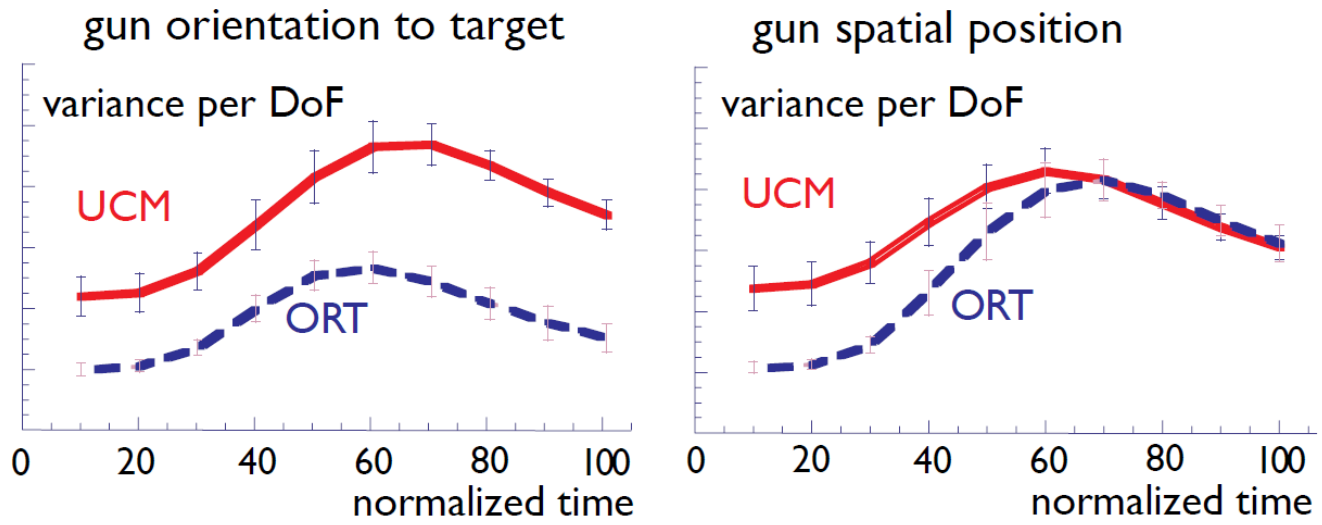

Figure 4. Results of the UCM analysis of the shooting study. Both panels show variance per degree of freedom as a function of normalized time within the UCM (solid red) and orthogonal to the UCM (dashed blue). Left: Hypothesis gun orientation to the target. Right: Hypothesis gun spatial position.

TWO STRANDS OF UCM THINKING

Since those early days, the UCM method of analysis has been used in many different tasks, for different effector systems, and with different hypotheses. The broad uptake of the method was probably driven, in part, by a need for methods to analyze the high-dimensional movement data that have become common as naturalistic motor behaviors are brought into the laboratory. Very often, clear UCM effects were observed, so that the UCM analysis helped uncover structure in such data. In this literature, the UCM hypothesis has been developed, broadly speaking, in two different strands or flavors (see also review by Latash [25]).

The first is based on the specific notion that movement tasks are about spatially positioning and orienting some part of the body in a particular way to reach, shoot, stand, walk, etc. This strand is close to the original motivation of understanding how infants learn to reach to objects. How does the brain generate signals that bring about a desired movement? Much convergent evidence suggests that the brain, certainly parietal cortex and perhaps pre-motor cortex, represents movement targets and movement parameters in spatial terms [26]. The transformation into neural activation signals that drive muscles and spinal reflex loops take place in motor cortex and its projections to the spinal cord [27]. The UCM structure of variance may be a signature of this transformation (see below).

In this specific flavor of the UCM, learning to reach is about tuning these neural networks. The UCM signature reflects the very fact that this projection has been successfully learned. It has turned out to be quite difficult, however, to observe this learning process. John Scholz and I tried at one point to get adult participants to learn a "new" UCM by having them move the cursor on a computer screen with a new combination of four joint angles of the planar upper arm (wrist, elbow, shoulder, scapula). These combinations were qualitatively different from the combinations that move the fingertip in real space. Some joints would, for instance, move the cursor in the opposite direction to how they move the fingertip. Engaged in two hours daily of intensive training for five days, participants never learned to move the cursor in a fluid way. This negative result, which as such things typically go, we did not publish, confirmed again that one cannot just "impose" an arbitrary task on the arm. Learning to move the arm in space is probably a developmental process in infancy that is deeply engrained in the brain's networks.

The other flavor of UCM thinking is more abstract, based on the general notion of task and elemental variables that are tied together to achieve a task. The finger force production tasks performed by Mark Latash's team are examples of this. Fingers can be used

individually in flexible ways as witnessed by piano players. In Mark's studies, elemental variables were sometimes conceived as "modes" of finger co-activation that were determined by finding an orthonormal basis of finger force vectors when participants tried to generate forces with individual fingers while all fingers were in contact with touch sensors [28]. That fingers can be organized in different such collective tasks has been demonstrated in Mark's lab in many different ways. Variance may be structured, for instance, consistent with control of the total force generated by the fingers as well as with control of the moment that the fingers jointly generate in an isometric task [29]. Such structure makes sense for grasping, for handling objects, and perhaps for compliant tasks [30]. These finger tasks can be learned and the structure the UCM structure of variance changes during learning in complex ways [31].

In recent work, Mark's lab has used UCM ideas at a more abstract level. For instance, different combinations of the "r" and "c" command of Equilibrium Point Theory are consistent with any given isometric force production task. The "r" command reflects how opposing muscles settle on an Equilibrium Level of force, while the "c" command reflects the level of co-contraction that varies the effective stiffness of the joint posture. They showed that variance in the "r-c" space that kept the force invariant was larger than variance that affected the force produced [32,33].

Hermann Müller and Dagmar Sternad have used an abstract notion of a UCM to account for timing [34]. In their "skittle" task, participants must choose particular combinations of release velocity and position of the skittle in order for the skittle to hit the target. They established that after learning, participants displayed more variance in a direction of release velocity/position space that is consistent with hitting the target than in the orthogonal direction. We had a debate, some of it public, about the validity of this abstract analogy to UCM around the question if one can legitimately use metrics to determine such differences in a space in which the different axes that span the space have different units of measurement (e.g. degrees per second vs. degrees). The task can also be analyzed by plain correlation between the two variables, so the point may be moot.

The difference between these two strands of UCM thinking becomes more relevant, perhaps, when trying to develop theoretical accounts for the UCM.

THEORY

The abstract strand of UCM thinking may resonate with an abstract, computation account that is based on optimal feedback control (OFC) [35]. In OFC, a feedback control system is determined that moves a set of task variables to a target state. The control law is determined by minimizing the distance of the task variables from the target state together with some regularization factors that typically minimize the control signals. The key idea is that different time courses of the elemental variables of the system may realize the task level performance. The differences between these different solutions may lie in something like an UCM, although the UCM structure of variance has not been formally studied in this work.

This approach has become quite popular, largely because it links to interesting issues like online updating and transcortical feedback [36,37]. So despite its abstract computational nature, OFC is being proposed as a language for understanding the neurophysiology of movement. We will come back to these issues below.

One limitation of the OFC perspective is that it eliminates the control theoretic notion of a desired trajectory. That makes it difficult for this approach to recognize that time courses of movements may be coordinated across effector system [38,39] or with perceived timing constraints such as when we catch a ball [40]. These forms of coordination are plausibly achieved at the level of task variables, e.g. hand-position in space [41], consistent with what we know about cortical representations of timing (for review see [42]).

What would a less abstract, more thoroughly neural account for the UCM structure of variance look like? We have developed a neural processes account of the UCM [43,44] which I will briefly review here. This was the topic of Valère Martin's brilliant doctoral thesis, which he finished in 2005. It took me 5 years to finally write it up and published the first set of results in the 2009 paper, and another 10 (!) years to write up the second set of results in the 2019 paper. All my fault, with only the limited excuse that it was a complex set of theoretical results to work though.

There are three kinds of dynamic processes in this account (Figure 5).

(1) Timing is generated at the level of the end-effector in the form of stable limit cycles that could be realized by neural oscillators [39]. A discrete movement is simply a single cycle of such an oscillator, which is de-activated along the way in a dynamic instability [45]. The timing signal thus starts out from the resting state, generates a time course, and then ends at the initial state. This is what I will call a "movement signal" below.

(2) Such timing signals are distributed to the muscles and spinal reflexes through a recurrent dynamical system that also integrates the timing signal, so that in addition to a movement signal it also contains a postural component that shifts from an initial state to the final state. We called this the "neural dynamics", even though the equations do not respect all constraints of neural networks (e.g. activation can change sign).

(3) The output of the recurrent neural dynamics couples into a model of the spinal stretch reflex as a time varying reflex threshold that can be interpreted as virtual muscle lengths, ("lambda" in Equilibrium Point jargon), beyond which the stretch reflex engages. Together with the reflex contribution, these descending signals drive muscle force generation and then the biomechanical dynamics of the limb.

This process model generates actual time courses of the movement signal, of the reflex threshold, of muscle activation and

forces, and ultimately, of the arms kinematics. At each of these three stages, a source of variance was modeled as "timing noise"', "neural noise"', and "muscle noise". The model was implemented for planar movement of a four-joint arm (wrist, elbow, shoulder, and scapular motion) and was compared to human movement data obtained in John Scholz's lab in which participants performed point to point movements in a plane engaging these four joints.

In the model, it is possible to study the mechanisms that cause the UCM structure of variance by turning particular sub-processes on or off (by setting relevant parameters to zero). This is how the model helped us identify two main causes of the UCM structure of variance (read the 2019 paper [44] for a more nuanced discussion).

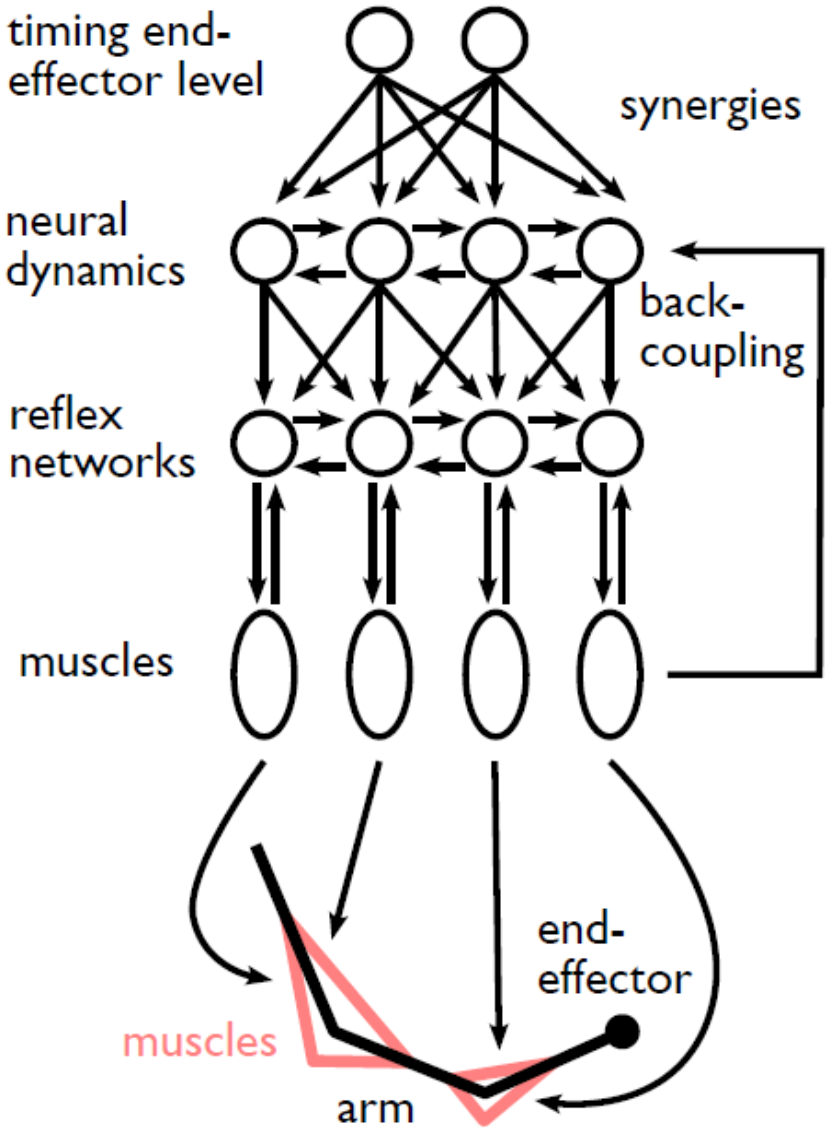

Figure 5. The Valère Martin model [43] in a schematic outline. Three stages of processing each have their own noise source. The timing level generates time courses of virtual end-effector trajectories. A few-to-many forward projections onto a neural dynamics implements classical synergies. The neural dynamics is subject to neural noise and integrates the timing signals into virtual joint trajectories. These project as thresholds onto the reflex layer. Only the stretch reflex was mathematically modeled. The output of the reflex layer is muscle activation, which generates muscle forces according to a model of the muscle dynamics and subject to muscle noise. Deviations of the sensed from the virtual joint configuration are coupled back into the neural dynamics so that the virtual joint trajectory yields to these differences within the UCM. The muscle forces drive the mechanical dynamics of the arm.

First, the recurrent connectivity was assumed to couple the different degrees of freedom such as to stabilize the task-variable, the hand's position in space. The coupling structure effectively decouples joint velocity vectors that move the hand in space from joint velocity vectors that do not (Figure 6). Neural noise acting equally on all components of this dynamical system is thus resisted in the directions in joint velocity space that moves the hand in space more than in directions that do not. We showed that this coupling structure is one cause of the UCM structure of variance.

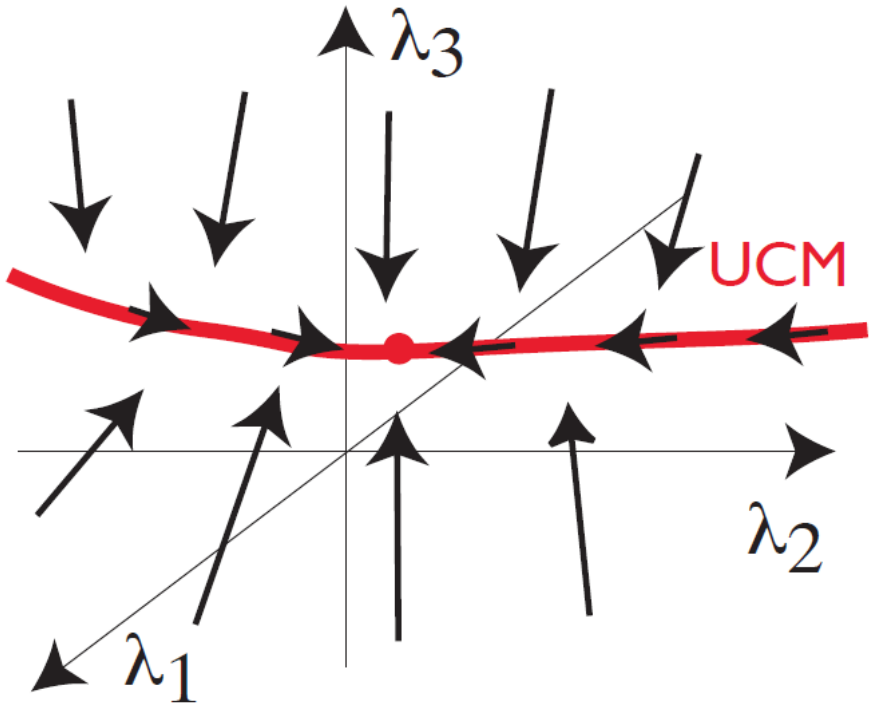

Figure 6. The coupling structure within the neural dynamics of the Valère Martin model is illustrated through a vector field for three components of the virtual joint vector (lambda 1 to 3). These vectors indicate the virtual joint velocity. The UCM leaves the end-effector position invariant (solid red line). During movement, the UCM shifts under the influence of the timing signal. A strong component of the vector-field orthogonal to the UCM keeps the virtual joint vector on or near the manifold. Within the UCM, the vector-field is much weaker, so that the virtual joint configuration is only weakly constrained within the UCM. This leads to movement along the UCM (self-motion [43]) as well as to larger variability within the UCM under the influence of neural noise [44].

Second, when muscle noise leads to variable joint torques, the movement of individual joints do not follow the virtual trajectory specified by the descending neural signals. Such motor perturbations are resisted more when the stochastic deviations move the hand in space than when they do not. This is due to the specific reciprocal pattern of coupling between the reflex level and the neural dynamics. The neural dynamics specifies an attractor state of the downstream reflex-muscle-mechanical dynamics. Conversely, backward coupling from the reflex to the neural dynamics level induces updating of the neural state when the joints deviate from the attractor states. This "back-coupling" is the logical opposite of feedback control (Figure 5): When the plant (the reflex-muscle-mechanical dynamics) deviates from the set point, the set-point yields, reducing the deviation by moving the set-point closer to the current state. It does so only within the UCM, not orthogonal to it. This is by virtue of the same coupling structure that figures in the first source of UCM structure of variance. In fact, the orthogonal component brings about the movement of the hand in space.

In our first analysis [43], we had introduced this idea of back-coupling as it is critical to understanding motor equivalence. In motor equivalence, a phasic perturbation leads to the emergence of an alternative solution to a movement task in which the final postural state deviates within the UCM, but not (or less) orthogonally to the UCM [46]. For this to happen, there must be some way in which the neural signals that descend to the spinal cord are updated. Without such updating, the stretch reflex would servo control the joint back to the configuration that the descending neural signals specify. Mark Latash's lab has provided empirical support for various forms of back-coupling [47].

Updating through back-coupling could be viewed as a neural implementation of the property of optimal feedback control that neuroscientists find so attractive[37]. In the neural dynamic perspective, neural activation patterns that descend from the brain to the spinal cord are not fixed "movement plans". They are emergent dynamic states that can be updated any time through coupling, including back-coupling. Other forms of online updating are observed when perceptual information about movement targets changes (reviewed in [48]).

The neural dynamic model also provided insight through negative results. One strength of neural process models is that they generate actual time courses of relevant variables. One can observe, therefore, the consequences of different theoretical hypothesis as in a virtual experiment.

One such insight was that noise at the timing level does not contribute to the UCM structure of variance. Such noise plays a critical role in theories of movement coordination [49]. In dynamic accounts, coordination results when different timing systems driving different effectors are coupled [39]. Instabilities of the coordination dynamics lead to observable increases in fluctuations of timing variables such as the relative phase [49]. The source of these fluctuations is noise at the timing level.

When we varied the level of noise at the timing stage of the neural dynamic model, the UCM structure of variance remained largely invariant. This means that the UCM effect comes from neural processing that is downstream from the timing level. Motor cortex may be involved in timing [50] but also in representing different configurations of a moving limb [51]. So, this segmentation is more functional than anatomical.

A second insight came from a negative result. Early in our journey to the UCM way of thinking, we had entertained an idea that the "variance is directed into task irrelevant directions", implying that this would reduce variance in task relevant directions. The intuition was that removing control form combinations of degrees of freedom that do not affect the task would reduce control action overall. As any control action could itself be a source of perturbation, this would reduce variance of task variables as well. In the model, we were able to show that while this is a theoretical possibility, it just does not scale up to an effect of relevant size. This idea thus is misleading.

This insight was important in our ongoing reflection on what the UCM structure of variance is "good for"? In some of our papers we even talked about "good" vs. "bad" variance. We can now say that "good" variance is not good for reducing "bad" variance. Instead, it is good for enabling flexibility, that is, for providing space to accommodate additional task constraints without conflicting with the pre-existing task dimensions. Most UCM analyses of variance are done, in fact, on task variable at a time, revealing a capacity to accommodate multiple constrains within the vast UCM space of other task variables.

CLOSED LOOP

Hendrik Reimann worked in my lab for a couple of years on a range of topics. But his doctoral thesis focused on another neural dynamic model of the UCM. He finished his thesis in 2013, and it again took us some years to publish the result [52]. Hendrik also helped me to finally publish the variance portion of the Valère Martin model [44]. The difference between Hendrik's and Valère's models lies in the contribution of feedback at the level of task variables. This led us to discover a third source of the UCM structure of variance, and I will explain that briefly now.

The paradigm around which we developed this account quiet stance, standing upright. This is the simplest movement system that we failed to initially address because we thought it was unlikely it would show a UCM structure of variance (see above). We did find, however, a rather strong UCM signature when we finally did the analysis [21].

Posture is kinematically redundant: There are many joints that contribute to the upright body configuration. The data and the model were limited to one plane, the anterior-posterior dimension of sway, with six degrees of freedom in experiment and only three in the model. This redundancy is critical: Each joint offers another way in which the upright body could collapse under the influence of gravity unless actively stabilized. For the body as a whole, we have known now for a number of years that the effective stiffness at the ankle created by the muscles converging on that joint is not sufficient to counter the negative stiffness of the inverted pendulum that the upright body represents [53]. Posture is thus active movement: To remain upright, signals must be sent to the muscles converging on the relevant joints to effectively shift the equilibrium point of each joint in the direction that counters any detected body movement that could initiate a fall. It is not sufficient nor is it the case that posture is achieved by co-contracting antagonistic muscles around each joint.

This particular problem of postural control challenges an account for the observed UCM structure of variance in quiet stance in two ways. First, a model of multi-joint quiet stance must explain why the kinematic chain does not collapse under the influence of gravity. In the "inverted pendulum" models of upright stance, only the ankle is actuated, all other joints are assumed to be passively stiff enough to withstand buckling [54,55]. Postural control is then only about not falling over forwards and backwards. Feedback based on sensory estimates of the body's velocity or acceleration in space can be used to prevent that from happening. The observed UCM structure of variance already hints that this is not a good approximation. Variance is similar for all joints along the kinematic chain. Moreover, the UCM effect itself suggests that variance of joint configurations that do not move the body in space, and thus, do not move the ankle joint, is much larger than variance that does move the body and the ankle joint. So this implies that buckling, a collapse of the upright body, is a real problem.

The second challenge for multi-joint postural control is that it takes place in closed loop. The typical time scale on which postural sway occurs is revealed in spectral analysis. Data suggests that correlations in sway decay only over about 5 to 10 seconds, leaving ample time for feedback corrections based on sensory information from vision, from the vestibular system, or from foot pressure sensing [56]. This sensory information is about the body's state in space, for example, about the head's forward or backward velocity (from optic flow), or acceleration (from the otoliths), or about the center-of-pressure (from foot sensors). That sensory information is thus at the level of task variables, not at the level of the joints or muscles, the elemental variables. In Valère Martin model, the reaching movements are assumed to take place in open loop at the task level, a good approximation for pointing movements. We did not address updating movement generation based on feedback about the hand's trajectory in space. All other feedback is at the level of the elemental variables and comes from spinal reflexes or also from transcortical feedback as modeled by the neural dynamics. So the account for the UCM structure of variance in posture had to address feedback at the task level for the first time.

The first issue was resolved by modifying the neural dynamics that transforms task level to elemental level variables (Figure 7). Here, the task level is not a timing system, but a control system of the state of the body in space. The elemental variables are still the thresholds of the stretch reflexes for muscles converging on individual joints. In Valère Martin's model, the neural dynamics linking these levels was structured by the kinematics of the kinematic chain, making use of Jacobians, their pseudo-inverses, and the projections into

the associated null and range spaces. In the modified model for postural control, we found we needed to include kinetic constraints. The ankle joint encounters a much larger inertial moment, the whole body, than joints higher up in the kinematic chain do. We proposed a neural dynamics structured not only by kinematics, but also by the inertial tensor, so that joints facing large inertial moments like the ankle are driven with higher gains than joints higher up in the kinematic chain. Systematically exploring such kinetic constraints, we were able to prevent the upright body from collapsing under gravity. This was, in a way, a first and significant result. It is not easy to stabilize upright stance if the muscles are modeled realistically, reflecting the relatively low effective stiffness of the joints.

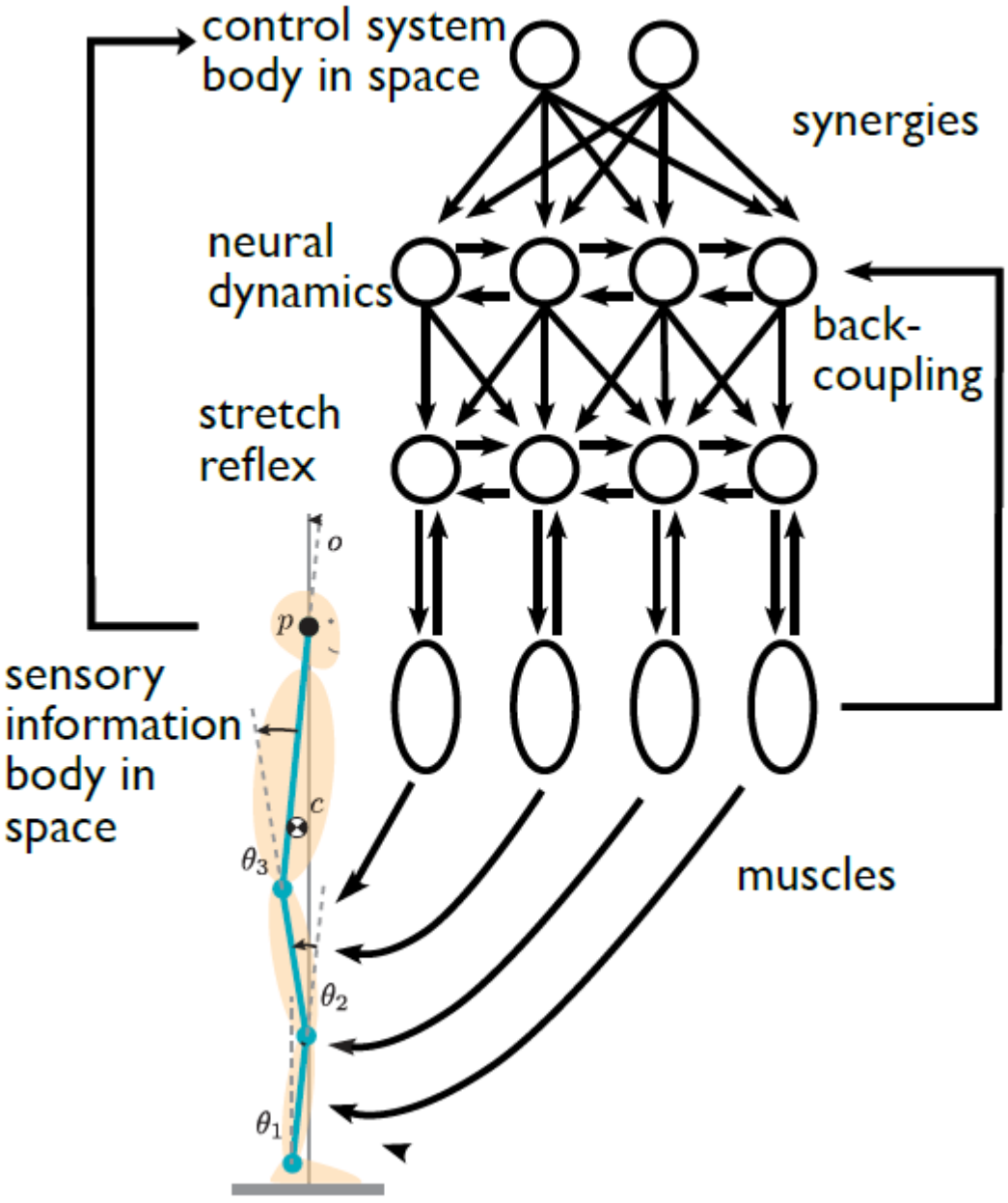

Figure 7. The Hendrik Reimann model [52] is illustrated in a schematic outline. Compared to the Valère Martin model (Figure 5), the timing signal is now replaced by control signals at the level of the body's state in space, driven by sensory information about that state (visual, vestibular, foot pressure sense). The neural dynamics takes into account the inverse inertial tensor.

The second issue was easier to address. The same kind of feedback used in previous models that were framed in the inverted pendulum picture [54,55] could be used to establish a task level control law that generates desired body accelerations and velocities on the basis of sensory information. The neural dynamics transforms these low-dimensional signals into signals to the reflex circuits controlling muscles at each joint. The emergent muscle activation drives the dynamics of muscle force generation and the biomechanical mechanics. This controls the body's state in space, which is again picked up by the modeled sensory systems.

This account contains the same two sources of UCM structure of variance as Valère Martin's model: First, in response to neural noise, the coupling structure in the neural dynamics stabilizes virtual joint configurations that affect the body's state in space more than virtual joint configurations that do not. Second, in response to muscle noise, the virtual joint configurations that do not affect the body's state in space yield to deviations of the realized joint configurations as a result of back-coupling. The latter was critical to understanding how new postural configurations arise after a phasic external perturbation of the postural state, a form of motor equivalence [57].

The Reimann model identifies, however, a third and new source of the UCM signature of variance. This is the outer feedback loop at the level of the task variables, the body's state in space. To understand this intuitively, assume, for instance, that as a result of either muscle or neural noise, the ankle flexors generate more force at one particular point in time than they would do on average. This would lead to a forward acceleration of the body that would be picked up by the sensors of the body's state in space. As a result, the control system at the level of body in space would generate a signal that would drive the body backwards. This signal is distributed to all joints by the neural dynamics, leading, for instance, to extensor muscles in the hip to fire a little bit more than they would usually do. In effect, this outer reflex loop induces co-variation across the degrees of freedom compensating for the original perturbation so as to keep the body state in space stable.

OUTLOOK

The UCM method of analysis for variance has been a great success empirically as it provided a way to discover meaningful patterns within high-dimensional and often complex sets of movement data. Because it is based on hypotheses about task variables, it does not require as much statistical power as purely explorative correlational approaches. The UCM method of analysis make the long-standing Bernsteinian intuition operational. In that tradition, learning to move means learning to "harness" the degrees of freedom so that they achieve a task.

The other form in which this intuition has been pursued lies in the notion of the (classical) synergy. There are many ways, synergies have been characterized [58,59]. The common denominator is certainly the idea that muscles covary in time during a movement or as movement direction is varied and that this covariation reflects "synergies". Such synergies are thought of as being caused by shared input to these muscle groups from the brain.

The neural dynamic models I reviewed contain such a shared component: the forward component of the neural dynamics effectively provides a few-to-many projections from the timing or control stage to the reflex stage (Figures 5 and 7). In effect, the space locally orthogonal to the UCM is the direction in which time courses are generated and thus, captures the co-variation that synergies are about. Much more can be said and analyzed about this issue, but I would want to leave that for another day.

The neural process analysis of the UCM has been taken up much less than the method of analysis and the empirical results it led to. Mostly, I think, this is because the theory is a bit difficult to understand. Also, using these ideas to propose or analyze new experiments is hard. The theory work provides, however, useful ways to interpret UCM effects at a process level.

We are currently developing an integrative framework that makes these neural dynamics more "neural" in that it would consistently respect principles of neural networks, and would also link to a neural dynamic account for target perception and selection, movement initiation, and movement updating (see [48,42] for first sketches).

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