Bernstein's "Desired Future" and Physics of Human Movement

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Abstract. Bernstein's concept of "desired future" has been recently developed within two approaches to the neural control of movement. Within the computational approach, this concept led to the ideas of predictive (direct) internal models. Within the physical approach, based on the referent configuration hypothesis and uncontrolled manifold hypothesis, this concept is reflected in two types of anticipatory motor phenomena, leading to net changes in task-specific performance variables and leading to changes in their stability. Typical examples are anticipatory postural adjustments and anticipatory synergy adjustments respectively. Both may be seen as reflections of neural processes aimed at achieving a future state effectively given the external conditions and planned actions.

Keywords: N.A. Bernstein, Desired future, Synergy, Referent configuration, Uncontrolled manifold, Anticipatory postural adjustments, Anticipatory synergy adjustments

It is common knowledge that animals behave in a predictive fashion. For example, when you throw a ball to a dog, the dog runs not to the current location of the ball on its flight trajectory but to the point of its expected fall. Interceptive actions are typical of many predators who direct their attack at a point in space where the quickly moving prey is expected to be, not where it is at the moment. To summarize, before an action is initiated, there is always a combination of desired future body location and configuration that drives the action. In that sense, all actions are initiated in a feed-forward fashion, even if they are driven by an external stimulus.

1 Elements of History

Much of Bernstein's thinking about the control of natural actions was developed in the Soviet Union dominated by ideas of I.P. Pavlov and his school, accepted as the only view officially endorsed by the Communist Party. In the nineteen-thirties, Bernstein's disagreement with Pavlov's views were tolerated by the authorities, and Bernstein even managed to write a book "Contemporary Studies on the Physiology of the Neural Process" with a strong critical analysis of Pavlov's theory. Although the book had been written in the mid-thirties, it was published only about 70 years later [1]. The delay in the publication was related to the fact that Pavlov had died a few months before the book was to be released. Bernstein thought that it would be unfair to argue with a person who cannot respond, and he stopped the publication process. Later, however, after the World War II, Bernstein's opposition to Pavlov's views was the main factor resulting in his forced early retirement.

While Bernstein did not officially hold any position after being fired in the early nineteen-fifties, he continued to work at home, in particular with a few of his younger colleagues and students including Josef Feigenberg, Philip Bassin, and Lev Latash. During those years, the main postulates of Bernstein's physiology of activity were formulated. In particular, Bernstein introduced the notion of *desired future* as a major factor that drives animal action [2,3]. The idea that an action is driven by a desired future state was in stark contrast to the alternative that followed the traditions set by Pavlov that all actions were reflex responses to stimuli, either inborn or conditioned. Using contemporary terminology, one can say that desired future body location and configuration were assumed to work as attractors for the actual body location and configuration. Later, a student of Bernstein, Josef Feigenberg, developed the notion of *desired future* into a *model of the future* [4,5]. This line of thinking has been recently continued and developed within two approaches to the neural control of movement that currently dominate the field. The two approaches can be addressed as *computational* and *physical*. The main purpose of this paper is to provide a brief overview of some of the recent developments in this field, with an emphasis on the latter approach.

2 Two Approaches to the Neural Control of Action

The two approaches in the field of the neural control of biological movement offer different views on the origins of anticipation seen in motor behavior (and other areas). One of the approaches assumes that the central nervous system (CNS) models or otherwise emulates the interactions between body parts and between the body and the environment using *internal models*. Two types of internal models are assumed to exist. Inverse models pre-compute neural signals from brain structures that would lead to a desired mechanical effect, for example moving the tip of the index finger from a given initial position to a target position. The term *inverse* implies that the model uses output variables to compute neural variables that, during the actual course of movement production, have to be generated before the output variables change. So, inverse models address *effect-cause transformations*. On the other hand, direct models emulate processes from the generation of neural signals by brain structures to the production of mechanical variables, i.e., *cause-effect transformations*. They are used to predict changes in the body structures and their interactions with the environment. Such predictions are crucial, in particular, because of the unavoidable time delays both in the transmission of sensory information and in the generation of motor effects caused by efferent neural signals.

While the internal models' approach has been successful in interpreting a body of data, in particular during adaptation to unusual force fields (reviewed in [6]), there are several problems with this approach. One of those problems is the underlying assumption of neural computation, which is equivalent to giving up any attempts at understanding the laws of nature involved in the production of movements. It is similar, for example, to assuming that some smart structures on the Sun pre-compute forces that have to be produced on planets and then send signals to actuators that move the planets. If such an approach were accepted in physics, the law of gravity would have never been discovered. Other drawbacks of the computational approach are multiple *problems of motor redundancy* inherent to computations within inverse models. For example, the task is commonly formulated in a relatively low-dimensional space. To implement the task, however, multiple joints have to be involved, even more muscles, many more neurons, and an astronomical number of synaptic connections. In addition, some of these problems involve threshold elements (neurons), for which it is in principle impossible to compute an input based on a desired output. For example, it is impossible to compute a force necessary to exert on a toggle switch to turn on light in a room. The force only has to be above a certain threshold, but its actual magnitude cannot be predicted without making additional, commonly arbitrary, assumptions.

The alternative approach views the human body, including the central nervous system, as a physical system, not a computational one. Its goal is to discover laws of nature that drive physical (including physiological) processes within the body (for reviews see [7-9]). Recent progress within this field allows accounting for a variety of phenomena, including those of anticipation, without resolving to the computational metaphor. One has to start, however, with a disclaimer: While the progress in this field has been substantial, it is far from offering an approach to all aspects of anticipation that would be supported by experiments and the current knowledge of neurophysiology. In particular, anticipation at the level of cognition remains largely mysterious, although the recent development of the neural field theory [10,11] offers promise in addressing issues of psychology, for which neurophysiology and physics are all but unknown.

The physical approach follows Bernstein's traditions formulated, in particular, in his classical paper published in 1935 [12] on the relations between coordination and localization within the central nervous system. In that paper, Bernstein introduced the notion of *engrams* as precursors of movements stored in memory. Engrams were assumed to reflect topology of planned movements, not their metrics. So, they were not supposed to reflect forces, muscle activations, and other peripheral variables that change with both metrical and topological features of movements. Later developments of this idea in the form of the generalized motor program [13] and, more recently, internal models (reviewed in [14]), linked hypothetical neural variables stored in the brain to patterns of joint torques, muscle forces, and muscle activations. The physical approach on the other hand views these peripheral patterns as emergent features of neural control signals (e.g., based on engrams) and the unpredictable external force field.

While the physical approach does not accept the idea of computations performed by the brain, it certainly uses computational methods of analysis, just like other, better developed, chapters of physics of inanimate matter. As stated by the great mathematician Israel Gelfand [15,16], the challenge of this approach is not in applying mathematical methods developed for problems of classical physics to biological problems but in developing new, biological chapters of mathematics. This direction of thinking has resulted in a paradigm shift that leaves behind attempts at solving complex problems of movement mechanics with presumed neural computations and sensory-based feedback loops. The physical approach tries to unite the neural and mechanical processes making the interaction between the neural and mechanical worlds seamless, without the need to use one of the worlds (the central nervous system) to solve problems of the other (complex mechanical interactions). To achieve this, neurophysiology and mechanics have to be coupled by physical processes that naturally translate the language of millivolts into the language meters. The following section will try to summarize specific aspects of the physical approach, its methodology, and some of the recent results.

3 Physics of Human Movement

The physical account for the neural control of movements is based on several central ideas. The first is using threshold elements (neurons) to ensure adaptive motor behavior. Note that a suprathreshold activation of a neuron forces it to generate an action potential (or a sequence of action potentials) independently of any other input that the neuron may receive. A subthreshold input, however, makes the frequency of firing of the neuron a function of other inputs, in particular those provided by length-sensitive receptors in the muscle the neuron innervates (sensory endings in muscle spindles). This is illustrated in Figure 1A, where it is assumed that the reflex input provides a relatively slow depolarization of the neuronal membrane at a constant rate. Changing the level of subthreshold depolarization effectively modifies the muscle length, at which the neuron starts to generate action potentials (Figure 1B). As a result, the adequate units of neuronal interaction (millivolts) are transformed into adequate units of action (meters).

Second, in line with the previous paragraph, a brain-generated input into a pool of alpha-motoneurons may be associated with a value of the muscle length, at which it starts generating active resistance during very slow stretch – the threshold of the tonic stretch reflex for the muscle [17]. If muscle movement is unopposed, the muscle contracts until its length is equal to the threshold value. If the muscle acts against a load, it contracts until its force balances the external force. The combination of magnitudes of muscle length and force where it comes to an equilibrium given the external load is referred to as the *equilibrium point* of the system (Figure 2). Hence, the original hypothesis on the neural control of a muscle with changes in the tonic stretch reflex threshold was termed the equilibrium-point hypothesis [17,18].

Third, this general idea can readily be generalized to multi-muscle actions. Within this generalization, neural control can be adequately described as a subthreshold input into some neuronal pool, which results in setting referent values for a spatial variable produced by a group of muscles that define a *referent body configuration* (conceptually equivalent to the tonic stretch reflex threshold for a single muscle) [19]. The same neurons receive signals proportional to the deviation of the actual values of this variable and its referent value. This feedback loop drives the actual variable value towards the referent one and, if this action is opposed by external forces, results in an equilibrium state characterized by non-zero forces produced on the environment.

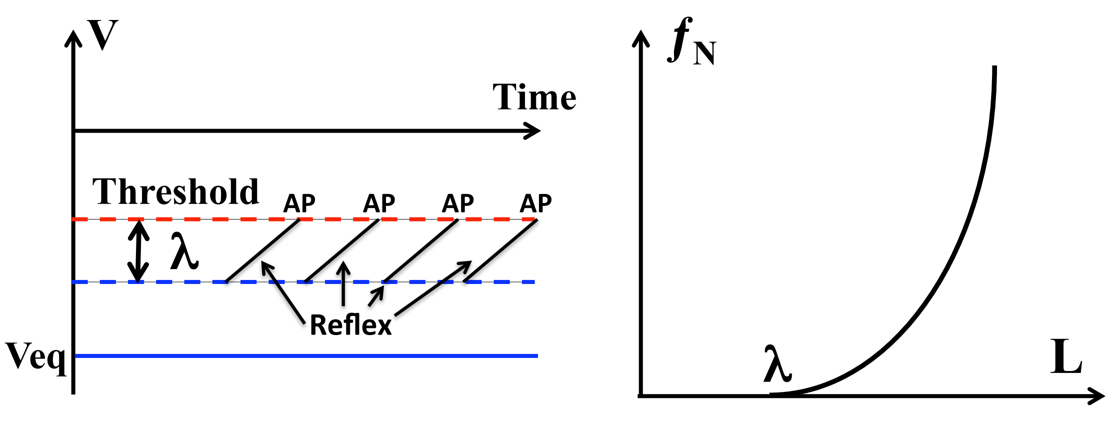

Fig. 1. A: Changes in the potential on a neuronal membrane (V) produced by two inputs, a descending signal leading to subthreshold depolarization (l) and a reflex input leading to a ramp depolarization. When the potential reaches the threshold, action potentials (AP) are

generated. B: The dependence of the frequency of firing (f_N) of a neuron (or a neuronal pool) on muscle length (L). Note that the descending signal (l) defines the muscle length, at which action potential generation starts.

Fourth, no movement is produced by only one muscle. The fact that movement control does not imply specifying contributions of individual muscles was already recognized in the nineteenth century. Hughlings Jackson wrote in 1889: “The brain knows nothing about muscles. It knows only movements” [20]. This view later led to the idea of a hierarchical control of natural actions with a sequence of few-to-many (redundant) transformations. At the upper level of the hierarchy, control may be associated with setting referent values for a handful of task-specific variables. Further, this relatively low-dimensional input is distributed over higher-dimensional sets of variables ultimately leading to a large number of inputs into the alpha-motoneuronal pools innervating the many muscles involved in any natural action.

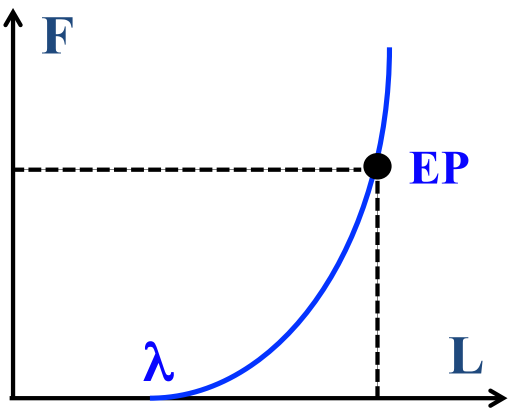

Fig. 2. A dependence of active muscle force (F) on muscle length (L) for a given value of the threshold of the tonic stretch reflex (l). When muscle force balances the external load, the system is at an equilibrium point (EP) characterized by a combination of muscle force and length values.

4 Problems of Redundancy and Solutions of Abundance

There is a major difference in treating the problems of motor redundancy between the traditional approach based on the famous Bernstein formulation “the elimination of redundant degrees-of-freedom” [21] and a more recent approach that considers the apparently redundant design of the human body as bliss of abundance [22,23]. The former approach tries to find a single, possibly optimal, solution for each and every problem of motor redundancy. The latter approach assumes that the neural controller facilitates families of solutions equally able to solve such problems, and selection of specific patterns realized in each particular action is driven by unpredictable factors such as variation in the internal states of the body and in external forces. This approach is intimately linked to the concept of task-specific stability [24]. According to this concept, individual degrees-of-freedom (DOFs) within a redundant set are organized to ensure stability of a particular performance variable, to which all the DOFs contribute. Such neural organizations have been addressed as synergies stabilizing specific performance variables (reviewed in [25]).

This organization is reflected in a number of experimentally observable signatures. In particular, a sequence of trials at a task shows larger variance in directions that do not change potentially important performance variables (spanning *uncontrolled manifolds*, UCMs, for those variables, [26]) as compared to variance in directions that change these variables (reviewed in [27]). Reactions to small perturbations involve large deviations of DOFs that result in no changes in task-specific performance variables [28]. Overall, the neural organizations providing for such synergic behaviors (e.g., as in models by [29,30]) lead to low stability within the corresponding UCMs as compared to directions orthogonal to the UCMs.

The ideas of control with referent configurations and synergic few-to-many mappings have been united recently into a single scheme (Figure 3). Within this scheme, synergies emerge as results of back-coupling between the levels in the assumed hierarchy (cf. [29,30]). Note that this is not the only way synergies may emerge. For example the feedback loop linking the performance with the top level of the hierarchy in Figure 3 may play a major role in ensuring that any variance accumulated during the intermediate steps of neural signal transmission and processing in the scheme is channeled primarily into the UCM for the variable(s) encoded in the referent configuration at the highest hierarchical level (Task in Figure 3). This loop may use any relevant sensory signals, for example visual information on success in task execution.

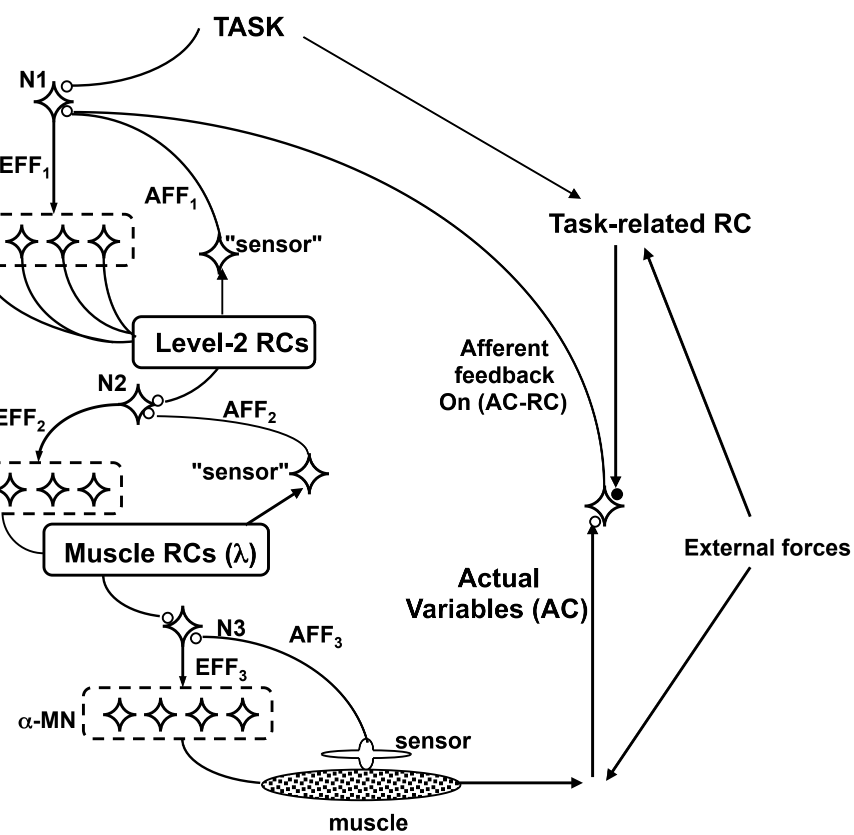

Fig. 3. A scheme uniting the ideas of control with referent configurations and synergic few-to-many mappings. Note that the task-specific input (TASK) defines a referent configuration (RC) at the task level. Referent values at lower levels emerge as consequences of a chain of few-to-many mappings organized in a synergic way with the help of back-coupling loops based on relevant afferent feedback (AFF) and efferent feed-forward (EFF). The overall feedback loop on the difference between the actual and referent values of task-specific variables provides excitation proportional to the difference between the actual and referent configurations at the task level, (AC–RC). N – neuron, MN – motoneuron.

5 Anticipatory Motor Adjustments: Producing Desired Net Mechanical Effects

Anticipation plays a major role in the generation of meaningful movements. Within this brief review, I would like to focus on two major groups of anticipatory phenomena. The first involves the production of net mechanical effects, such as muscle forces, joint torques, displacements, etc. in anticipation of an event in future that makes these mechanical effects beneficial for success in the planned or ongoing action. The second group involves anticipatory changes that do not produce any net mechanical effects but modify stability of the current body state or trajectory in anticipation of a future action.

Within the first group, there are universal mechanisms of anticipation. These have been commonly studied in conditions when a predictable perturbation acts on the whole body, a limb, or a joint during a steady-state task. In many of such studies, the perturbation is a direct mechanical consequence of an action by the same person produced by the mechanical coupling of the body segments (reviewed in [31]). One of the best-known universal mechanisms of motor anticipation is arguably muscle co-contraction. Co-contraction of agonist-antagonist muscle pairs may lead to no net effect on the joint torque but it reduces kinematic effects of a perturbation by increasing the apparent stiffness of the joint (see [32] on *apparent stiffness*). This method of dealing with external perturbations is obviously suboptimal. First, it is energetically wasteful. Second, it is in principle unable to cancel out effects of a perturbation, only to attenuate its kinematic consequences. As a result, anticipatory co-contraction is more commonly seen in populations with impaired motor control such as elderly adults, persons with Down syndrome, and neurological [33,34]. It can also be seen in young healthy persons in challenging conditions, for example during tasks performed in unstable conditions.

More task-specific mechanisms involve changes in the activation levels of muscles involved in a steady-state (postural) task that are seen prior to a quick movement by the person or prior to a predictable perturbation. For example, when a standing person performs a quick arm movement, reactive forces perturb posture. Perturbations of a similar nature happen during picking up or dropping a load, pushing against a high-inertia object, etc. In such cases, changes in the activation of postural muscles are seen about 100 ms prior to the actual perturbation. These changes have been termed *anticipatory postural adjustments*, APAs [35]. Typically, APAs generate forces and moments of force acting against those expected from the perturbation. They change with the magnitude of the perturbation, magnitude of the action that triggers the perturbation, stability conditions of the postural task, and time available to generate APAs (reviewed in [36]). In particular, under typical simple reaction time conditions, APAs shift towards the time of initiation of the instructed action [37,38].

A different group of phenomena have been also addressed as APAs, although their nature and function are clearly different. These involve, for example, postural preparations to making a step or another whole-body action, which are seen 500 to 1000 ms prior to the action initiation ([39]. To avoid confusion, it is better to address adjustments from this group with a different name, e.g., early postural adjustments (EPAs) [40,41]. The purpose of these adjustments is clearly different: They adjust posture to make performance of the planned action possible or more comfortable. These adjustments are not associated with any obvious postural perturbations; if anything, they themselves produce postural perturbations. Both APAs and EPAs produce measurable net changes in mechanical variables such as, for example, shifts of the coordinate of the center of pressure (point of application of the resultant vertical force acting on the body).

Similar phenomena involving feed-forward adjustments of a steady-state component of a planned action are observed in a variety of motor tasks. A typical example is the adjustments of the grip force in preparation to a quick motion of the hand-held object (reviewed in [42]). Another typical example is the so-called waiter's reaction: When a person holds a tray on one hand and then takes a heavy object, for example a pitcher, off the tray with the other hand, the first hand shows a drop in the vertical force in anticipation of the unloading. As a result, no visible tray motion is seen.

Two interpretations have been offered for APAs seen during quick actions by a person (reviewed in [43]). One of them considers APAs as results of a process separate from the one involved in the production of the instructed action. The other one views APAs and action as separate peripheral outcomes of a single neural process. On the one hand, APAs scale with the action magnitude, even when the magnitude of perturbation associated with the action remains constant [44]. On the other hand, attempts at observing APAs without any action, for example in preparation to an impact from an external object, have been ambiguous: APAs do exist in such conditions [45] but there is commonly (or even always) an action by the person timed to the impact, even when the person is instructed not to do any action [46]. The idea of a single process involving anticipatory adjustments and the planned action is attractive because it presents an example of the so-called *strong anticipation*, not based on computation-based predictions [47].

6 Anticipatory Motor Adjustments: Adjusting Stability

While stability is clearly one of the most important features of natural actions performed in the unpredictable environment, very high stability of a variable also means that it is very hard to change it quickly. For example, all passenger airliners have a vertical tail fin that helps ensure stability in the air. The evolution, however, failed to produce a single bird with a vertical tail fin. This is likely caused by the fact that ability to show flexible and manouevreable behavior is more important for survival than being stable during flight.

Several recent studies have produced evidence for an ability of the central nervous system to adjust stability properties of an ongoing action without a change in other action characteristics [48-50]. This is reflected in changes of the variance structure across repeated trials without a change in the average across trials behavior. These phenomena have been termed *anticipatory synergy adjustments* (ASAs). ASAs have been studied during steady-state multi-digit force production in preparation to a quick change in force, during prehensile tasks in preparation to a change in the external load or torque, and during postural tasks in preparation to a quick movement or a predictable external perturbation.

ASAs represent a separate group of anticipatory phenomena. They can be seen in combination with APAs, typically ASAs are seen 200-300 ms prior to action initiation (or a perturbation), while APAs are seen 100-200 ms later [41,50]. ASAs can also be seen in preparation to action in conditions when APAs are absent. Their important feature is that ASAs destabilize relevant performance variables and prepare the body for an action in any direction involving a change in those variables. For example, if a person knows when an action will be needed but does not know the direction of that action, ASAs can be used and are indeed seen [51]. The large postural sway of a goalkeeper getting ready for a penalty shot or a tennis player getting ready for a serve by the opponent are likely reflections of ASAs. In contrast, APAs can be used only if both the timing and direction of an expected perturbation are known in advance.

The two types of anticipatory adjustments, APAs and ASAs, may be viewed as caused by changes in two types of neural variables that define time profile of referent coordinates for aspects of the action (reflected in APAs) and gains in the feedback loops in Figure 4 that lead to changes in synergy indices (reflected in ASAs). So, at a control level, two means of anticipatory neural control lead to changes in net values of mechanical variables and in their stability, respectively.

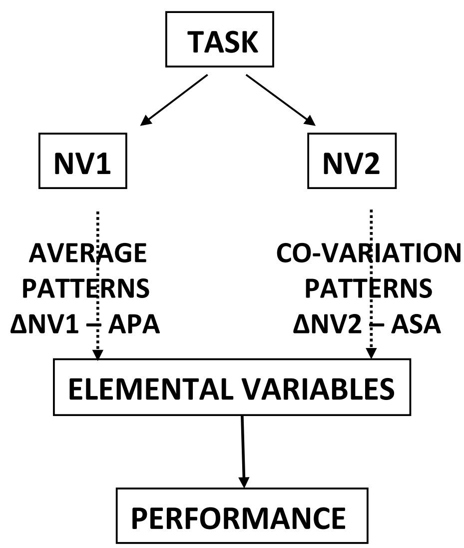

Fig. 4. Two types of neural variables that define: 1) the time profile of referent coordinates for aspects of the action that may, in particular, be reflected in APAs (NV1); and 2) the gains in the feedback loops that determine the time profiles of synergy indices, in particular reflected in ASAs (NV2).

While neural mechanisms of both APAs and ASAs remain largely unknown, there are promising observations in populations with motor impairments that point at subcortical structures and loops as crucial for establishing synergic relations and also for their feed-forward adjustments. In particular, studies of patients with Parkinson's disease and cerebellar disorders have both shown a significant drop in the index of motor synergies and an impaired ability to adjust this index in preparation to a quick action [52,53]. In contrast, patients after a mild cortical stroke show major impairments in overall motor patterns but relatively preserved structure of variance pointing at relatively unimpaired synergic mechanisms [54].

7 Back to "Desired Future"

Bernstein's concept of desired future remains central for the contemporary studies of motor control. So far, experimental analysis has not been able to delve far into the future, and studies of anticipatory phenomena have been limited at most by one second prior to action initiation or modification. In particular, APAs and ASAs may be seen as reflections of neural processes aimed at achieving a future state effectively given the external conditions, planned actions, their speed, etc. On the other hand, experimental investigation of processes related to planning future shift of the body referent configuration that could take into account predictable changes in forces, target motion, and similar factors remains limited and fragmented. A promising approach is being developed by the group of Schöner [11] based on the idea of activation fields generated by neural oscillators. A major problem seems to be that lower-level processes can be measured relatively objectively and accurately while processes that happen within the brain remain "physics of unobservables". This limits the experimental confirmations of the excellent theoretical approaches developed within this field. These issues, however, are only transient problems in the aforementioned paradigm shift from using the neural processes to solve problems of physics of inanimate nature to a single science, physics of living systems.

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