In: Progress in Motor Control - From Neuroscience to Patient Outcomes. M.F. Levin, M. Petrarca, D. Piscitelli, S. Summa (eds.), Elsevier/Academic Press 2024

Chapter 4

Toward a neural theory of goal-directed reaching movements

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Introduction

How do we generate the movements that direct our hand toward objects in our visual surround? This question touches upon many of the processes that play a role in the generation of goal-directed action in general. At the same time, reaching movements are sufficiently circumscribed to be studied in the laboratory (Desmurget et al., 1998; Kim et al., 2021). This makes reaching a good model system for the study of movement generation. To sketch a neural theory of reaching, we must address at least the processes illustrated in Fig. 1. (1) Before initiating a reach, we take in the visual scene and visually attend to objects that may be relevant to our action. Not every object that is visually attended will be the correct target given our movement intention. (2) We must select the correct target and decide to initiate the movement. The hand moves in the direction of the target from the very start, so the selection and initiation processes must take into account the initial position of the hand. (3) Moving the hand entails generating time courses of neural signals that are suitable to bringing about the movement within a desired movement time. (4) These signals must be distributed to the many muscles that actuate the limb so that the degrees of freedom of the arm are appropriately recruited for the motor act. (5) Finally, muscle forces must be generated and controlled to physically move the limb, stabilize it against any mechanical perturbation, and bring it to a new postural position at the target location.

These processes are typically embedded in a behavioral context. For instance, a reaching movement may be part of a sequence of motor acts (Herbort & Butz, 2009) aimed at a behavioral goal, say preparing a cup of coffee. Each individual motor act may be driven by a desired outcome

Progress in Motor Control. https://doi.org/10.1016/B978-0-443-23987-8.00008-0

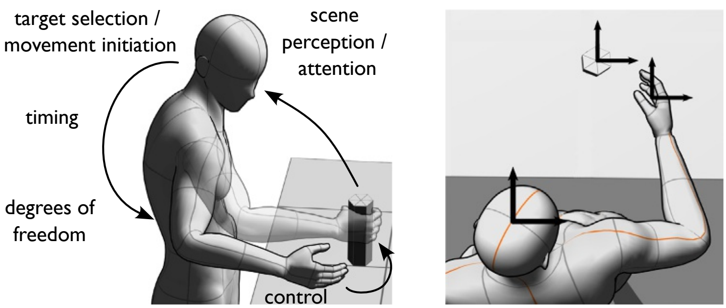

FIG. 1 The processes (*left*) and coordinate frames (*right*) entailed in reaching for an object.

(Kunde et al., 2004) that is critical to the next motor act. While the style of neural theory we will outline here is beginning to address such issues (Aerdker et al., 2022; Tekülve et al., 2019), we will not further review those ideas in this chapter.

At first brush, Fig. 1 suggests that the processes are sequentially organized from perception through cognition to motor control. We will argue that this classical conception of forward information processing is not a good approximation, however. Instead, the processes are tightly integrated. They are coordinated so that each is engaged at just the right time relative to the state of another process. This may require anticipation as neural processes need a head start to accommodate delays before their physical consequences may be sensed. The processes may also be continuously coupled to each other. Even after a movement has been initiated, for instance, it continues to be updatable at any time to accommodate changes in object pose or location (Prablanc et al., 2003; Prablanc & Martin, 1992). The processes unfold in closed loops (Weiler et al., 2019), so that an ongoing movement may modulate movement generation.

The tradition of forward information processing has allowed separate theoretical frameworks and concepts to be used to study these different processes. Scene perception and attentional selection of objects are part of visual cognition and are studied through paradigms of visual search (Wolfe, 2021) and visuo-spatial working memory (Henderson & Hollingworth, 1999). Motor planning is often addressed in terms of cortical representations of spatial vectors of hand to target (Kim et al., 2021; Mahan & Georgopoulos, 2013). Motor timing is addressed in terms of optimal control (Berret & Jean, 2016) or of coupled oscillators (Schöner, 2002). Motor control is addressed in terms of spinal reflex loops (Feldman, 2015; Tsianos et al., 2014) or of internal models (Shadmehr & Mussa-Ivaldi, 2012; Wolpert & Kawato, 1998).

To understand how these different processes are integrated, coordinated, and continuously coupled, a different theoretical language is needed, one that reaches all processes with a unified set of theoretical concepts. We propose that this language should be framed in neural terms as it is the nervous system with its constraints that bring about selection, initiation, time-course generation, and control. Principles of neural function may be what all processes share. But what it does mean for a theory of movement behavior to be "neural"?

Coding and decoding by correlating recorded neural activity with stimulus or motor conditions provide one route toward characterizing the neural basis of motor function (Georgopoulos, 1986; Moran & Schwartz, 1999; Paninski et al., 2004). This may help map models onto brain areas but does not by itself suggest how the neural activity comes about. Computational theories of motor control use mathematical models of movement generation drawing from optimal control, optimal feedback control, and estimation theory (Franklin & Wolpert, 2011) to provide models of movement generation at an abstract level. Although such models also do not explain how neural activity comes about, their components may be mapped onto brain areas (Shadmehr & Krakauer, 2008). This provides potential accounts for functional deficits when specific brain areas are lesioned or perturbed (Agostino et al., 1996; Beer et al., 2000; Miall et al., 2007).

Neurally reductionist accounts provide detailed models of neural mechanisms and circuits to explain movement. The most far-reaching attempts in this direction have been made for invertebrate and very simple vertebrate systems (Grillner, 2003). It is difficult to scale such reductionistic models to human movement, as the neural circuitry and its modulation are not known at comparable levels of detail. A strength of such detailed mechanistic accounts is that they may provide *process models* that go beyond description and functional interpretation of neural circuits by being capable of actually generating time courses of neural activity and potentially even of motor activity, through models of muscles, biomechanics, sensory systems, and the environment (Ijspeert, 2008). Because process models provide the strongest integrative accounts, we will focus this chapter on such models.

The theory we will outline in this chapter overlaps with some of these ideas but takes a somewhat different stance. The idea is to postulate a small set of functional neural principles that are consistent with what we know about the neural networks of the brain. These functional neural principles then provide the theoretical language in terms of which we outline a neural theory of movement generation. Such a theory does not aim to fully identify in each case the specific brain circuitry that implements a specific neural function. The account may, however, predict behavioral and neural signatures of the functional principles. It provides a process account that makes it possible to understand how different subfunctions are continuously coupled to each other in a closed loop. The outline we provide builds on earlier work on various subsystems of the overall architecture (Martin et al., 2019, 2009; Schöner et al., 2019; Zibner et al., 2015).

Functional principles for a neural theory of reaching movement

The core assumption of the proposed neural theory is that activity in small populations of neurons generate thought and behavior (Schöner, 2019). Arguments for populations as the privileged level at which neural activity and behavior are linked are based on various ways to estimate the covariation of neural and behavioral measures (see Saxena & Cunningham, 2019 for a recent review). The population hypothesis has a prominent history in the motor domain due to the foundational work of David Sparks (Lee et al., 1988) and Georgopoulos, Schwartz, and colleagues (Georgopoulos et al., 1986; Schwartz, 1994).

Dynamic field theory (DFT) mathematically models the temporal evolution of activity in such neural populations (Schöner et al., 2016). DFT is based on the notion of neural fields that date back to Wilson and Cowan (1973). These provide a mesoscopic level of description at which neurons with overlapping forward connectivity from sensory surfaces and to the motor system are embedded in a continuous space and their spiking activity is replaced by a continuous activation variable. The threshold function of neural spiking is approximated through a sigmoidal function that passes on only positive levels of activation (see Gerstner et al., 2014, Part 3, for review). Neural fields can be directly estimated from neural spiking data in small populations using the method of the distribution of population activation (Erlhagen et al., 1999).

While neural fields provide a convenient mesoscopic approximation to the complex dynamics at more fine-grained anatomical levels, the key strength of the concept of neural fields lies in its capacity to describe the dynamics of localist neural representations. In neural fields, peaks of activation, localized along the dimensions of the field, are stable states (or attractors) of the neural dynamics (Fig. 2). These localized activation patterns are hypothesized to drive decisions and behavior. The population vector for movement direction constructed from populations of neurons in the motor and premotor cortex

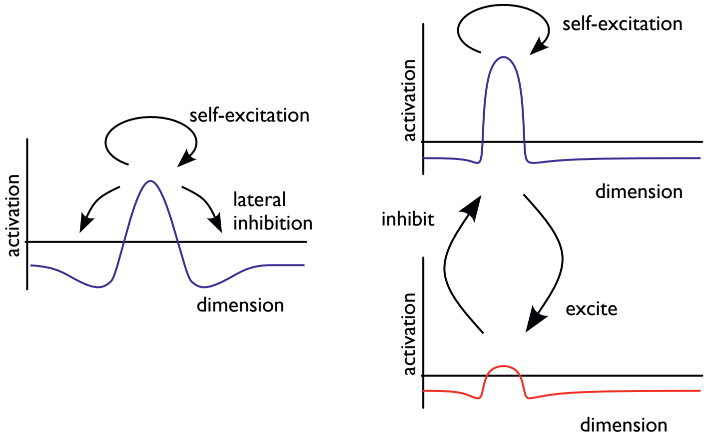

FIG. 2 *Left*: A neural field with self-excitation and lateral inhibition has localized peaks of activation as attractor states. *Right*: The excitatory layer (*top*) of a two-layer neural field self-excites and excites the inhibitory layer (*bottom*), which in turn inhibits the excitatory layer. Localized peaks may be stable, may oscillate, or may go through active transients.

(Georgopoulos et al., 1986), for instance, is essentially an estimate of the location of a peak of activation in the space of movement directions as well as of its amplitude (Bastian et al., 1998).

To understand how peaks play a central role in DFT, we briefly review the basic notions of the dynamics of neural activation. The activation, $u(x, t)$, in a neural field over a dimension, x, evolves in time according to

$$\tau\dot{u}(x,t) = -u(x,t) + h + \mathrm{input(x,t)} + \mathrm{interaction(x,t)} \tag{1}$$

Apart from the interaction term, this equation is inherited from the dynamics of neural membranes in the way described, for instance, in integrate-and-fire models (Gerstner et al., 2014, Part 2). Without input, this model has a stable stationary state, $u(x, t) = h$, at the resting level, $h < 0$ (solve $\dot{u} = 0$ to see this). Constant input shifts this attractor to $u(x, t) = h + \mathrm{input}(x)$. From any initial value, activation converges to these attractors on a time scale, τ, of approximately 10 ms. Time-varying input is tracked, so the neural dynamics acts as a low-pass filter. It is through the dependence of input on some feature dimension, x, that a neural field comes to depend on and thus represent that dimension.

The interaction component is critical to the capacity of dynamic neural fields to generate localized activation states that are stable. Interaction is excitatory among field sites close to each other and inhibitory among field sites at larger distances from each other (Fig. 2). Formally

$$\mathrm{interaction}(x,t) = \int dx' w(x - x')\sigma(u(x', t)) \tag{2}$$

where the strength of recurrent connectivity, $w(x - x')$, depends on the distance between field locations as described. Such interaction patterns are common in cortical and subcortical structures (e.g., Georgopoulos et al., 1993; Jancke et al., 1999). The sigmoid threshold function, $\sigma(u) = 1/(1 + \exp(-\beta u))$, approaches zero for large negative activation levels, approaches one for large positive activation levels, and transitions between these limits with a maximum slope of β which is attained at $u = 0$. Because all down stream neural systems onto which a given field, $u(x, t)$, projects are driven by the *output*, $\sigma(u(x, t))$, the slope of the threshold function determines the range over which changes in activation make a difference.

To see how interaction creates localist representations, consider a field at a resting level that then receives spatially structured input, here as a bimodal input distribution (Fig. 3). Activation grows where input is provided and approaches the threshold near the location that receives the strongest input. Output, $\sigma(u(x, t))$, around that location becomes positive, engaging interaction. Local excitatory interaction further amplifies activation at that location, while global inhibitory interaction limits the growth of activation at the competing locations with smaller input. The field converges to a peak of above-threshold activation centered on the local maximum of input. This event, the formation of an above-threshold peak of activation, results from the *detection instability* in which the

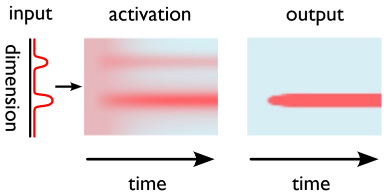

FIG. 3 An illustration of detection and selection in a neural field. *Left*: Input with two local maxima along the field's dimension, x, is provided to the neural field at the initial moment in time. *Center*: The time course of activation, $u(x, t)$, is shown using a color code (*light blue*: negative levels, *light red*: levels near threshold, *strong red*: levels above threshold). *Right*: The output, $\sigma(u(x, t))$, is shown with a similar color code (*blue*: zero, *red*: near one).

subthreshold activation pattern becomes unstable. Through detection instability, discrete events emerge out of continuous time courses of input and activation. This is the basis for the generation of initiation decisions and of sequences in neural dynamics (Sandamirskaya & Schöner, 2010).

Detection decisions typically entail selection decisions as well. Fig. 3 illustrates how this happens. As a peak is formed, it begins to inhibit other field locations and thus prevents a peak from forming over other local maxima of input. This is exactly what is observed neurophysiologically (Cisek & Kalaska, 2010). Again, it is the spatially organized form of neural interaction that enables selection among different localist representations.

Detection and selection illustrate how dynamic neural fields make decisions, amplifying and reweighing activation, rather than merely transmitting input patterns. Neural fields are therefore less dependent on inputs than the feed-forward neural networks that are the basis of much current neural modeling. This fact is perhaps best illustrated through the notion of sustained activation, the possibility of an above-threshold activation peak remaining stable after the inducing localized input has been completely removed. Here is how this works: without localized input, the resting level is a stable activation state. Localized input reshapes that state until it becomes unstable at the detection instability. The above-threshold peak of activation persists as a stable state when localized input is removed. The reverse detection instability marks the lower limit of this bistable regime. This occurs when input-induced activation boosted by local excitatory interaction falls below the threshold. For sufficiently strong interaction, this never happens, so the peaks remain stable even after localized input has been completely removed.

Neural dynamic fields may generate oscillations or active transients (Amari, 1977). To understand these, we must take into account Dale's law, the fact that neurons have only one type of synapse, either excitatory or inhibitory. The dynamics of neural fields described earlier are in apparent violation of this principle, as the field locations both excite nearby locations and inhibit locations further removed. This formulation is actually a simplification of a more complete description that has separate populations of excitatory and inhibitory neurons, which can be visualized as a two-layer neural field (Fig. 2). The excitatory field receives external input, has excitatory local interaction, and projects onto down stream neural populations. It also drives the inhibitory field, which in turn inhibits the excitatory field, both projections organized locally.

Such pairs of excitatory and inhibitory fields provide a generic description of the population dynamics in cortical and subcortical layered structures (Wilson & Cowan, 1973). Neural oscillations occur under a broad set of conditions in such two-layer fields (Amari, 1977). An intuition for how oscillations arise is suggested in the "mental simulation" of Fig. 4: input to the excitatory field drives its activation up. Once above the threshold, output from the excitatory field begins to induce activation in the inhibitory field. As that activation reaches the threshold, its output begins to exert inhibitory influence on the excitatory field, whose activation level falls. If it falls below the threshold, the input to the inhibitory field falls away, leading to a decay of activation in that field. If activation in the inhibitory field falls below the threshold, its inhibitory influence on the excitatory field falls away. That allows the excitatory field to again generate activation in response to its input. And the cycle begins again.

Active transients are a variant of this capacity of two-layer fields to autonomously generate time courses. Such active transients may be important to a neural theory of movement generation. In the mental simulation of Fig. 4, an active transient emerges if the input that starts activation growth in the excitatory field has fallen away by the time the cycle returns to low levels of activation in both fields. This will prevent excitatory activation from arising again, so the two fields will remain in their subthreshold resting states (Fig. 4). The time course itself and its amplitude are largely determined by the recurrent connectivity within and across the two layers, not by the time course of input to the excitatory field. The only constraint on the time course of input is that it must fall away within one cycle of the neural oscillation.

Two-layer fields are the simplest example of a neural dynamic architecture. Architectures are more generally built by coupling fields in a variety of different ways (Zibner et al., 2011). Peaks as attractor states, the detection and reverse detection instability, the capacity for selection, and for sustained activation all persist when fields are coupled in this way (within limits). This makes it

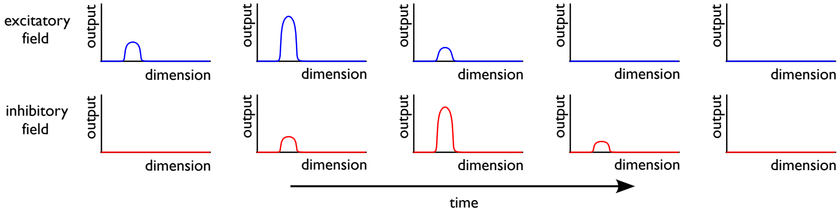

FIG. 4 Time course of the output of a pair of excitatory (*top*) and inhibitory (*bottom*) fields. The excitatory field initially receives an input (not shown) that induces an active transient.

possible to understand how properties of component fields remain relevant to the neural dynamics that emerge from a complete neural dynamic architecture.

If neural fields are embedded in such neural dynamic architectures, how are they still defined over some feature dimensions, x? How do these dimensions come about to begin with? Of course, the neural fields are just dynamical systems, in which activation is driven up or down by inputs and interactions. The dimensions are merely a way to describe the coupling patterns in the fields. The fields do not “know” about the dimensions other than through these coupling patterns. It is us, the modeler, who interprets the field dimensions by relating them to things outside the neural architecture either in terms of sensory stimuli or in terms of motor behavior. That is done in the manner of “coding” and “decoding” as in all neural network models. In other words, as a stimulus parameter is varied, an induced activation pattern in a given field varies and a systematic analysis of these dependencies enables the interpretation of the field’s dimensions. The forward connectivity from sensory surfaces to a given field or from a given field to the motor system ultimately determined these dependencies and thus, the meaning of a field’s dimensions. In many cases, these align with known dimensions of cortical maps such as the retinotopic feature maps in the visual cortex or the known population encoding of movement parameters in the motor and premotor cortex. The localist nature of representation in neural fields is most consistent with forward connectivity that induces space code in which the location within a neural field determines what is being encoded. Finally, when fields simultaneously represent dimensions that have qualitatively different meanings (e.g., color and visual space), new functions are enabled as we shall see next in the context of visual search.

Skeleton of a neural theory of reaching movements

The skeleton of a neural theory for goal-directed reaching movements is a neural dynamic architecture (Fig. 5) that includes the five component processes entailed in such movements. We step through each component and sketch the neural dynamic elements and the empirical evidence to which each component is linked.

Scene perception and selective attention

Reaching to objects is based, of course, on perceptual information about objects in the reachable environment. Humans tend to quickly build scene representations of their immediate environment by attending to objects and storing these in memory (Henderson & Hollingworth, 1999). Given a scene representation, an object relevant to a given task can be brought into the attentional foreground through a process of visual search, supported both by online visual information and by the scene representation (Peelen & Kastner, 2014).

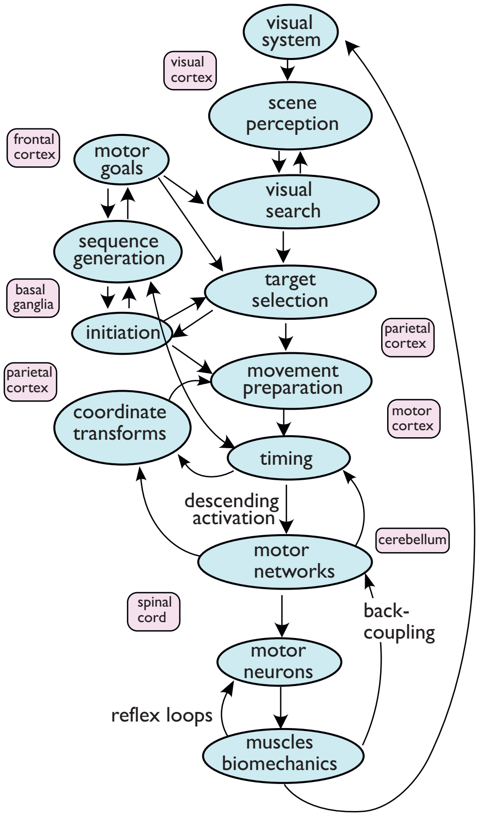

FIG. 5 A schematic illustration of the component processes (*light-blue ellipses*) involved in targeted reaching movements. Their couplings are indicated by *arrows*, with a label next to some coupling structures that will be discussed in the chapter. A rough mapping of neural structures is suggested by the labels in *light red*. Many component processes may be supported by circuitry in different brain areas, however.

In neural dynamic thinking, such a scene representation is a neural activation pattern defined not only over visual space, but also over feature dimensions such as color, orientation, size, or shape (Zibner et al., 2011). Fig. 6 illustrates a simple case, a joint representation of visual space (along only one spatial dimension) and color. The scene consisting of four colored objects is thus represented by four localized activation peaks that bind color to space (see Chapter 5 in Schöner et al., 2016).

Visual search selects one of the objects for visual attention based on a top-down cue to the object's visual features, here the color "blue." This cue may be represented in a neural field defined over the feature space, color. It projects a ridge that is homogeneous across the spatial but localized along the color dimension into the two-dimensional (2D) neural field that jointly represents

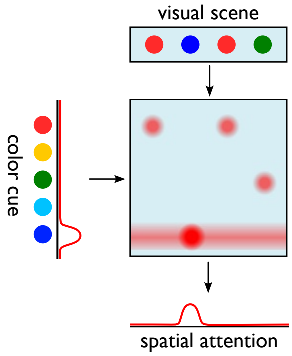

FIG. 6 A sketch of the visual selection portion of the model. *Left*: A one-dimensional neural field represents the color cue. *Bottom*: A one-dimensional neural field represents the spatial location in visual space that is selectively attended. *Center*: A two-dimensional field defined over color and visual space receives direct input from the visual array shown on top (along only one spatial dimension). Here, activation is illustrated using a color code (*light blue*: negative levels, *light red*: levels near threshold, *strong red*: levels above threshold). The color cue field provides input to the two-dimensional attentional field that is constant along the spatial dimension. A peak in the color cue field thus induces a horizontal ridge in that field. When input from the visual array, localized along both color and space, overlaps with such a ridge, a peak forms, leading to the attentional selection of the corresponding spatial location.

color and space. Where the ridge overlaps with one of the peaks generated by visual input, activation is boosted. Projecting out to a spatial attention field, the corresponding location receives stronger input and wins the competition, so it is selected for attention. A more complete account for visual search takes into account multiple feature dimensions for conjunctive search, their binding through space, and the sequential selection for attention of objects that overlap with the cue (Grieben et al., 2020).

Building on earlier work (Lins & Schöner, 2019), we have recently studied empirically, how visual search for a potential target of a reaching movement interacts with the generation of that movement (Hummert & Schöner, unpublished). The experiment made use of the mouse-tracking paradigm, in which participants began to move a visual cursor from a starting location into the general direction in which targets lay. Once the mouse movement began, an array of visual objects was displayed, of which only one matched the conjunctive feature cue of the target (e.g., “red” and “diagonal”). The array contained one distractor object that matched the feature cue along one, but not the other dimension (e.g., “red” but not “diagonal”). All other objects did not match either feature cue. We observed the online updating of the mouse trajectory from its initial default direction toward a movement directed at the target (similar to how goal-directed reaching movements are updated when a target is abruptly shifted; Prablanc et al., 2003). Critically, we also found an attraction of the mouse trajectory toward the distractor object! This means that not only the final outcome of the visual search process, the target, was passed on to the neural processes that select the motor goal and generate the reaching movement, but also the potentially subthreshold representation of the distractor object.

Target selection and movement initiation

Visually attending to an object is not identical to the decision to select and initiate a reaching movement. The decision to initiate a movement is often viewed as a reflective of a selection decision among different choices because many classical reaction-time experiments are set up this way (Rosenbaum, 1980). A classical theoretical picture from mathematical psychology describes two-choice selection tasks by postulating a hypothetical decision dimension along which the two choices lie at some distance from an initial starting value (Ratcliff & Rouder, 1998). The decision is made by integrating random input (diffusion) that has a deterministic component (drift) until one of the two-choice locations is reached. This is meant to model the accumulation of evidence until significant certainty about the choice has been reached. Models of this nature, called diffusion models, provide parameters that describe the different reaction-time distributions observed when tasks are varied.

In spite of its abstract nature, this picture has been used to interpret neural data obtained while animals made selection decisions (Gold & Shadlen, 2007). The decision dimension is separated for different choices and represented by the firing rate of neurons tuned preferentially to a particular choice. Response initiation is typically aligned with particular levels of neural firing, as is natural given the threshold property of neural transmission. The rate of increase of firing rate is found, in some cases, to vary with task difficulty and response time consistent with diffusion models.

This theoretical picture is unsatisfactory in many ways, however. First, input information about the upcoming choices is itself provided by neural processes that have a characteristic time course rather than providing “evidence” at a constant rate. So, the integration of a time-invariant drift is unrealistic. Studies manipulating the time course of information about an upcoming choice have indeed demonstrated the need to modulate this purported mechanism by a temporally structured neural “urgency” signal (Cisek et al., 2009).

Second, motor decisions need to generate macroscopic neural states that can drive downstream systems and ultimately behavior. Merely reaching a threshold does not explain how movement initiation is achieved.

In a sense, the sensorimotor decision is first a decision to initiate action and only secondarily a decision to select a particular action. In fact, participants can modulate the relationship between initiation and selection decisions. In the timed movement initiation paradigm participants learn to initiate an action at a fixed point in time, specified by a metronome. Information about the requested choice is provided at a variable time before that moment of initiation (Ghez et al., 1997, 1990). When that stimulus-response time is short, movement is thus initiated before the selection has been made. The responses of participants are distributed over the possible choices either monomodally (if choices are metrically close) or multimodally (if choices are metrically far from each other). With increasing stimulus-response times, these distributions reshape gradually into distributions centered on the correct choice.

In DFT, initiation decisions come, of course, from the detection instability that leads to the formation of an above-threshold peak of activation (Erlhagen & Schöner, 2002). The instability may be induced by a localized input that would model, for instance, an imperative signal provided in a reaction-time experiment. But it may also be induced by a homogeneous boost of activation across the field, which will amplify any small inhomogeneity in the field. Such small inhomogeneities may represent prior information about upcoming choices, which may have been acquired by learning or from precues (Erlhagen & Schöner, 2002). Preshaping of this kind has in fact been directly observed neurophysiologically by estimating the distribution of population activation over movement direction from many neurons in the motor and premotor cortex (Bastian et al., 2003). Providing the animals with different precues about upcoming movement targets, a broad pattern of activation centered on the mean movement direction to the precued targets was observed before the go-signal specified the actual movement target. Once that information was provided, the distribution gradually reshaped until it was centered on the actual target, very similar to how the probability density evolved as a function of stimulus-response time in the timed movement initiation paradigm. The neural dynamic model captured this temporal evolution (Bastian et al., 1998). Cisek and colleagues have similarly observed distributions of population activation in the premotor and motor cortex for tasks in which the possible choices are metrically further removed from each other (Cisek & Kalaska, 2005). They found a transition from a bimodal pattern of preactivation to a monomodal distribution centered on the selected target (see Fig. 2 in Cisek & Kalaska, 2010), very similar to what is shown in Fig. 3. Cisek also used DFT to model this data (Cisek, 2006).

The neural and behavioral data on movement initiation are ambiguous with respect to whether the selection is about the movement target or the movement itself. This is because these studies do not typically vary the initial position of the hand. Functionally, selection must reside at the level of movement targets. For instance, sequences of movements can be planned to reach multiple targets in a particular serial order. A later target may affect an earlier movement (Hansen et al., 2018), evidence that its representation must already have been active, even though the initial position of the hand for the later target had not yet been reached. The capacities to update movements online in response to target shifts (Prablanc et al., 2003; Prablanc & Martin, 1992; van Sonderen et al., 1988) or in the mouse-tracking paradigm are also consistent with this view. It is difficult to imagine how the update could happen at the level of movement parameters given that the initial hand position is changing.

On the other hand, movements reflect the relative configuration of the initial hand position and reaching the target from the very start (Fig. 1): The hand begins moving in the right direction and the initial acceleration profile of the hand reflects the distance and movement time. How may a neural architecture compute these movement parameters based on the coordinates of the target and the initial hand position? Dating back to the vector-integration-to-endpoint (VITE) model (Bullock & Grossberg, 1988), researchers have assumed that some form of vector subtraction is performed (see Kim et al., 2021 for illustration). Neurons cannot perform such arithmetic operations without some special machinery. That machinery can be understood by recognizing that what is needed is a coordinate transform. The target is initially represented in some visual reference frame and must be transformed into a frame centered in the hand, from which projections may directly activate the adequate neural pattern of movement generation. The observation that neurons in the motor cortex are tuned to the hand's movement direction in space is consistent with this assumption.

The neural machinery for coordinate transforms is known under the label of gain fields (Pouget & Snyder, 2000) which were discovered around the analogous problem of the transform from eye- to body-centered spatial reference frames (Andersen et al., 1985). Gain fields can be understood within DFT as steerable neural maps (Schneegans & Schöner, 2012) based on a joint representation of the original space (the target in body-centered coordinates) and of the steering variable (the initial position of the hand). Peaks in this joint representation can be shifted through "ridge input" from the steering variable (Fig. 7). Projecting out from the joint representation, the movement parameters can be determined (Schöner et al., 2019). There is a complex literature about the neurophysiological foundations for such joint representations of visual targets and hand position that is overall compatible with this framing of the problem

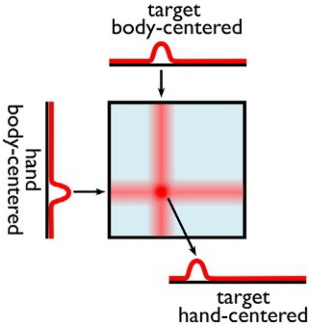

FIG. 7 Sketch of the coordinate transformation in the model. Knowledge of both the position of the hand and the target in the body-centered frame allows one to compute the position of the target relative to the hand. Only where the input from the two input fields overlap can a peak form and the output field can learn the position of the appropriate response in the end-effector centered representation.

(Orban et al., 2021). Note that the neural implementation of coordinate transforms can run in parallel to the selection process as multiple possible targets can be transformed into multiple possible movement parameters as long as the steering dimension has a unique value (Schneegans & Schöner, 2012).

Movement timing and coordination

The essence of the movement is that it unfolds in time. Upon initiation, a time course of neural activation must be generated to drive forward the movement. Human reaching movements are *timed* (Schöner, 2002) in the sense that their time courses are stabilized against perturbations and are potentially coordinated with other movements or with perceptual data (Turvey, 1990). Although often studied in the context of rhythmic movement, coordination is observed for discrete motor acts as well (Kelso et al., 1979; Schöner, 1990). During a reach for an object, for instance, the transport of the hand toward the object and the opening and closing of the hand are coordinated (Jeannerod, 1984). Delaying the transport component leads to a slowing down of the hand opening gesture as well (Savelsbergh et al., 1993). Timing a reaching movement is obviously critical for tasks such as catching or hitting moving objects (Schöner, 1994). In such tasks, the timed movement compensates for any acceleration or slowdown of the object (Bootsma & van Wieringen, 1990).

So how would a neural theory address timing? We have already discussed neural time-course generation in the form of neural oscillation and active transients. In fact, when animals perform a periodic task, activation in the motor cortex reflects that periodicity. This has given rise to the notion that the motor cortex forms a neural oscillator (Churchland et al., 2012), although this may be a bit too global a statement to help develop a neural theory.

A more specific idea is that the neural activation from the initiation decision provides input into reciprocally coupled populations of excitatory and inhibitory neurons which are then induced to generate an active transient. Such active transients can be coupled across populations, providing mechanisms for coordination (Schöner, 2002). The precise time course generated depends on the coupling constants so a whole set of such neural timers could be constructed by varying these constants across the dimensions of the coupled pair of neural fields (Schöner et al., 2019). A slower and a faster active transient are illustrated in Fig. 8. Any particular set of time courses could be selected by providing input

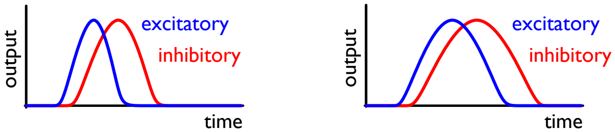

FIG. 8 Two schematic examples of the time courses generated by a two-layer neural field dynamics (excitatory activation, u, and inhibitory activation, v). Depending on the coupling parameters, shorter (*left*) or longer (*right*) durations may emerge, as well as different amplitudes.

into the excitatory field at the appropriate locations. In recent, as yet unpublished, work (Jokeit & Schöner, unpublished), we have assembled different movement primitives from such a field of neural oscillators to explain the coupled time courses of the transport and lift components of reaching movements during obstacle avoidance (Grimme et al., 2012). A neural timer system of this general form could remain coupled to the initiating inputs during the initial phase of the transient. This may provide the neural substrate for online updating (Zibner et al., 2015), although a precise account of online updating is still needed. The notion of batteries of timers could be viewed as a special case of the concept of "reservoir computing" (or echo state networks) (Buonomano & Laje, 2010). How projections from the battery may select appropriate components of the timing signals to drive muscles is addressed next.

Degree of freedom problem

Time-course generation is neurally costly. So the idea that every muscle could have its own field of neural timers does not scale well. Instead, the field of neural timers must be of reduced dimensionality, perhaps linked to the time courses of the hand in space. That would be consistent with neurophysiological findings that showed that the hand's speed along its path covaries with the amplitude of the population vector (Schwartz, 1994). This would also be consistent with much behavioral evidence about the spatiotemporal regularity of hand trajectories (Morasso, 1981), with evidence that coordination occurs at the level of spatial timing relationships rather than at the level of muscle timing relationships (Mechsner et al., 2001), and with evidence that the timing of the hand in space is controlled during catching (Peper et al., 1994).

The ensemble of neural timers may thus be low-dimensional and to some extent aligned with characteristics of the hand's movement in space, while specific and varied timing signals may be needed to supply the descending activation patterns that drive the many muscles involved in generating the hand's trajectory. This is the degree of freedom problem, famously discussed by Nikolai Bernstein decades before the referenced neural and behavioral data were known (Gurfinkel & Cordo, 1998; Latash, 2008).

What form of projection from neural timers to muscles may solve this problem? A classical idea is the notion of synergies (d'Avella & Bizzi, 2005; Tresch et al., 1999) according to which muscles are bound into groups within which activation covaries. Recording from sets of muscles while participants perform a set of different movements, numerous studies have documented such covariation of muscle activation. The reliable finding can be visualized by thinking of the activation of each muscle as a separate row of a matrix. The columns are formed by tracking muscle activation across time, concatenating the time series obtained from different movements (d'Avella & Lacquaniti, 2013; d'Avella et al., 2006; Ting & McKay, 2007). This matrix has many more columns than rows. The key finding is that the long rows are not independent: The rank of the matrix is considerably smaller than the number of muscles tracked. So the

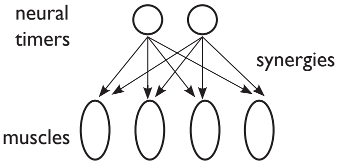

FIG. 9 In the classical neural picture of synergies, the output of a relatively small number of neural timers is projected onto a larger number of muscles, leading to characteristic patterns of coactivation.

activation patterns of all muscles can be predicted from a smaller set of synergies, often as little as four to six "principle components" or feature vectors.

A possible neural account for such covariation is illustrated in Fig. 9. A smaller set of neurons (really, of neural populations) projects onto a larger set of muscles (really, the associated spinal networks). In our framework, that smaller set of neurons represents activation in the neural fields of timers. They vary across a small set of dimensions that reflect movement parameters such as direction, extent, and speed. In this picture, the characteristic covariation among muscle activation patterns comes from the pattern of forward projection. Inserting variation in time or across movement at the top predicts covariation at the bottom of the network due to the spread of activation from the few to the many dimensions.

Do such forward neural projections solve the degree of freedom problem? It turns out that there is a problem with this account that comes from the structure variance from trial to trial (or from cycle to cycle in rhythmic movement). Many empirical studies of synergies include repetitions of movements in the data matrix, but these contribute little compared to the variation across time and across different movements. The account of the few-to-many forward projection predicts that variability across repetitions should lead to the same pattern of covariation as variation across time and movement. To see this, consider two possible sources of trial-by-trial variability. One source could be stochastic variation at the level of the timer neural field. Such variation would be transformed by the forward projection into the same pattern of covariation that characterizes synergies. The other source would be stochastic variation at the level of the muscles (or the spinal networks driving muscles). These sources of variation would be independent for each muscle (or at least not structured by the forward projections).

When variability across trials or cycles is studied separately from variation across time and movement conditions, a broad set of studies has found patterns of covariation that are roughly *orthogonal* to the patterns predicted from the forward model. To explain this without going into technical details, we use a kinematic variant of the degree of freedom problem in Fig. 10. In this simplified picture, think of neural timer signals as being about the hand's trajectory in 2D space. The degree of freedom problem is about how to distribute these timing

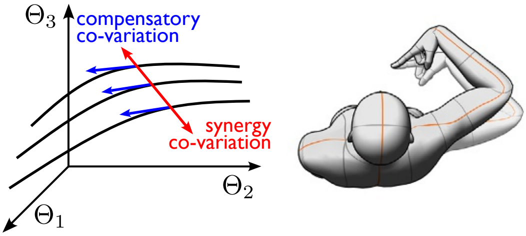

FIG. 10 *Right*: A planar arm with three joints can realize the same hand position in space with a continuum of joint configurations, of which two are shown. *Left*: In the three-dimensional joint space, the *black lines* are the manifolds on which the hand position remains invariant. Three different manifolds are shown for three different positions of the hand in space. Joint angle covariation orthogonal to the manifolds is predicted from classical synergies. Joint-angle covariation along the manifolds is predicted from the concept of the uncontrolled manifold (UCM).

signals to the three joint angles of this kinematically redundant arm. At any moment in time, there is a manifold of possible joint configurations that may realize the current hand position in space. The figure illustrates such *uncontrolled manifolds* (UCM) (Schöner, 1995) for different positions of the hand in space. As the hand moves through space, these manifolds shift in joint space. The direction of this shift in joint space is what classical synergies describe, the covariation of joint angles as the hand moves. Variance at the timing level would shift the manifolds along that general direction and thus predict covariation consistent with the classical synergies. Covariation among joint angles that shift joint configurations within or along the manifolds would, by contrast, keep the hand's trajectory in space unaffected. This form of covariation is not predicted by the forward model.

To empirically isolate the variability across trials or cycles from variance across time or movements, one needs to study each moment in time of each movement condition separately. This requires time normalization (Schöner & Scholz, 2007). It is then possible to examine the cloud of points in joint (or muscle) space that is generated at a given time within a given movement across trials/cycles by projecting the cloud onto the subspace parallel to the UCM and onto its orthogonal complement. The *UCM structure of variance* in which the cloud of joint configurations is elongated along the UCM has been found in a large collection of studies for different tasks, different task-relevant variables, and different effector systems. Examples include UCM structure for hand position during reaching (Yang et al., 2007), hand-target alignment during shooting (Scholz et al., 2000), or center of mass/pressure in whole-body posture stabilization (Krishnamoorthy et al., 2003; Park et al., 2016). The UCM structure of variance reflects compensatory covariation in which a variation in one degree of freedom is compensated for by covariation in another degree of freedom to keep the system on the manifold and thus, to keep the hand's position in space invariant. This compensatory covariation is roughly orthogonal to the covariation predicted by the forward model.

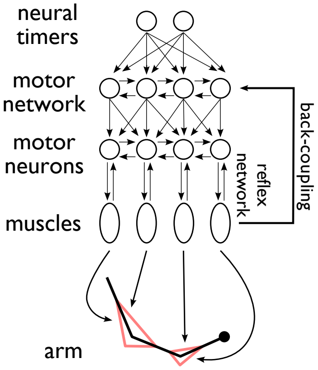

FIG. 11 Sketch of a neural account for the degree of freedom problem. Low-dimensional neural timers send time courses through forward projection to a motor network. Recurrent connectivity within that network creates compensatory covariation. So does back coupling from afferent muscle signals to the motor network, through which descendant signals yield perturbations.

How would a neural theory account for the two different signatures of covariation? A complete account is still missing, but a number of proposals have been made (Goodman & Latash, 2006; Latash, 2021; Neilson & Neilson, 2010). Here, we focus on models that are somewhat aligned with the neural principles discussed in this chapter (Martin et al., 2019, 2009; Reimann & Schöner, 2017). We summarize three main ideas in Fig. 11. First, the forward projection of Fig. 9 must be part of such a theory to account for the classical signatures of synergy. Second, recurrent connectivity within a motor network may establish compensatory coupling. Such connectivity may, in effect, decouple the subspaces parallel and orthogonal to the UCM, so the deviations from the manifold are counteracted, while deviations within the UCM are resisted only weakly (hence the name "uncontrolled"). A mathematical formulation for such decoupling was shown to account not only for the UCM structure of variance (Martin et al., 2019), but also for a variety of other experimental signatures including self-motion and motor equivalence (Martin et al., 2009). That mathematical formulation was not entirely aligned with the neural principles we outlined at the outset. A thorough neural theory of this form of compensatory coupling still needs to be developed. Spinal neural networks could potentially provide a substrate for such recurrent connectivity through the Renshaw interneurons (Latash et al., 2005) (in this work, the term "back coupling" is used for the recurrent connectivity that generates compensatory covariation. In this chapter, we use this term in a different sense explained later.), but many other possibilities exist (Windhorst, 2007). A third proposed mechanism is back coupling, a form of positive feedback from the muscle or joint level to the motor network. This mechanism was proposed by Martin et al. (2009) within a formalization that represents the signals descending to the joints in terms of expected joint velocities and joint configurations.

Back coupling is the notion that these signals “yield” to sensed deviations from these expected time courses. Thus, for instance, a joint that flexes less or more slowly than expected leads to an update of the descending signal to that joint that shifts the expectation in the direction of reduced flexion. This yielding was effective only within the UCM, so the descending signals would still drive the hand to its desired state. Back coupling was critical in that model to understand motor equivalence, the realization of the same hand position in space with a different joint configuration following a phasic perturbation (Scholz & Schöner, 2014). Some empirical evidence for a mechanism consistent with back coupling has been obtained by Mark Latash and colleagues in isometric tasks (Ambike et al., 2016, 2015; Zhou et al., 2014, 2015 a, 2015 b). Still, this idea needs further elaboration.

A fourth mechanism for the emergence of a UCM structure of variance has been proposed by Reimann and Schöner (2017) in the context of upright standing. In that account, the outer sensory feedback loop stabilizing posture induces compensatory covariation. Postural sway is actually a movement behavior on a slow time scale of seconds (Morasso & Schieppati, 1999) that is governed by sensory feedback loops involving vision, foot pressure sense, proprioception and vestibular sensors, and more (Horak & Macpherson, 1996). These signals inform about the kinematic state of the head in space, of the center of pressure, or of other low-dimensional characterizations of the body’s motion in space. The feedback control of posture (Collins & De Luca, 1995; Jeka et al., 1998; Peterka, 2002) must distribute these signals to the degrees of freedom. The forward projection model together with the outer feedback loop then predicts the UCM structure of variance. Imagine that due to neural noise, the ankle joint is flexing more than on average. The body’s forward motion is picked up by the sensors, and the low-dimensional control law generates a movement signal that would pull the body backward. That signal would be distributed to all joints, leading to an effective compensatory reaction of the other joints to this particular excursion of the ankle joint. This fourth mechanism for UCM effects is not included in Fig. 11 because the published models assumed that such outer feedback about the state of the hand was too slow to be effective in reaching. The relatively fast transcortical reflexes may, however, effectively bring about such a closed-loop mechanism (Pruszynski et al., 2011).

In summary, while neural dynamic mechanisms have been proposed that may create the two signatures of covariation, a comprehensive neural theory of the degree of freedom problem remains in need of development.

Control

Muscles, the actuators of the human movement system, are very soft from the point of view of control: Their stiffness and damping (or impedance) are small so that conventional “PD” control would allow for slow movement only. The time scale of muscle action, characterized in terms of eigenfrequency, is on the same order of magnitude (100 ms) as the fastest movement times. So control, that is, generating active torques through the muscles to bring about fast-reaching movements, is a substantial problem for the nervous system.

Keeping a limb in a specific posture is thus also a problem. Unlike the stiff robot actuators, the viscoelastic properties of human muscles make human arm soft actuators with relatively low impedance. This is a feature of sorts when our arms and hands come into contact with surfaces and objects: The soft nature of our muscular actuators limits the peak forces that may arise, protecting both our limbs and the objects against mechanical damage. It also provides a simple strategy for compliant tasks, at which humans excel (Franklin et al., 2008). In such tasks, target configurations of the hand or fingers inside a surface could be planned (Bonilla et al., 2015). The deviation from the planned configuration would then create elastic forces that may serve to grasp an object or exert force on it. This idea has been adopted by researchers in robotics in the form of variable stiffness actuators (Bicchi & Tonietti, 2004).

The stability of joint postures is actively achieved through reflex loops and neural control loops. The stretch reflex (Pierrot-Deseilligny & Burke, 2005) is perhaps the most prevalent and generic contribution to postural stability and we will use it to explain ideas here (Feldman, 2011). Fig. 12 illustrates schematically how the stretch reflex combines descending activation with the afferent signals from muscle spindles that reflect muscle length and its rate of change. The sum of these two forms of neural activation, passing through the neural threshold mechanism, determines muscle activation and ultimately active muscle force. To intuitively see how the stretch reflex stabilizes posture, consider a single joint, say the elbow, with a flexor and an extensor muscle. Assume the elbow is in a given posture, say at a right angle, while the arm is horizontal (so we do not need to think about gravity). A certain level of descending activation is sent down to the spinal cord that, together with the afferent signal from the muscle spindles, determines the amount of activation of the two muscles in this postural state. Assume someone pushes against the hand, creating a mechanical

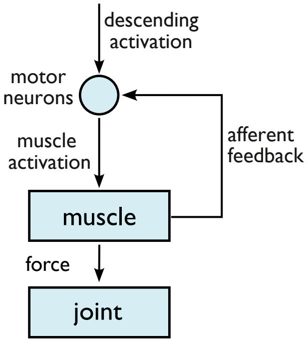

FIG. 12 A sketch of the stretch reflex. Afferent feedback depends on muscle length and its rate of change.

perturbation that extends the elbow. This lengthens the flexor muscle so that its spindles send an increasing signal to the motor neuron. At constant descending activation, this increases activation of the flexor muscle, which therefore resists the extension movement of the elbow. The analogous reflex for the extensor muscle reduces extensor activation in response to the shortening of that muscle. In reality, spinal reflex networks for the control of posture are more complex (Raphael et al., 2010; Windhorst, 2007), but this first approximation serves to set up the problem.

The stabilization of posture by the stretch reflex poses a problem for the movement. This so-called posture-movement problem (Feldman, 2016; Feldman & Latash, 2005) is illustrated in Fig. 13. Assume you want to voluntarily extend the elbow beyond its initial posture. To do this, you need to shorten the extensor muscle and lengthen the flexor muscle. Initially, both muscles are active at a certain level that reflects cocontraction, giving the elbow joint a certain stiffness. The associated forces cancel exactly so the elbow is at rest. To shorten the extensor muscle, its activation must increase and generate the appropriate force. Extensor activation can be brought about by sending increased descending activation down to the extensor muscle. At the same time,

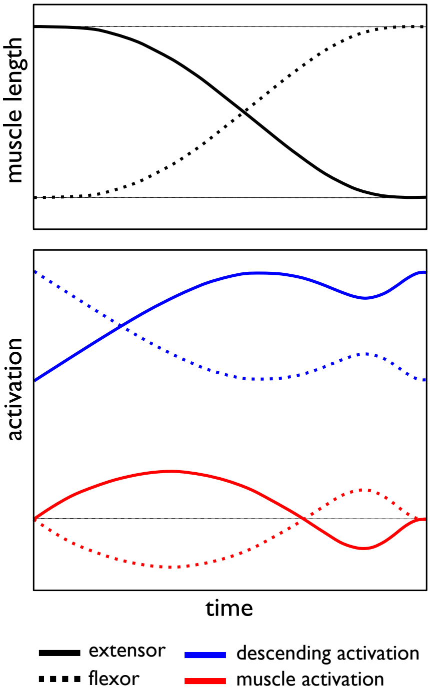

FIG. 13 A sketch of the lengths, descending and muscle activations of a flexor and an extensor muscle during a voluntary extension movement. The descending activation profiles were obtained by minimizing their change for a given movement time and amplitude (Ramadan et al., 2022).

flexor activation should decrease to avoid resistance of the flexor muscle to the extension movement. This can be brought about by sending decreased descending activation to the flexor muscle. As soon as the desired new joint posture has been reached, the initial level of activation of both muscles needs to be reinstated, so there is no net torque at the new joint posture and the same level of joint stiffness prevails. Alas, the extensor is now shorter, while the flexor muscle is now longer than initially. So the length feedback signals differ, smaller for the extensor and larger for the flexor muscle. In order for the same muscle activation to reign as initially, the descending activation for the extensor must be larger than initially, and the descending activation for the flexor must be smaller than initially. In other words, the descending activation patterns sent to the muscles are not pure "movement signals": They do not change from an initial no-movement level to a movement level and back to a nonmovement level. Instead, the descending activation patterns contain a postural component, so they end up at a different level from their initial level after the movement has terminated. This is the key insight of *equilibrium point* theory (Feldman & Levin, 1995). There is no question that such a postural component is contained in the descending activation signal (Albert et al., 2020). Debates have concerned the more radical claim that the only thing that descending activation needs to do is shift the postural state, with movement simply tracking that shifting equilibrium point. Model simulations aligned with data have demonstrated that this may be feasible for certain movements (Gribble et al., 1998; Pilon & Feldman, 2006; Zhang et al., 2022).

This debate may be more of an obstacle than an aid to understanding the problems of human motor control. For one, the large literature on adaptation to external force fields (Shadmehr & Mussa-Ivaldi, 2012) shows that participants can learn to generate approximately the same movement kinematics in the presence of a force field as they do in its absence. This is true for force fields that vanish at the end of the movement, so the final postural state is unchanged across learning. Therefore, the different demands on muscle forces during the movement must come from modulated descending activation patterns. It does not really matter if we describe those in terms of hypothetical equilibrium (or virtual) trajectories or in terms of the relevant neural activation signals. Moreover, when the speed of reaching movements is varied, the kinematics scale remarkably well, while the interaction torques between moving segments change considerably and nonlinearly (Hollerbach & Flash, 1982).

We have directly addressed the question of how descending activation patterns scale when the speed of a reaching movement is varied (Ramadan et al., 2022). For two-joint planar movements of the upper arm, we varied movement speed to induce interaction torques of different strength (Hollerbach & Flash, 1982). We used a model of the stretch reflex, muscle force generation, and of the biomechanics of the arm that had previously been used to demonstrate that simple shifts of equilibrium postures may predict movement patterns in this same task (at a low movement speed) (Gribble et al., 1998). We found the minimally changing descending activation pattern that moves the limb within a given time from the initial to the target position using numerical optimization techniques. For slow movements, descending activation patterns resembled linear shifts of activation level from an initial to a target level that ended after about two-thirds of the movement duration (consistent with empirical findings; Ghafouri & Feldman, 2001). For fast movements, the descending activation patterns were temporally structured in more complex ways. The descending activation patterns shown in Fig. 13 were actually taken from the results obtained at high movement speed. Clearly, descending activation is not just a rescaling of the ramp-like activation pattern that produces a slow movement.

We concluded that descending activation patterns generated by the neural timing system must be specifically adapted to the dynamic properties of the movement plant, the muscles, and the peripheral reflex loops. The required time courses are not overly complex and limited in temporal frequency. It is quite imaginable that they could be generated in the kind of neural timer systems we have sketched and be selectively projected to the appropriate muscles. This would be a simple neural solution to what has been framed in computational theories of motor control as an "internal model." Needless to say, this neural account needs further elaboration.

Discussion

We have outlined a path toward a neural theory of goal-directed reaching movements. The goal is an account that is consistent with a limited set of principles of neural function rather than an account that links in detail to the specific neural circuitry underlying each component process. We gave a short review of these neural principles as framed in DFT and then went through five major component processes from scene perception to control. We reviewed evidence that these component processes are continuously coupled in a way that goes beyond the transmission of finished "computations." This was illustrated in the context of mouse tracking in a visual search task, in which the mouse trajectory is updated as the target is visually searched, while a distractor object also affects the mouse trajectory. The component processes are not coupled only in a feed-forward direction. We reviewed "back coupling," spinal reflexes, and the closed loop of postural control to illustrate how closed loops of coupling play a role. Recent evidence for closed-loop components in reaching (Weiler et al., 2019) is not yet addressed in the theoretical sketch even though the language of neural dynamics may be well suited for providing an account. Finally, we discussed how neural timing may need to "know" about control problems, exemplifying an interdependence between the component processes that may emerge from motor learning.

We referenced neural dynamic models of various subarchitectures of our overarching picture (Erlhagen & Schöner, 2002; Grieben et al., 2020;

Schöner et al., 2019; Tekülve et al., 2016). In some cases (Martin et al., 2019, 2009; Reimann & Schöner, 2017), the mathematics of the models are not entirely consistent with the neural principles yet. This is also true for the work of Rokni and Sompolinksi (Rokni & Sompolinsky, 2012) which is otherwise closely related in spirit to our outline. Older work from the Bullock and Grossberg labs overlaps partially with our ambition (Bullock & Grossberg, 1988; Cisek et al., 1998), aligned with some of the principles we emphasize, but not all. A similar partial overlap of the neural principles characterizes the models of Butz et al. (2007) and Caligiore et al. (2014).

Another line of theoretical work uses the neural principles of DFT, but differs in specific assumptions about the neural architecture of reaching (Fard et al., 2015; Strauss et al., 2015). The core difference in this modeling line is that the timing of movement generation is postulated to derive from peaks of activation that move within a spatial representation of the end effector.

We have begun to move beyond the scenario of reaching for a single object in a DFT architecture for serially ordered sequences of reaching movements (Tekülve et al., 2019). Combining different functional components, lift and transport as well as obstacle avoidance, is the goal of a yet unpublished work (Jokeit & Schöner, unpublished).

Under more natural conditions, reaching movements are parts of overall action intentions. For instance, a human operator may reach for a tool in order to act on another object to achieve a particular outcome. This provides constraints relevant to the architecture we have outlined, for instance, in that selection of a particular grasp would be informed by future action (Herbort, 2013; Zhang & Rosenbaum, 2008). Guidance toward objects and action selection based on desired outcomes may be a general principle as postulated in ideomotor theory (Herbort & Butz, 2012; Hommel et al., 2001; Shin et al., 2010). We have begun to think about that principle in neural dynamic terms (Aerdker et al., 2022; Tekülve & Schöner, 2019), but have yet to link all this together into an integrated theory.

In conclusion, we believe that a principled neural theory of goal-directed reaching movement is possible. Many components have been recognized, and the theoretical framework of DFT enables their integration. Many open questions remain. The main strength and interest of such an integrated neural account may ultimately lie in interesting new questions which may stimulate discovery, and interesting ways the models may fail, which may stimulate insight.

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