REVIEW

Modeling discrete and rhythmic movements through motor primitives: a review

Sarah Degallier · Auke Ijspeert

Abstract Rhythmic and discrete movements are frequently considered separately in motor control, probably because different techniques are commonly used to study and model them. Yet the increasing interest in finding a comprehensive model for movement generation requires bridging the different perspectives arising from the study of those two types of movements. In this article, we consider discrete and rhythmic movements within the framework of motor primitives, i.e., of modular generation of movements. In this way we hope to gain an insight into the functional relationships between discrete and rhythmic movements and thus into a suitable representation for both of them. Within this framework we can define four possible categories of modeling for discrete and rhythmic movements depending on the required command signals and on the spinal processes involved in the generation of the movements. These categories are first discussed in terms of biological concepts such as force fields and central pattern generators and then illustrated by several mathematical models based on dynamical system theory. A discussion on the plausibility of theses models concludes the work.

Keywords Motor primitives · Discrete movements · Rhythmic movements · Dynamical systems · Central pattern generators · Force fields · Muscle synergies

1 Introduction

Humans are able to adapt their movements to almost any new situation in a very robust, seemingly effortless way.

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To explain both adaptivity and robustness, a very promising perspective is the modular approach to movement generation: movements result from combinations of a finite set of stable motor primitives organized at the spinal level [see Bizzi et al. 2008 for a review]. In this article, a motor primitive is defined as a network of spinal neurons that activates a set of muscles (which we call a synergy) in a coordinated way in order to execute a specific movement. Motor primitives are thus defined relative to the movement they produce.

In terms of control, the modularity assumption is attractive because it drastically reduces the dimensionality of the problem: instead of a complex stimulation of a vast number of muscles across the body, high-level commands can be summed up as activation signals for a finite, discrete set of motor primitives. Strong evidence, notably through the concepts of central pattern generators (CPGs) and force fields [see reviews by Grillner (2006) and Bizzi et al. (2008)], supports the existence of such functional modules at the spinal level in vertebrate animals. For instance, Kargo and Giszter (2000) have demonstrated how a finite set of spinal motor primitives could account for the natural wiping reflex in the frog, showing that the central nervous system (CNS) could use such primitives to produce natural behaviors.

Assuming the existence of such motor primitives provides an interesting framework for reflecting upon the potential differences between discrete and rhythmic movements. It allows us to reflect on these movements relative to a simplified view of movement generation: a high-level command activates a (set of) motor primitive(s) at the spinal level that generates a given kinematic outcome. Given this scheme, we can consider the potential differences between discrete and rhythmic movements that are not related to sensory feedback or muscle interaction but to the spinal processes underlying them and to the high-level commands needed to activate these spinal processes. We call this approach a functional approach to

distinguish it from the many studies focusing on the kinematics of these types of movements such as, for instance, the thorough analysis by Hogan and Sternad (2007).

Most of the studies on discrete and rhythmic movements are either based on electromyographic (EMG) analyses of the generated movements (Hogan and Sternad 2007; van Mourik and Beek 2004) or on functional magnetic resonance imaging (fMRI) analysis (Schaal et al. 2004), as will be reviewed in Sect. 3. While those studies have provided insightful results on the nature of discrete and rhythmic movements, we think that adopting a functional perspective is a useful, complementary step toward understanding the differences between the movements regarding the way they are generated, and also to gain more understanding on how brain and EMG studies can be bridged. Moreover, the generation of discrete and rhythmic movements at the spinal level has been extensively studied in vertebrates through the concepts of force fields and CPGs, respectively, providing an interesting basis for reflection.

We start by presenting a simplified model of the motor system on which we will base our reflection (Sect. 2). We then present several studies on the differences between discrete and rhythmic movements (Sect. 3) and some of the literature on the combination of these movements (Sect. 4). Although we are well aware that movement generation is a dynamic process involving the whole motor system, we discuss movement execution and movement planning separately since we think that in this way distinct properties pertaining to those two phases of movement can be emphasized, as will be discussed in Sects. 5 and 6, respectively. Furthermore, we present in Sect. 7 some existing mathematical models for the generation of discrete and rhythmic movement since such models provide important information on the generation of these movements.

2 A simplified view on motor systems

In this section, we briefly present a simple model for movement generation based on the concept of motor primitives. We consider the processes underlying the generation of both movements with an emphasis on the contribution of the spinal component of the CNS. Such a simplified structure will provide us with a framework for discussion throughout this article.

According to textbooks [see, e.g., Kandel et al. (2000)], movement generation is achieved through three motor structures organized hierarchically and corresponding to different levels of abstraction. These structures are (a) the *cerebral cortex*, which is responsible for defining the motor task; (b) the *brain stem*, which elaborates the motor plan to execute the motor task; and (c) the *spinal cord*, which generates the spatiotemporal sequence of muscle activation to execute the
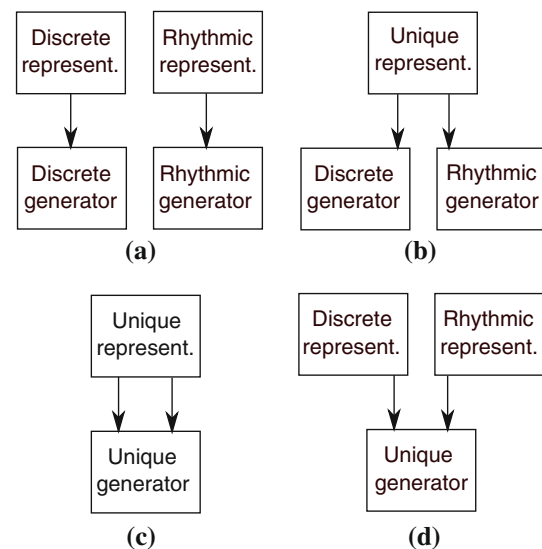

Fig. 1 The four different categories of models. **a** Two/Two, **b** One/Two, **c** One/One, **d** Two/One

task. In addition, the cerebral cortex and the brain stem are influenced by the *cerebellum* and the *basal ganglia*, which can be considered as feedback circuits, the cerebellum being connected to the spinal cord as well.

In order to consider the relationships between discrete and rhythmic movements, we will mainly distinguish between the planning (a) and the execution phase (b–c) of movements. By planning we mean all the processes required to choose the features of the movement (i.e., to *represent* the task) and by execution the processes responsible for the spatiotemporal activation of the muscles *generating* the corresponding trajectories by the limbs. Within this framework, four different possible structures for the generation of discrete and rhythmic movements need to be considered (Fig. 1).

• Two/Two

Discrete and rhythmic movements are generated through two totally different processes, at both the planning and the execution phase.

• One/Two

The planning processes involved in the generation of both movements are the same, while their generation depends on different structures.

• One/One

Discrete and rhythmic movements are two outcomes of the same process, at both the planning and the execution level.

• Two/One

The two movements involve different types of representations, while the generator is shared.

These four simple categories provide us with basic grounds for reflection on the possible differences between discrete and rhythmic movements. We will refer to them throughout this article.

3 Defining discrete and rhythmic movements

Mathematically, defining rhythmic and discrete movements is an easy task. Rhythmic refers to periodic signals, discrete to aperiodic signals. However, when considering movements that we actually perform, the task becomes more complex, the major problem being that movements are finite in time and that the formal, mathematical definition of periodicity is thus unusable. Moreover, the intrinsic variability of movements and modulation by the environment (contacts for instance) change the actual trajectory, so that it is impossible to perform a perfectly periodic trajectory.

The attempt by Hogan and Sternad (2007) to develop a taxonomy to classify discrete and rhythmic movements confirms the inherent difficulty of the task. A discrete movement is defined as a movement that occurs between two postures, where postures stand for a nonzero interval of time where (almost) no movement occurs. Rhythmic movements are categorized in four subsets, going from strictly periodic movements to movements with recurrent patterns. However, as the authors point out in the article, these two definitions are not exclusive. The so-called rhythmic movements occur in between postures (and thus enter the definition of discrete), and discrete movements can be repeated in order to become periodic.

Another difficulty derives from the fact that rhythmic and discrete movements have mainly been studied separately in the literature, although some interesting (relatively recent) articles on their combinations exist [as, for instance, Hogan and Sternad (2007) or Sternad (2007)]. From our point of view, this distinction is mainly due to two interlinked factors. First, rhythmic and discrete movements have not been studied per se in general, but mainly as outcomes of some specific processes in trajectory generation, such as, for instance, CPGs in locomotion and sensorimotor transformations in reaching. Second, studies focusing on the low-level generation of movements often concentrate on rhythmic movements such as locomotion, while those concerning high-level movement generation typically address discrete movements such as reaching or grasping. This implies different investigation techniques; most of the studies on rhythmic movements have focused on the spinal cord–brain stem system in deafferented or spinalized subjects, whereas discrete movement is usually studied using brain imaging techniques or kinematic data on awake, behaving animals. Overcoming these differences is a necessary step to understanding discrete and rhythmic movements.

These two issues make a review of rhythmic and discrete movements difficult in the sense that any comparison between the numerous studies on the subject is laborious since the methods, the point of view, and the physiological level of investigation are different. It is an interesting question whether, in terms of motor control, the apparent differences between discrete and rhythmic movements are artifacts due to different scientific approaches or if both types of movements are in fact produced independently.

Schaal et al. (2004) and van Mourik and Beek (2004), for instance, have defined three hypotheses that need to be considered: (a) rhythmic movements are repeated discrete movements (*concatenation hypothesis*), (b) discrete movements correspond to interrupted cyclic movements (*half-cycle hypothesis*), and (c) discrete and rhythmic movements result from different processes (*two-primitives hypothesis*). Note that these three hypotheses would correspond to the One/One case defined above for (a) and (b) and to the Two/Two case for (c). The mixed cases One/Two and Two/One are not considered here as the planning and the execution phase of the movements are not distinguished.

While hypotheses (b) and (c) are still untested, several studies have shown that hypothesis (a) is unlikely to be true. According to van Mourik and Beek (2004), the concatenation hypothesis is mainly a consequence of trajectory planning theory where it is often supposed that discrete segments are used as building blocks for a movement. This hypothesis has been ruled out by several studies comparing discrete and rhythmic movements (van Mourik and Beek 2004; Hogan and Sternad 2007), where key kinematic features of rhythmic movements are significantly different from those of discrete movements. Schaal et al. (2004) obtained similar results using fMRI techniques: some cortical areas activated during discrete movements were not active during rhythmic ones. In addition, as reported by van Mourik and Beek (2004), Guiard (1993) argued that the concatenation assumption would involve a waste of elastic energy (indeed at the end of a reaching movement, the energy has to be dissipated, whereas for rhythmic movement, the energy can be stored as potential energy for the remaining half-cycle).

It is important, however, to point out that those comparisons are always made between a reaching movement and its corresponding back-and-forth rhythmic movements. Thus some of the differences observed may be due to the characteristics of reaching itself (for instance, the control commands required to characterize it) rather than to the fact that reaching is a discrete movement. For instance, in the experiment conducted by Schaal et al. (2004), the subjects had to either cycle around a rest position at a self-chosen amplitude or to

stop at a chosen position, to wait for a while, and then to start again. fMRI recordings of this experiment have shown that some cortical areas active during the discrete movements were not activated during the rhythmic movements, leading to the conclusion that rhythmic movements cannot be concatenated discrete movements. However, as has been pointed out, notably by Miall and Ivry (2004), discrete movements require more processing, namely, choosing where to stop and when to start again, which could also explain the difference observed in the fMRI recordings.

Another nonnegligible phenomenon is the onset and ending of a rhythmic movement: indeed, boundary conditions change the kinematic properties of the initial and final cycles (compared to normal, in-between cycles), making them closer to those of discrete movements. Indeed, when a discrete movement is performed, the initial and final accelerations are zero, while this is not the case during in-between cycles.

van Mourik and Beek (2004) have studied the in-between cycles and first and last half-cycles separately. They came to the conclusion that, whereas the in-between cycles were significantly different from the discrete movements, the first and last half-cycles were kinematically close to discrete movements. Even if their results do not rule out the half-cycle hypothesis conclusively, they give more support to the two-primitives hypothesis: the cyclical movements performed could in fact be a sequence in a discrete, onsetting movement, followed by rhythmic movements, and terminated again by a discrete movement. A model by Schöner and Santos (2001) based on this latter hypothesis will be presented in the last part of this review.

The questions on the nature of discrete and rhythmic movements thus remain open, even if strong evidence seems to rule out the concatenation hypothesis. In the next section, we present some work on the interaction of discrete and rhythmic movements in tasks involving their combination.

4 The combination of discrete and rhythmic movements

Most of the EMG and kinematic studies on the combination of rhythmic and discrete movements are built on the same scheme: a particular joint (usually the finger or the elbow) has to be moved from an initial to a target position (discrete movement) while oscillating (rhythmic movement). The oscillation is either physiological (Goodman and Kelso 1983; Adamovich et al. 1994; Michaels and Bongers 1994; Sternad et al. 2000) or pathological (Wierzbicka et al. 1993; Elble et al. 1994; Staude et al. 2002). The reader is referred to Sternad (2007) for a thorough review.

In all these experiments, an entrainment effect is observed, that is, the discrete movement is phase-coupled with the rhythmic movement, in the sense that the onset of the discrete movement occurs preferably (though not always)

during a specific phase window of the oscillations. Goodman and Kelso (1983) showed that this phase window corresponds to the peak of momentum of the oscillations in the direction of the discrete movement. Interestingly, it has been shown that professional pistol shooters press the trigger in phase with their involuntary tremor, while beginners try to immobilize themselves before shooting (Tang et al. 2008).

In terms of EMG recordings, the burst initiating the discrete movement occurs approximately at the time where the EMG activity for the rhythmic movement would have been expected without this perturbation. This effect is thus referred to by De Rugy and Sternad (2003) as "burst synchronization." Performing the same experiment, although at different frequencies [lower for De Rugy and Sternad (2003)], Adamovich et al. (1994) and De Rugy and Sternad (2003) came to different conclusions on movement combination. Adamovich et al. (1994) observed the three following features: (a) oscillations rapidly attenuate and disappear during discrete movements and resume after the peak velocity of discrete movements; (b) there is a phase resetting of the oscillations after the completion of discrete movements; and (c) the frequency tends to be higher after discrete movements. In addition, they observed that (d) once a discrete movement is initiated, it is performed independently of the rhythmic one, in the sense that the discrete trajectory is not influenced by the rhythmic movement. Based on the monotonic hypothesis (St-Onge et al. 1993), according to which the command of the discrete movement stops at the time of its peak velocity, they concluded that discrete and rhythmic movements are excluding each other at the neural level, in the sense that they cannot co-occur. However, their kinematic outcomes outlast them and lead to overlap.

However, Sternad et al. (2000) came to a different conclusion concerning the interdependence of the two movements. Indeed, they observed a significant influence of rhythmic movements on discrete movements (lower frequencies of oscillations lead to longer discrete movements), which is in contradiction with the result (d) obtained by Adamovich et al. (1994). Moreover, the higher frequency observed by Adamovich et al. after a discrete movement (observation c) appeared to be a transient phenomenon. Following these observations, Sternad et al. (2000) proposed that both movements co-occur and that the attenuation of the oscillations during discrete movements is due to inhibitory phenomena.

Note that co-occurrence of discrete and rhythmic movements is supported by a study on whisker movements in rats by Haiss and Schwarz (2005), where it was found that rhythmic and nonrhythmic movements could be evoked through two different areas of the primary motor cortex. It was shown in addition that simultaneous activation of both areas resulted in a shift of the offset of the whisker oscillations, that is, in a combination of both movements. This experiment will be discussed in more detail in Sect. 6.

We now discuss more precisely the generation of discrete and rhythmic movements, at both the execution and the planning levels.

5 Generation of discrete and rhythmic movements

We present movement generation through two fundamental concepts, *CPGs* and *force fields*, that we develop in what follows.

CPGs, that is, a spinal network involved in many behaviors in vertebrates and invertebrates, are a seminal concept in the generation of (rhythmic) movements (Grillner 1985; Delcomyn 1980). Although most work on CPGs was originally dedicated to rhythmic movements, Grillner (2006), for instance, now extends it to discrete movements as well.

Another important discovery in movement generation is the concept of *force fields*, which has been brought to light by Bizzi's group (Bizzi et al. 1991). As we will see, force fields provide evidence for a modular organization of the spinal cord circuitry in vertebrates.

In what follows we present these two notions in more detail, as well as their relationship to discrete and rhythmic movements.

5.1 Central pattern generators

Approximatively one century ago, there were two competing explanations for the rhythmic pattern present in locomotion: one suggested that sensory feedback was the main trigger of the different phases of locomotion (Sherrington 1910), and the other suggested the existence of central neural networks capable of generating rhythms without any sensory input (Brown 1912); such neural networks are now called CPGs. Brown (1912) showed that cats with transected spinal cord and with cut dorsal roots showed rhythmic patterns of muscle activation. Even if, in the initial experiments, the transection of the dorsal roots did not exclude the influence of sensory feedback as pointed out by Grillner and Zangger (1984), there is now very clear evidence that rhythms can be generated centrally without sensory information. Indeed, experiments on lampreys (Cohen and Wallen 1980; Grillner 1985), on salamanders (Delvolvé et al. 1999), and on frog embryos (Soffe and Roberts 1982) have shown that when the spinal cord is isolated from the body, electrical or chemical stimulations activate patterns of activity, called fictive locomotion, very similar to those observed during intact locomotion. Since then, the CPG hypothesis has been strengthened by experiments on both vertebrates and invertebrates [see Stein et al. (1997) or Ijspeert (2008) for more comprehensive reviews].

Grillner (1985) proposed that CPGs are organized as coupled unit-burst elements with at least one unit per articulation

(i.e., per degree of freedom) in the body. Cheng et al. (1998) reported on experiments where these units could be divided even further with independent oscillatory centers for flexor and extensor muscles. Furthermore, several experiments have shown that CPGs are distributed networks made of multiple coupled oscillatory centers [for a review see Ijspeert (2008)].

According to Marder and Bucher (2001), two types of CPG networks can be distinguished: the so-called pacemaker-driven networks and networks with emergent rhythms. Pacemaker-driven networks, which are generally always active, as in breathing, consist of a subnetwork of intrinsically oscillating neurons that drives nonbursting neurons into a cyclic pattern, while in networks with emergent rhythms, the oscillatory pattern comes from couplings between the neurons, for instance by mutual inhibition of two reciprocal neurons. A mathematical model by Matsuoka (1985) of such a system will be presented in Sect. 7.

While sensory feedback is not needed for generating the rhythms, it has been shown that some important features of the actual motor pattern are not present in the fictive motor pattern (Stein and Smith 2001). For instance, in the cat scratching movement, the rhythmic alternation between agonist and antagonist muscles is already present in the fictive motor pattern, whereas the relative duration of extensor activity observed during actual scratching is greater than that observed in the immobilized preparation (fictive pattern). The motor pattern generated by CPGs thus seems to be modulated by the sensorimotor information so that it stays coordinated with body movements.

According to Pearson (2000), sensory feedback is also involved in the mechanisms underlying short-term and long-term adaptation of CPGs. He postulates that the long-term phenomena are driven by the body and limb proprioceptors together with central commands and the action of neuromodulators. Kawato (1996) also proposed that persistent errors detected by proprioceptors are used to recalibrate the magnitude of the feedforward command.

In summary, strong evidence exists for the existence of CPGs in animals, as rhythmic patterns of activation were observed both in decerebrated and in deafferented animals, the observed pattern being thus reasonably imputed to the spinal cord alone.

In humans, the activity of the isolated spinal cord is not observable, making the generalization of the previous results difficult: influences from higher cortical areas and from sensory pathways can hardly be excluded (Capaday 2002). However, evidence suggesting that the spinal cord with intact sensory afferents can generate rhythmic locomotorlike tonic input is provided by different studies on patients with complete spinal lesion (Dimitrijevic et al. 1998). In addition, Hanna and Frank (1995) reported steppinglike movements in patients before or after brain death, and stepping responses

have been observed in anencephalic infants just after birth (Peiper and Nagler 1963). It was shown that treadmill exercises for patients with spinal cord injuries improved their walking pattern (Barbeau and Rossignol 1994; Dietz and Harkema 2004; Edgerton et al. 2004; Rossignol et al. 2007; Wolpaw and Tennissen 2001), which may be accounted for by the fact that CPGs can be trained to function independently of descending signals (Stein 2008). Interestingly, Dietz et al. (2002) showed that in a setting with 100% body unloading (thus limiting the role of stretch reflexes), patterned leg movements could be elicited in patients with para- and tetraplegia. Moreover, studies of disabled patients have shown that in the absence of sensory information, gross movement control is preserved, even if peripheral information is necessary for precise movement organization and control (Jeannerod 1988; Gandevia and Burke 1992).

The neonatal stepping movements are an illustration of a complex intra- and interlimb coordination of muscle activity, and, even though it lacks some of the unique features of human locomotion, some of its characteristics remain with the onset of real walking, suggesting that the innate pattern could be transformed during ontogeny by neural circuits that develop later to obtain mature locomotion (Forssberg 1985).[1] Indeed, although the innate stepping response usually (but not always) disappears, the pattern used by toddlers is similar in many aspects to patterns in newborns (Forssberg 1985; Thelen and Cooke 1987). While Forssberg (1985) suggested that the inactive period may be due to a change of excitability in the CPG due to the developing descending locomotor driving signals, Thelen and Cooke (1987) argued that the innate CPGs evolved in a more task-specific pattern, notably through the maturation and experience of key subsystems such as balance, posture control, and strength. However, Ivanenko (2005) have shown that the differences between infant and adult walking cannot be imputed to balance support, since the EMG and kinematic patterns of walking in infants were unaffected by increased postural stability.

As mentioned above, most of the early work on CPGs focused on rhythmic movements, but the discovery of functional muscle synergies in the frog linked to discrete movements has led to an extension of the term, as we will see in the next section.

5.2 Motor primitives and force fields

The Bizzi group provided some evidence for the concept of motor primitives. Indeed, they brought to light that movements were generated in a modular way by the spinal cord in

frogs [for a comprehensive review, see Bizzi et al. (2008)]. More precisely, stimulating specific interneuronal areas of the spinal cord, they observed that the limb was moved in the direction of the same target posture (equilibrium point) whatever the initial position of the limb was. They called the set of the vectors corresponding to the directions obtained by the stimulation *force fields*. Surprisingly, only three to four directions, corresponding to different areas in the spinal cord, were identified (Bizzi et al. 1991); furthermore, they were sufficient to account for natural limb trajectories (Kargo and Giszter 2000).

Indeed Mussa-Ivaldi et al. (1994) found that stimulating two areas simultaneously was almost equivalent to a simple linear combination of the vector of the force fields proportional to the intensity of stimulation. 87.8% (36 of 41) of the cases could be explained by the summation hypothesis, while an alternative hypothesis, where the outcome corresponded to only one of the fields (i.e., a winner-take-all approach), was also tested and could explain 58.5% (24 of 41) of the cases. Under the hypothesis that the fields can be summed, and since the intensity of stimulation does not change the pattern of force orientation (Giszter et al. 1993), the space of possible end-effector target positions could be spanned through the weighted summation of a limited set of force fields. Note that similar results were obtained with rats (Tresch et al. 1999) and cats (Krouchev et al. 2006; Ting and Macpherson 2005).

The costimulation assumption supports the hypothesis that movements are produced through the combination of spinal motor primitives, which can be characterized by a resulting force field acting on the end effector of the limb. This seminal result could provide a powerful tool for explaining how the CNS can easily control the many muscles involved in any movement. Indeed, instead of having to activate and control the different muscles involved in the task, the CNS only has to define the level of activation of a small number of synergies. Furthermore, the combination being almost linear, it provides an efficient way of bypassing the inherent nonlinearities present in movement control using direct muscle activation. Tresch et al. (1999) have developed a variety of computational methods to extract muscle synergies involved in different movements. Identifying those synergies is a difficult task, mainly because muscles can belong to more than one synergy at a time.

In an experiment using chemical stimulation[2] (NMDA iontophoresis) of interneurons in the spinal cord of the frog, Saltiel et al. (1998) found that some regions were eliciting rhythmic behaviors. Force measurements of the limb show

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[1] It should, however, be pointed out that the role of transient neonatal reflexes is still unclear, and in particular whether these reflexes are later used to develop mature, voluntary movements or if they correspond to different control levels.

[2] Although both electrical and chemical microstimulations give the same overall picture for discrete movements (Saltiel et al. 1998), differences in the typical responses are observed that are due to the fact that electrical microstimulation excites mainly somas and axons, while chemical microstimulation excites dendrites and somas.

a finite number of synergies corresponding to the orientation of the oscillations. More precisely, in rhythmic activation, it seems that the equilibrium point changes periodically, leading to an oscillatory behavior. It is thus believed that by stimulating a particular area of the spinal cord, a whole CPG network can be activated thanks to connectivity. Interestingly, the different orientations of oscillation are very close to the direction of the force fields for discrete movements found with the same method. Furthermore, the areas of activation of the discrete and the rhythmic movements for a given orientation were topographically close (Saltiel et al. 2005). This result suggests that rhythms might arise from the temporal combination of simpler discrete modules. According to Saltiel et al. (1998), CPGs could be organized such that the discrete modules provide the orientation of the oscillations while the timing features come from the network.

It is not known yet if the concept of force fields can be extended to higher vertebrates, but it has been shown that a finite set of (time-variant) synergies of muscles could account for the movement generation in humans during fast reaching movements (d'Avella et al. 2006) as well as in primate grasping (Overduin et al. 2008), providing evidence for the existence of motor primitives.

The difference between discrete and rhythmic movements, at least at the spinal level, may thus be due to differences in the topology[3] of the network of motor primitives [CPGs, in the broad sense as in Grillner (2006)] rather than to completely distinct pathways. Indeed, discrete networks need to encode a target position and possibly a time of onset, while rhythmic networks also need to be endowed with a notion of frequency and phase. As reviewed by Marder and Bucher (2001), such features seem to emerge naturally from the intrinsic and synaptic properties of the neurons constituting these particular (rhythmic) CPGs.

In summary, there is strong evidence that basic building blocks of movements are present at the spinal level and that they are used by the CNS to create behaviors by combination. However, at this point it is still not clear if distinct motor primitives exist for the generation of discrete and rhythmic movement (One/Two, Two/Two cases) or if discrete and rhythmic movements are generated by the same process (One/One, Two/One cases). It seems reasonable to postulate that the same motor primitives could be involved in the generation of both discrete and rhythmic movements (by specifying target equilibrium points or orientations of oscillations, respectively), while features pertaining to rhythmic movements alone (such as frequency and phase) might arise

from the coupling properties of the network. In Sect. 7, we present a unique dynamical system developed by Degallier et al. (2008) that can switch between rhythmic and discrete regimes depending on the input commands.

6 Planning of discrete and rhythmic movements

We now address the question of discrete and rhythmic movement during planning. We start by presenting the possible role of motor primitives in movement planning and then discuss movement encoding by the motor cortex.

6.1 Motor primitives in movement planning

A common hypothesis on how we choose to perform a given action is that the CNS uses internal models, that is, *representations* of the sensorimotor system and the environment, to select the next action that it is going to produce. An inverse dynamic model is then required for movement initiation, that is, to find the activation commands to be sent to the muscles to fulfill the desired task.

The question of how the CNS actually computes the inverse model remains open. Indeed, inverse dynamics problems are complex, in particular in systems with many degrees of freedom, that is, with high redundancy. Additionally, the dynamics of the body change with time, as do external dynamics. According to some authors, the existence of motor primitives might help the CNS to solve the inverse dynamics problem (Bizzi et al. 1991; Mussa-Ivaldi 1999; Georgopoulos 1996). Indeed, motor primitives could provide the CNS with built-in links between muscles and movement direction and hence facilitate the resolution of the inverse problem of finding the muscle commands generating the desired trajectory (Mussa-Ivaldi and Bizzi 2000).

More precisely, we have seen in Sect. 5 that motor primitives, at least in frogs, can be combined linearly, bypassing the high nonlinearity of muscles. Thus it can be imagined that instead of solving an inverse problem to control each of the muscles needed to follow the desired trajectory, the CNS chooses a combination of motor primitives that best fits this trajectory. In this case the only task of the CNS is to optimize the activation of each motor primitive in order to minimize the error between the desired and the actual trajectories. According to what was postulated in Sect. 5, such a hypothesis could mean that discrete movements are represented during planning by the CNS by a (possibly time-varying) equilibrium point in space, whereas rhythmic movements would be represented by a (possibly time-varying) direction and a parameter controlling the emerging frequency of oscillation of the network. In both cases the specification of the speed of the movement (or another, related command signal) would also be required to fully determine the movement.

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[3] By network topology we mean the interconnections between the different elements of the network, including their direction and types (that is, if the connection is excitatory or inhibitory in our case). Indeed, the main point is to consider the behavior emerging from the interactions between the elements (for instance, a tonic or an oscillatory output), rather than the behavior of each element.

Note that the existence of and need for internal models is still debated. Basically, the opponents of internal models doubt that the brain is capable of imitating the laws of nature, which seems to be required to solve the inverse problem of finding the motor command that gives the desired kinematic outcome (for instance, the torque needed to accelerate the end effector of a limb). The reader is referred to articles by Bridgeman (2007) and Feldman (2009) for more details.

We now present some results on movement encoding that are relevant for the control of discrete and rhythmic movements.

6.2 Movement encoding by the motor cortex

The motor cortex can be subdivided into two areas, the primary motor cortex and the premotor cortex. The latter is formed by the lateral (dorsal and ventral) premotor areas and by the supplementary motor area, which are involved in learning sequences of movement, in timing, in the processing of sensorimotor information, as well as in the selection of actions.

The primary motor cortex is involved in the control of movement parameters. According to a study by Graziano et al. (2002), if the motor cortex is indeed organized somatotopically, it seems that one of the key features that is encoded in the primary cortex is the location in space toward which the movement is directed. Indeed, in their experiments, regions of the primary motor and premotor cortex of monkeys were stimulated for 500 ms (the time scale of normal reaching and grasping movements), this duration being longer than in traditional studies. They found that these stimulations were resulting in a complex movement ending in the same location, for any initial position of the limb. They concluded that, instead of encoding regions of the body, the motor cortex contains a representation of different complex postures. Note, however, that these results are still disputed, as reported in Strick (2002); some authors argue that the length of the stimulation and the high currents used do not ensure that only the motor cortex is activated, and thus the resulting movement may be mediated by areas other than the cortex itself.

The result of Graziano et al. (2002), if true, would support the hypothesis according to which some primary motor cortex neurons are connected in a one-to-one relationship with spinal motor synergies (Ashe 2005). Georgopoulos (1996) has proposed a model for movement control where levels of activation of motor cortical neurons control the weights of different motor primitives at the spinal level, that is, that cortical neurons elicit combinations of preprogrammed basic trajectories rather than encode the complexity of a particular desired trajectory. This could mean that the invariants observed in movement execution are the result of the usage by the CNS of a small set of motor primitives defined at

the spinal level rather than a kinematic plan or optimization processes in the supraspinal structures.

In particular, Haiss and Schwarz (2005) have studied the electric stimulation of different types of whisker movements in the rat, namely, rhythmic movement (used for tactile exploration) and whisker retraction (used to sense an object at a specific location). They found that both movements, although performed by the same set of muscles, were elicited by different (but adjacent) regions of the primary motor cortex. Such a result suggests different representations for discrete and rhythmic movements (Two/One and Two/Two cases), even though it is difficult to conclude at this point whether this is due to the nature of movement (rhythmic or discrete) or simply to the fact that the motor cortex encodes behaviors [as postulated by Graziano et al. (2002)]. The extension of such an experiment to a broader range of movements and animals could possibly provide further insights on the differences between discrete and rhythmic movement generation.

In the same experiment, Haiss and Schwarz (2005) found that stimulating both "discrete" and "rhythmic" areas of the primary motor cortex resulted in a simple combination of the two behaviors: the resulting movement was the oscillation expected when only the rhythmic area is activated, but with an offset corresponding to the discrete movement resulting from the activation of the discrete area. This result is important as it shows that, even if discrete and rhythmic motor primitives result from different processes, which has not yet been established, the combination of those primitives still results in a coherent, meaningful behavior. Two models, by De Rugy and Sternad (2003) and Degallier et al. (2008), representing complex movements as oscillations around time-varying offset will be presented in the next section.

7 Mathematical models for the generation of discrete and rhythmic movements

In this section, we illustrate the four categories (i.e., Two/Two, One/Two, One/One, Two/One) that were defined in Sect. 2 with six mathematical systems for the generation of discrete and rhythmic movements.[4]

All the mathematical models that we present here are based on dynamical system theory, that is, on sets of differential equations that define the evolution of a complex system in time. As we will see, this is a powerful approach to studying the qualitative time course of a system as well as the interconnections between its parts.[5]

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[4] Note that the matlab code used to generate the figures is available at http://biorob2.epfl.ch/users/degallie/bc_matlab.tar.

[5] For an excellent introduction to dynamical systems, see Strogatz (2001).

Furthermore, dynamical systems are particularly well suited for modeling discrete and rhythmic movements, as among the existing types of *stable* solutions of a dynamical system—that is, solutions robust against perturbations—two of them correspond to discrete and rhythmic signals: point attractors and limit cycles. Hence a natural solution to modeling discrete and rhythmic motor primitives is to use these stable solutions. Several examples of such modeling are presented in the following.

As a side note, combinations of stable modules are not necessarily stable themselves. However, Slotine and Lohmiller (2001) have shown that a certain form of stability, called *contraction*,[6] ensures that any combination of such contracting systems is also contracting.

7.1 Two/Two hypothesis

In the Two/Two hypothesis, it is assumed that two different, independent processes are involved in the generation of discrete and rhythmic movements. This hypothesis is convenient for modeling because each process can be optimized in order to finely reproduce the characteristics of both discrete and rhythmic movements. Yet the question of the combination and of the mutual influence of movements is left open.

We start by presenting two independent models for discrete and rhythmic generation, developed by Bullock and Grossberg (1988) and by Matsuoka (1985), respectively. These seminal models, or extensions of them, have been used extensively in the literature [e.g., Schaal et al. (2000), De Rugy and Sternad (2003), and Degallier et al. (2008)].

- **The VITE model: a neural command circuit for generating arm and articulator trajectories**
  D. Bullock and S. Grossberg,
  in *Dynamic Patterns in Complex Systems,* 1988.

The VITE (*V*ector *I*ntegration *T*o *E*ndpoint) model was originally developed by Bullock and Grossberg (1988) to simulate planned and passive arm movements. The limb position is controlled through a neural command that modifies the respective lengths of a pair of agonist and antagonist muscles according to the desired target position.

The model thus represents a motor primitive that, given a volitional target position, controls in an automatic way a synergy of muscles so that the limb moves to the desired end state. More precisely, here the brain does not encode a trajectory, but a desired final state; the actual trajectory emerges from the dynamics of the motor primitive.

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[6] Contracting systems are defined as nonlinear dynamical systems in which "*initial conditions or temporary disturbances are forgotten exponentially fast*" (Slotine and Lohmiller 2001, p. 138).
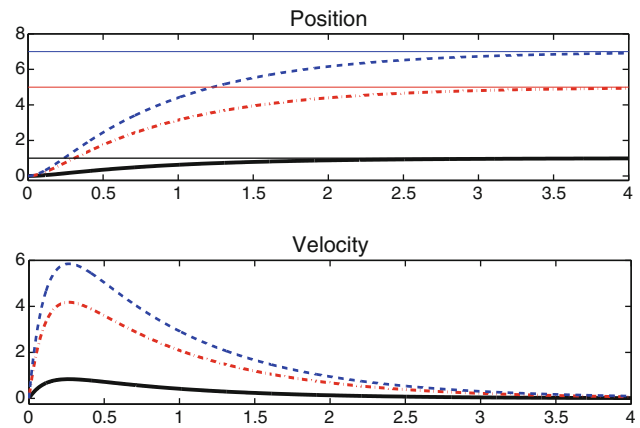

Fig. 2 VITE model. Trajectory for three different targets: $T = 1$ (*plain black line*); $T = 5$ (*dash-dotted red line*); $T = 7$ (*dotted blue line*). It can be seen that the three trajectories converge to their targets (*horizontal lines*) at the same time (*top graph*) and that the velocity peak is proportional to the displacement, i.e., to the difference vector (*bottom graph*). Here, for all systems, $G = 1$ and $\alpha = 10$

The target of the trajectory of each muscle is encoded through a *difference vector,* i.e., a population of neurons representing the difference between the desired length of the muscle (T) and its actual length (p). The movement is produced by modifying the length of the muscle at a rate v (called the *activity*) that depends on the difference vector. The whole process is gated by a *go command* (G) that is a function that can modulate the speed of the movement. There are thus two control parameters, the target length T and the go command G, the output of the system being the muscle length p. Note that the function G can be chosen to be equal to a constant, a step function, or a more complex signal. We will show the impact of the choice of the go command in Fig. 3.

Mathematical model. The following set of differential equations generates, for each muscle, a trajectory converging to the target position T, at a speed determined by the difference vector $T - p$ and the go command G:

$$\begin{cases} \dot{v} = \alpha \, (T - p - v) \\ \dot{p} = G \max(0, v) \end{cases},$$

where α is a constant controlling the rate of convergence of the auxiliary variable v.

As can be seen in the equations, the activity v of the population depends proportionally on the difference vector (the bigger the distance, the higher the activity and, thus, the speed of contraction of the muscle). In other words, the duration of the movement does not depend on the amount of contraction needed to reach the target length, but is constant, as shown in Fig. 2. Such a feature is very interesting when doing synchronized movements: indeed all the muscles automatically converge to their target length at the same time, whatever the difference between the target and the actual muscle length was. Moreover, this system is consistent with the observa-
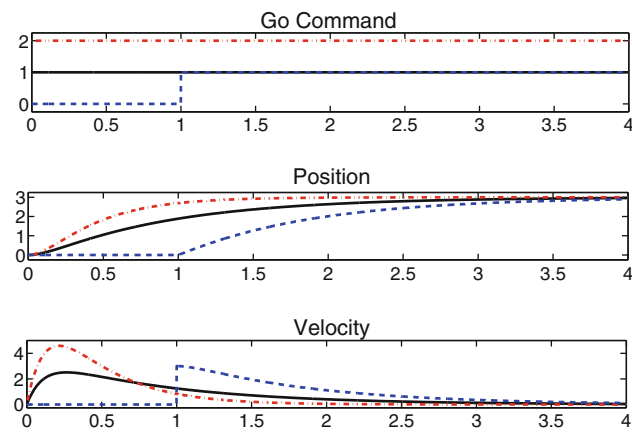
Go Command

Position

Velocity

Fig. 3 VITE model. Trajectory with three different go commands G : $G = 1$ (*plain black line*); $G = 2$ (*dash-dotted red line*); $G = 1$ from $t = 1$ s and 0 before (*blue dotted line*, *top graph*). For the three systems, the target is constant ($T = 3$). In the *middle graph*, it is shown that the go command can be used to postpone the onset of the movement and that the duration of the speed of convergence to the target can also be modulated. In the *bottom graph*, it can be seen that increasing the amplitude of the go command also increases the peak velocity. Here $\alpha = 10$

tion that human pointing movements tend to have the same duration, independently of the distance that the hand has to cover (Morasso 1981).

The go command G controls both the onset of the movement and its speed profile. Indeed, once the target length T is known, nothing prevents the movement from starting except the go command (if it is set to zero). It thus allows movements to be primed before being actually executed. In addition, the amplitude of the go command G allows for a modulation of the speed defined by the difference vector. Thus the CNS can control not only the target of the movement but also its speed. These features are illustrated in Fig. 3, with go commands modeled by simple step functions. Note that more complex functions can be chosen as go commands in order to modify (and in particular smoothen) the velocity profile, as will be shown when we present the model of Degallier et al. (2008).

In summary, the VITE model is a very simple model for generating discrete movements with open target position and speed that allows for synchronized and delayed control of several degrees of freedom. It has been extended many times to different applications, as, for instance, for visually guided reaching movements [AVITE model; see Gaudiano and Grossberg (1992)] or for modeling the interaction with the spinomuscular system to generate the torque needed to follow a specific trajectory [VITE-FLETE model; see Bullock and Grossberg (1989)].

- **Sustained oscillations generated by mutually inhibiting neurons with adaptation**
  K. Matsuoka,
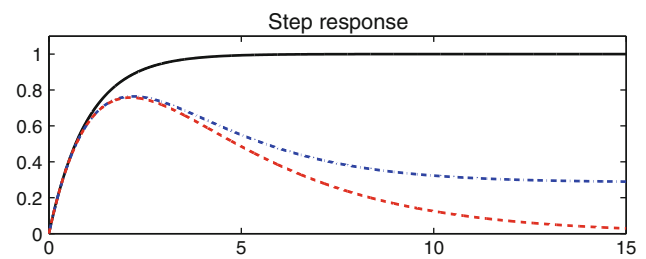 in *Biological Cybernetics,* 1985.

Step response

Fig. 4 Matsuoka oscillator. Three typical step responses of a single neuron (i.e., $S_i = 1$ in each case). *Plain black line*: fatigue parameter b is set to zero (no adaptation) and the output converges monotonically to the input value. *Blue dash-dotted line*: $b = 2.5$, the output rises but decreases after a while, showing an adaptation effect. *Dotted red line*: $b = 10$, and it can be seen that the firing rate almost returns to zero (which is the case when $b \to \infty$). In all cases, we used $\tau = 1$, $\theta = 0$, and $\tau' = 12b/2.5$ [this value was selected to prevent damped oscillation; see Matsuoka (1985)]

In this article, Matsuoka (1985) proposes a model for oscillating neural networks. As discussed in Sect. 5, it has been observed that oscillatory behaviors can emerge from networks of mutually inhibiting neurons [see, for instance, Marder and Bucher (2001)].

In Matsuoka's model, the activity of each neuron is modeled by a simple continuous-variable neuron model originally developed by Morishita and Yajima (1972). An input S_i[7] to the system increases the membrane potential x_i;. When the membrane potential is higher than the threshold value θ, the neuron starts to fire (with firing rate y_i).

Mathematical model. The equations for one neuron are:

$$\begin{cases} \dot{x}_i = \tau \left(S_i - x_i \right) \\ \dot{y}_i = \max \left(0, x_i - \theta \right) \end{cases},$$

where τ is a parameter controlling the rate of convergence of x_i and θ is the membrane threshold.

In this model, the firing rate increases monotonically and converges to a stationary state, which is not observed in neurons. Matsuoka (1985) thus extends the model to take into account the adaptation x' (also called fatigue) of the neurons: when the neuron receives a step input, the firing rate increases rapidly at first and then gradually decreases, as shown in Fig. 4. Adaptation has indeed been shown to be essential for the generation of oscillations by Reiss (1962) and Suzuki et al. (1971).

Mathematical model. The model becomes

$$\begin{cases} \dot{x}_i = \tau \left(S_i - x_i - bx'_i \right) \\ \dot{x}'_i = \tau' \left(y_i - x'_i \right) \\ \dot{y}_i = \max \left(0, x_i - \theta \right) \end{cases},$$

where $\tau'(> 0)$ and b (≥ 0) control the time course of the adaptation.

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[7] Note that while we take a single value S_i as the input to the system, it can be the weighted sum of different inputs.
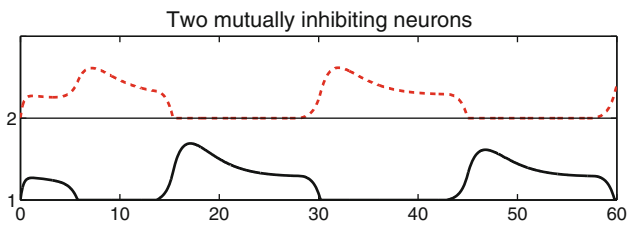
Fig. 5 Mastuoka oscillator. The firing rate for two neurons that inhibit each other, with a constant input $S_i = 1$. Parameters were set to $a_{12} = a_{21} = 2.5$, $\tau = 1$, $\theta = 0$, $b = 2.5$, and $\tau' = 12b/2.5$

The neurons are then coupled to form a network. Here self-inhibition and excitation are not considered.

Mathematical model. The equations to couple one neuron i with a neuron j are

$$\begin{cases} \dot{x}_i = S_i - x_i - bx'_i - \sum_{j \neq i} a_{ij} y_j \\ \dot{x}'_i = \tau' \left(y_i - x'_i \right) \\ \dot{y}_i = \max \left(0, x_i \right) \end{cases},$$

where a_{ij} (≥ 0) is the coupling strength of the inhibitory connections between neurons i and j and y_j is the output of neuron j. Note that here, without loss of generality, we assume $\theta = 0$ and $\tau = 1$.

Matsuoka (1985) has derived sufficient conditions for an oscillatory behavior to emerge for different types of networks. The output firing rates for two mutually inhibiting neurons are shown in Fig. 5.

Figure 6 shows two possible oscillating networks of three neurons: one where all the neurons mutually inhibit each other and the other where the neurons unilaterally inhibit each other, that is, neuron 1 is, for instance, only inhibited by neuron 2 and inhibits only neuron 3.

The model offered by Matsuoka is thus a powerful tool to model different oscillatory behaviors. Note that the model can be extended to a muscle command instead of a firing rate as output; we will see an example in the model of De Rugy and Sternad (2003).

Interestingly in this model an oscillatory pattern emerges from the combination of noncyclic units, thus reproducing the emergent rhythms observed in the spinal cord (see Sect. 5 for more details).

7.2 One/Two hypothesis

In the One/Two hypothesis, a similar encoding is used for both discrete and rhythmic movements, that is, there exists a common basic representation for the two types of movements. Such a hypothesis could reflect the analogy observed by Haiss and Schwarz (2005) between the representation of discrete and rhythmic movements in whisker movements in rats (Sect. 6). In this model, mutual influences of movements are supposed to occur at the muscle level rather than at the spinal level, as discussed above for the Two/Two hypothesis.
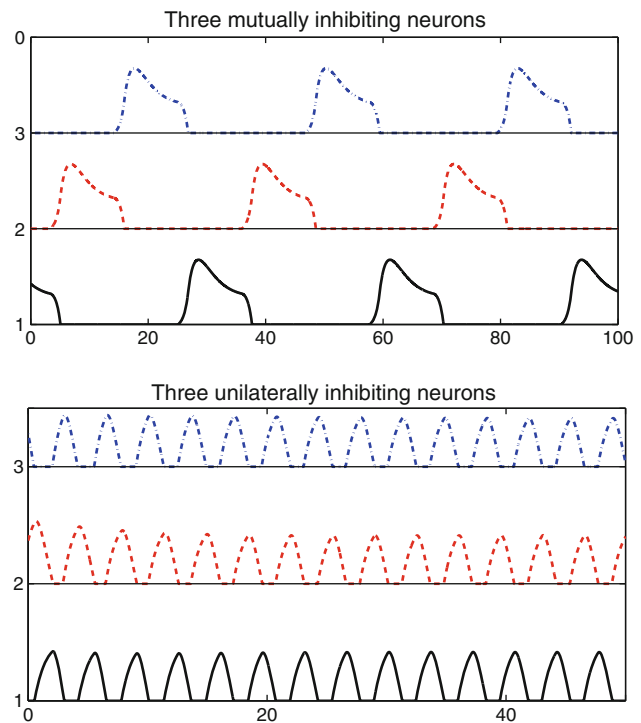

Fig. 6 Matsuoka oscillator. The firing rate for two networks of three neurons for a constant input $S_i = 1$. *Upper graph*: the neurons are inhibiting each other, i.e., $a_{ij} = 2.5 \; \forall i, j = 1, 2, 3$. In the second case, the neurons are only unilaterally inhibited, i.e., $a_{12} = a_{23} = a_{30} = 2.5$ and $a_{13} = a_{20} = a_{31} = 0.0$. Other parameters were set to $a_{21} = 2.5$, $\tau = 1$, $\theta = 0$, $b = 2.5$, and $\tau' = 12b/2.5$

We present here the model by Schaal et al. (2000), in which both discrete and rhythmic movements are encoded relatively to a difference vector: between the current and desired positions for the discrete movement and between the current and desired amplitudes for the rhythmic movement.

- **Nonlinear dynamical systems as movement primitives.**
  S. Schaal, S. Kotosaka, and D. Sternad,
  in the *Proceedings of the IEEE International Conference on Humanoid Robotics,* 2000

Schaal et al. (2000) have developed a model based on the concept of programmable pattern generators (PPGs), that is, generators of trajectories with some predefined characteristics and with some open, task-specific control parameters. Both discrete and rhythmic movements are triggered in a similar way, but they are then generated through different processes. At the end the discrete and the rhythmic output are linearly added to obtain the final trajectory.

In this model, discrete and rhythmic movements are encoded by the difference between the desired state (resp. position T and amplitude A) and the actual state (resp. p and θ); the output of the system is the position of the limb ($\alpha = p + \theta$). This system is quite complex, having many
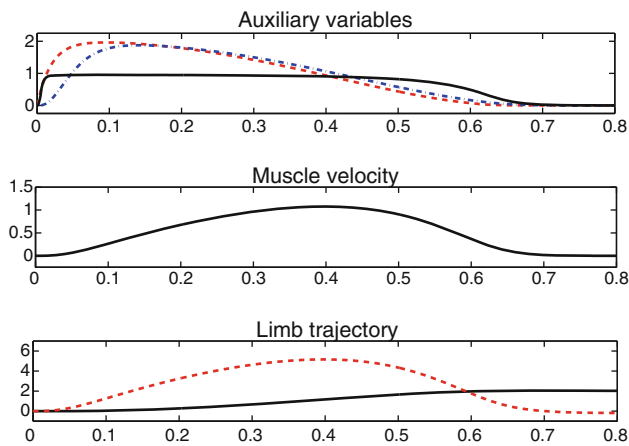
Auxiliary variables

Muscle velocity

Limb trajectory

Fig. 7 Model by Schaal et al. A typical discrete trajectory converging to the target $T = 1$. *Top panel*: activation pattern (*red dashed line*) as well as its smoothened version (*blue dash-dotted line*). The auxiliary variable r_i, which ensures that the velocity profile is roughly a symmetric, bell-shaped curve, is denoted by the *black plain line*. *Middle panel*: resulting speed z_i for muscle; *bottom panel*: resulting limb trajectory (*black plain line*) and its speed (*red dashed line*). Here $a_v = 50.0$, $a_x = 1$, $a_y = 1$, $a_r = 50$, $a_z = 0.01$, $a_p = 0.08$, $b = 10$, and $c_o = 60$

variables and parameters, so that the final output trajectory can be finely tuned to reproduce a desired movement.

The discrete system is a modified version of the VITE model presented earlier. The movement of the limb is controlled through the speed of contraction of a pair of agonist/antagonist muscles. The difference vector represents the positive difference Δw_i between the desired target position of the limb T ($-T$ for the antagonist muscle) and its actual position p. Δw is then transformed into an activation pattern v_i that resembles what is observed in the primate cortex (Fig. 7, top panel).

Mathematical model. The difference vector for muscle i, Δw_i, is transformed into an activation signal v_i

$$\begin{cases} \{\Delta \ w_i = \max{(0, T - p)} \\ \dot{v}_i = a_v(-v_i + \Delta w_i) \end{cases},$$

where a_v is a parameter controlling the rate of convergence of v_i.

The activation signal is then transformed into a velocity signal y_i through a double smoothing. The speed of the movement can be adjusted through the parameter c_0.

Mathematical model.

$$\begin{cases} \dot{x}_i = -a_x x_i + (v_i - x_i)c_o \\ \dot{y}_i = -a_y y_i + (x_i - y_i)c_o \end{cases},$$

where a_y and a_x control the rate of convergence of the system and c_o controls the speed of the movement.

Finally, the velocity y_i is integrated in order to obtain the final desired velocity z_i for the muscle change (Fig. 7, middle panel). An auxiliary variable r_i is used to make z_i roughly symmetric and bell-shaped.
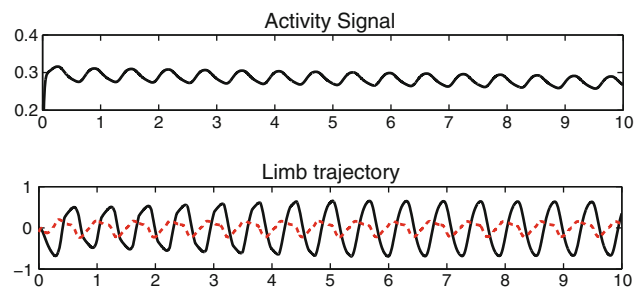

Activity Signal

Limb trajectory

Fig. 8 Model by Schaal et al. A typical rhythmic trajectory of amplitude $A = 0.6$. *Top panel*: activation pattern ξ_i. *Bottom panel*: resulting limb trajectory (*plain black line*) and its speed (*dashed red line*). Here $a_\xi = 50.0$, $a_\psi = 1.0$, $\beta = 2.5$, $w = 2.5$, and $c_r = 20$

Mathematical model.

$$\begin{cases} \dot{r}_i = -a_r(-r_i + (1 - r_i)bv_i) \\ \dot{z}_i = -a_z z_i + (y_i - z_i)(1 - r_i)c_o \end{cases},$$

where a_p and b control the shape of the signal and are chosen in order to obtain a bell-shaped velocity profile. a_z controls the rate of convergence of z_i.

The velocity commands of the agonist and antagonist muscles (i and j) are finally integrated to obtain the limb movement p (Fig. 7, bottom panel).

Mathematical model.

$$\dot{p} = a_p \left(\max{(0, z_i)} - \max{(0, z_j)}\right) c_o,$$

where a_p controls the rate of convergence of the system and c_o its speed.

As for the rhythmic movement, it is triggered in a similar way by a difference vector $\Delta \omega_i$ between the actual amplitude θ and the desired amplitude A. $\Delta \omega_i$ is turned into an activity signal ξ_i (Fig. 8, top panel).

Mathematical model.

$$\begin{cases} \Delta \omega_i = \max{(0, A - \theta)} \\ \dot{\xi}_i = a_\xi(-\xi_i + \Delta \omega_i) \end{cases},$$

where a_ξ is a parameter controlling the rate of convergence of ξ_i.

Then, a couple of mutually inhibiting Matsuoka oscillators are used to generate oscillatory velocity signals ψ_i and ψ_j. The oscillator is slightly modified to take into account the fact that ψ_i represents a velocity and not a position.

Mathematical model.

$$\begin{cases} \dot{\psi}_i = -a_\psi \psi_i + \left(\xi_i + \psi_i + \beta\zeta_i + w \max{(0, \psi_j)}\right) c_r \\ \dot{\zeta}_i = -\frac{a_\psi}{5}\zeta_i + \left(\max{(0, \psi_i)} - \zeta_i\right)\frac{c_r}{5} \end{cases},$$

where a_ψ controls the convergence rate of the oscillators and c_r the frequency of the oscillations; w controls the strength of the inhibitory coupling.

Finally, the difference between the two oscillators (i, j) is integrated to obtain the desired trajectory θ (Fig. 7, bottom panel).

Mathematical model.

$$\begin{cases} \dot{\theta}_i = \psi_i \\ \theta_r = c_r \left(\max\left(0, \theta_i\right) - \max\left(0, \theta_j\right) \right) \end{cases},$$

where c_r controls the frequency of the oscillations.

The movement of each degree of freedom is then defined by the linear combination of the output of both signals ($\alpha = p + \theta$). This linearity allows for a simple, independent control of both movements, but it fails to reproduce the mutual influence of the discrete and rhythmic movements observed in humans.

Note that the primitives can also be coupled together in order to synchronize several degrees of freedom during coordinated movement [see Schaal et al. (2000) for more details].

The many variables of the model allow for the tuning of desired basic building blocks of movements, yet also make the system quite complex. They manage to reproduce movements containing many features reminiscent of the human generation of movement, such as a bell-shaped velocity profile, for instance.

7.3 One/One hypothesis

The One/One hypothesis, which assumes that a unique motor representation and generator are used to produce movements, implies either that one of the movements is a particular case of the other one (i.e., it corresponds, more or less, to the concatenation and half cycle hypotheses mentioned before) or that discrete and rhythmic movement are themselves particular cases of a larger class of movements. The difficulty here is that the model should be designed to reproduce the mutual influences observed during movements that are both discrete and rhythmic.

We first present a model that we developed (Degallier et al. 2008), where discrete and rhythmic movements are two particular cases of a larger class of movements. In the second model, by Schöner and Santos (2001), discrete movements are a particular case of rhythmic ones, i.e., discrete movements are considered as truncated rhythmic movements.

- **A modular bioinspired architecture for movement generation forthe infantlike robot iCub.**
  S. Degallier, L. Righetti, L. Natale, F. Nori, G. Metta, A.J. Ijspeert,
  in *Proceedings of the 2nd IEEE RAS / EMBS International Conference on Biomedical Robotics and Biomechatronics (BIOROB)*, 2008.

Degallier et al. (2008) present a system where both discrete and rhythmic trajectories are generated through a unique set of differential equations, which is designed to produce complex movements modeled as periodic movements around time-varying offsets. More precisely, the solution of the
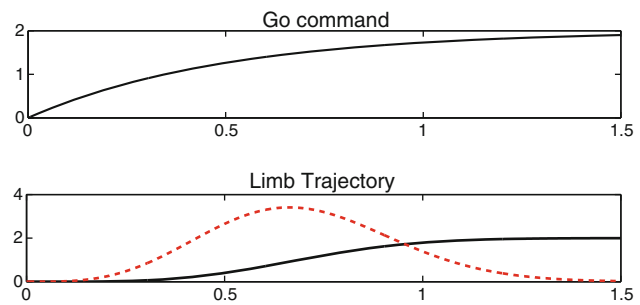

Fig. 9 Model by Degallier et al. *Top panel*: go function used in this implementation, that is, a trajectory asymptotically converging to p_i (=2 here), instead of the step functions presented in the VITE model. Such a go command turns the velocity command into a symmetric, bell-shaped curve (*red dashed line*). *Bottom graph*, *plain black line*: resulting limb trajectory converging to target $T_i = 2$. Here $d = 2$ and $b = 2.5$

system can switch between a point attractor and a limit cycle (Hopf bifurcation) depending on one single parameter, so that a unique system can be used for generating both discrete and rhythmic movements.

Here the input is a command specifying the target T_i of the discrete movement, and the amplitude M_i and frequency ω_i of the rhythmic movement. A zero (or negative) amplitude generates a purely discrete movement, and a constant offset generates a purely rhythmic movement. The output of the system is the trajectory of the limb.

The first set of equations controls the discrete movement and is inspired by the VITE model presented above. The trajectory converges toward a goal T_i and the go command G_i is chosen to ensure a bell-shaped velocity profile, as illustrated in Fig. 9. Similarly to the VITE model, all the joints converge synchronously to the target T_i.

Mathematical model. The discrete primitive, which is inspired from the VITE model, is modeled by the following system of equations:

$$\begin{cases} \dot{g}_i = d\left(p - G_i\right) \\ \dot{y}_i = G_i^4 v_i \\ \dot{v}_i = p \frac{4 - b^2}{4} \left(y_i - T_i\right) - b\,v_i \end{cases}.$$

The system is critically damped so that the output, y, converges asymptotically and monotonically to a goal T_i with a speed of convergence controlled by b, whereas the speed, v, converges to zero. p and d are chosen to ensure a bell-shaped velocity profile; h_i converges to p and is reset to zero at the end of each movement.

The rhythmic primitive is modeled as a modified Hopf oscillator, which is a simple model that allows for the generation of sinusoidal movements of amplitude $\sqrt{M_i}$ (when $M_i > 0$) and frequency ω_i (defined as a combination of the ascending and descending frequencies ω_{up} and ω_{down}; see below). These oscillations can be switched on and off easily through the parameters controlling the amplitude, more
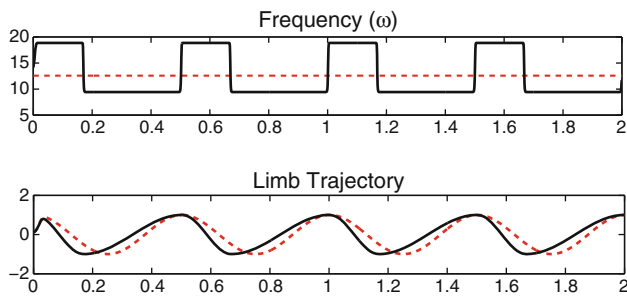
Fig. 10 Model by Degallier et al. *Top panel*: value of frequency ω_i modulated through parameters ω_{up} and ω_{down}. *Dashed red line*: $\omega_{up} = \omega_{down}$, and the resulting movement (*bottom panel*) is a normal sinusoidal movement. *Black, plain line*: $\omega_{down} > \omega_{up}$ and the resulting trajectory is a distorted sinusoidal. Note that only ω_{down} is controlled, ω_{up} being calculated so that ω_i is constant. Here $\omega_i = 2\pi$ and $\omega_{down} = 4\pi$ for the *red curve* and $\omega_{down} = 6\pi$ for the *black curve*. Other parameters are set to $a_i = 100$, $M_i = 1$ and $f_i = 100$

Fig. 11 Model by Degallier et al. *Top panel*: target T_i for discrete movement; the resulting trajectory is shown in *bottom panel* (*dashed blue line*). *Red dash-dotted line*: amplitude control parameter M_i (*top panel*) and resulting trajectory (*bottom panel*). *Bottom panel, plain black line*: combined trajectory. Note that it is not a simple linear combination of the discrete and rhythmic trajectories, which shows the influence of the embedding of the two dynamics. Here $\omega_i = 4\pi$, $p_i = 2$, $d_i = 2$, $b_i = 2.5$, $a_i = 100$, and $f_i = 100$

precisely, by bifurcation between a limit cycle behavior and a single point attractor.

In this model the expression for the frequency ω_i is slightly modified to allow independent control of the duration of the ascending (ω_{up}) and descending (ω_{down}) part of the sinusoidal movement, as illustrated in Fig. 10. This feature is particularly useful for independent control of the swing and the stance duration in locomotion.

Mathematical model. The oscillator is governed by the following set of equations:

$$\begin{cases} \dot{x}_i = a(M_i - r_i^2)x_i - \omega_i z_i \\ \dot{z}_i = a(M_i - r_i^2)z_i + \omega_i x_i \\ \omega_i = \frac{\omega_{down}}{e^{-f z_i}+1} + \frac{\omega_{up}}{e^{f z_i}+1} \end{cases},$$

where $r_i = x_i^2 + z_i^2$. a controls the rate of convergence to the limit cycle and f the rapidity of the switching between swing and stance.

The two primitives are then combined together by embedding the discrete movement y_i into the rhythmic one as an offset. The system output x_i is now an oscillatory movement around a time-varying offset.

Mathematical model. The oscillator is governed by the following set of equations:

$$\begin{cases} \dot{x}_i = a(M_i - r_i^2)(x_i - y_i) - \omega_i z_i \\ \dot{z}_i = a(M_i - r_i^2)z_i + \omega_i(x_i - y_i) \end{cases},$$

where now $r_i = \sqrt{(x_i - y_i)^2 + z_i^2}$.

Qualitatively, by simply modifying on the fly the parameters T_i and M_i, the system can switch between purely discrete movements ($M_i < 0$, $T_i \neq$ const), purely rhythmic movements ($M_i > 0$, $T_i =$ const), and combinations of both ($M_i > 0$, $T_i \neq$ const), as illustrated in Fig. 11.

This system allows for a simple modeling of discrete and rhythmic movements. Both dynamics influence each other, and when the movements co-occur, the discrete movement
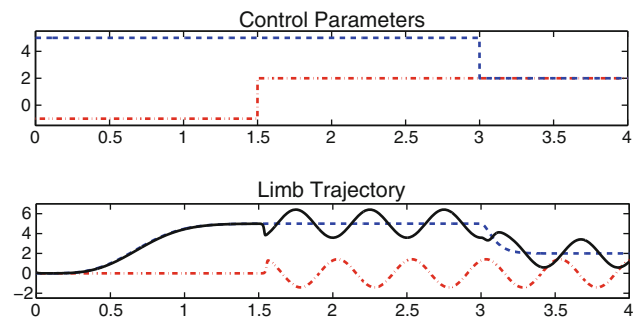
inhibits the rhythmic one, as observed in humans [see Sternad et al. (2000), and Sect. 4].

- **Control of movement time and sequential action through attractor dynamics: a simulation study demonstrating object interception and coordination.** G. Schoner and C. Santos, in *Proceedings of the 9th Intelligent Symposium on Intelligent Robotic Systems,* 2001.

The model developed by Schöner and Santos (2001) was built to generate discrete movements, but it is based on limit cycles, which makes it easy to extend to the generation of rhythmic movements. Here the input is the target position T of the limb and the output is its trajectory.

In this model, discrete and rhythmic movements are both modeled using limit cycles, i.e., discrete movements are interrupted rhythmic movements. More precisely, here the attractor is a whole trajectory going from the initial position to the target position (contrarily, for instance, to the VITE model where the trajectory is a transient phenomenon and only the target position is a stable attractor). This model can thus successfully explain the observation by Bizzi et al. (1984) and Won and Hogan (1995) that when a limb is perturbed during movement execution, it has a tendency to resume the original trajectory, that is, it seems that not only the target position matters, but also the trajectory leading to it.

A two-layer system is used consisting of a layer capable of generating both oscillations and stationary states ("timing layer") and another layer controlling the switching between those states ("neural dynamics control"). The timing layer consists of three terms: the first one is an attractor toward the initial state x_i, the second is a Hopf oscillator of amplitude 1, and the third is an attractor toward the target position X_f. All these terms are multiplied by the activity level of three "neurons" that are never fully active simultaneously.
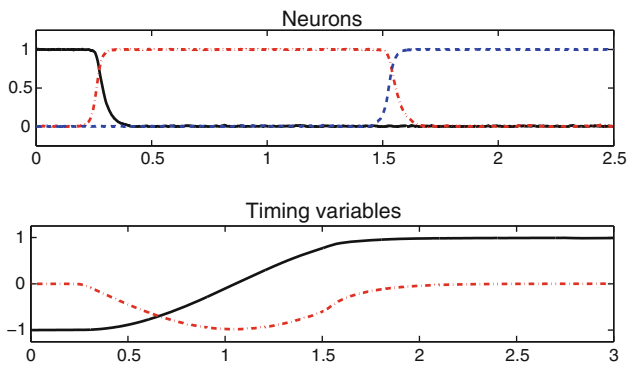
Fig. 12 Model by Schöner and Santos. *Top panel*: activity of three neurons (u_i, *plain black line*; u_h, *dash-dotted red line*; u_f, *dashed blue line*) during a typical discrete movement can be observed. Only one neuron is active at a time, corresponding to three stages of the movement: rest at initial position, move to the target, and rest at the target position. *Bottom panel*: obtained trajectory x_i is shown (*plain black line*) as well as the auxiliary variable y_i. Here $a = 5$, $b = 1$, $\omega = 2$, $c = 2.1$, and $\alpha = 0.02$

Mathematical model. The equations of the timing layer are given by

$$\begin{cases} \dot{x} = -a\,|u_i|\,(x - x_i) + |u_h|\left(b\left(1 - r^2\right)x - \omega y\right) - a\,|u_f|\,(x - X_f) \\ \dot{y} = -a\,|u_i|\,y + \left|u_h\left(b\left(1 - r^2\right)y - \omega x\right) - a\,|u_f|\,y\right| \end{cases},$$

where x is the output of the system and y an auxiliary variable, and a and b control the speed of convergence of the system. In this system, $|u_i|$ ($i = i$, h, f) represents neurons that are never active (i.e., $u_i = 1$) simultaneously.

The sequence of movements is controlled by the neural layer, and more precisely through three neuron activities u_i, u_h, and u_f activating the first attractor, the Hopf oscillator, and the target attractor, respectively. At rest position only the first attractor is active ($u_i = 1$, $u_h = 0$, $u_f = 0$), so that even if perturbations occur, the limb stays at the same position. Then, when a command is received, the Hopf oscillator is activated ($u_h = 1$) and the first attractor is deactivated ($u_i = 0$), so that the trajectory follows the limit cycle until it is close enough to the final target. At this moment the Hopf neuron activity u_h is set to zero and the final attractor is activated ($u_f = 1$) so that the trajectory converges to the target position X_f. This sequence of actions is illustrated in Fig. 12.

Mathematical model. The timing of activation of the three "neurons" is controlled by the neuronal dynamics, which are given by the following equations:

$$\begin{cases} \alpha\dot{u}_i = \mu_i u_i - |\mu_i|\,u_i^3 - c\left(u_h^2 + u_f^2\right)u_i \\ \alpha\dot{u}_h = \mu_h u_h - |\mu_h|\,u_h^3 - c\left(u_i^2 + u_f^2\right)u_h \\ \alpha\dot{u}_f = \mu_f u_f - |\mu_f|\,u_f^3 - c\left(u_i^2 + u_h^2\right)u_f \end{cases}.$$

Each equation corresponds to the normal form of a degenerate pitchfork bifurcation controlled by parameters[8] μ_i, with

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[8] That is, the system has one stable solution ($u = 0$) when μ_i is negative and two stable ones ($u_i = 1$ and $u_i = -1$) when μ_i is positive.

an extra term to ensure that only one neuron is active, i.e., that any solution with more than one neuron active is destabilized. The parameters μ_i are given by

$$\begin{cases} \mu_i = 1.5 + 2b_i \\ \mu_h = 1.5 + 2\,(1 - b_i)\,(1 - b_f)\,, \\ \mu_f = 1.5 + 2b_f \end{cases}$$

where $b_i = 1$ is equal to 1 when no movement occurs and is set to 0 to activate the movement, and

$$b_r = 1 - \tanh\left(10\left(0.7X_f - x_r\,(i)\right)\right) + 1)\,/2.$$

Movements can thus be shaped through the neuronal dynamics that qualitatively change the space of solutions of the timing layer. The trajectory in three parts produced by this model (i.e., discrete, rhythmic, discrete) is analogous to the observation by van Mourik and Beek (2004) that the first and last half-cycles of a rhythmic movement resemble a discrete movement. In systems with multiple degrees of freedom, coordination can be obtained through the coupling of rhythmic parts of the system [see Schöner and Santos (2001) for more details]. Synchronized discrete movements can be obtained through coupling.

7.4 Two/One hypothesis

In the Two/One hypothesis, two different motor commands are sent to the same generator. An open question is then how the two motor commands are combined. We present here a model developed by De Rugy and Sternad (2003), initially to explain the phase entrainment effect, where both commands are simply summed.

- **Interaction between discrete and rhythmic movements: reaction time and phase of discrete movement initiation during oscillatory movements.**
  A. de Rugy and D. Sternad,
  in *Brain Research*, 2003

This model was originally developed to explain the phase entrainment effect observed in humans (see Sect. 4 for more details). Here a motor command S, composed of the sum of a discrete S_d and a rhythmic S_r command inputs, is sent to a two-neuron Matsuoka oscillator to generate two firing rates (x_i, x_j). These firing rates are then transformed into muscle commands ($\mathcal{T}_i$, $\mathcal{T}_j$) for a pair of agonist–antagonist muscles and finally to a limb trajectory θ.

The discrete command is modeled as a pulse followed by an exponential decay, resulting in a damped oscillation that, with well-tuned parameters, will later generate a discrete movement. The rhythmic command is simply a constant signal.

Mathematical model. The input command is given by

$$S = S_r + S_d,$$

where $S_r = \text{const}$, and

$$\dot{S}_d = \tau_s \left(-S_d + P_d\right),$$

where P_d is the peak value of the pulse and τ_s a time constant.

A network of two mutually inhibiting Matsuoka oscillators is then used to transform this neural command S into the firing rates (x_i, x_j) of two motoneurons controlling a pair of agonist–antagonist muscles.

Mathematical model. The network is governed by the following equations (for one neuron):

$$\begin{cases} \dot{x}_i = \tau_1 \left(-x_i - \beta x_i' + S - \omega \max\left(0, x_j\right)\right) \\ x_i' = \tau' \left(-x_i' + \max\left(0, x_i\right)\right) \end{cases},$$

where τ and τ' are two parameters controlling the time course of, respectively, the firing rate x_i and the fatigue (or self-inhibition) x_i', β is the gain of the fatigue component, and x_j is the output of the second neuron.

The firing rates of the neurons (x_i, x_j) are then transformed into torques $\left(\mathcal{T}_i, \mathcal{T}_j\right)$ exerted by a pair of agonist–antagonist muscles.

Mathematical model. The torques are obtained through the following equations:

$$\begin{cases} T_i = h_T \max\left(0, x_i\right) \\ T_i = -h_T \max\left(0, x_j\right) \end{cases},$$

where h_T is the gain of the torques.

Finally, the action of the torques on the movement of the joint θ is deduced from the dynamics of the limb.
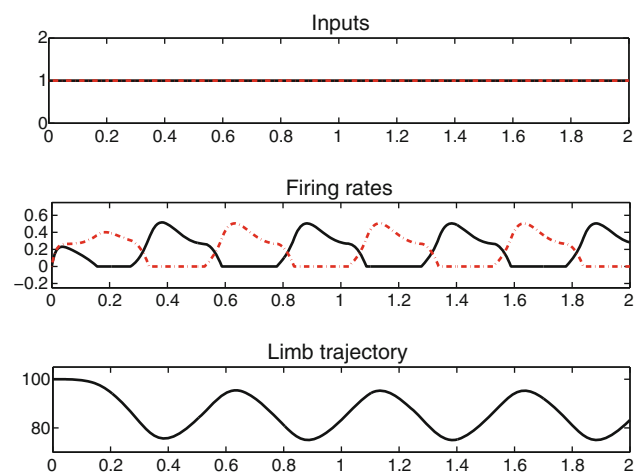

Fig. 13 Model by De Rugy and Sternad. A purely rhythmic command $S = S_r = 1$ (*top panel*) leads to oscillations of the coupled neurons (*middle panel*) and the limb (*bottom panel*). Here $\gamma = 0.5$, $I = 0.08$, $h = 5$, $\tau = 0.05$, $\tau' = 0.125$, $\tau_s = 0.2$, $\beta = 2.5$, and $\omega = 2.5$
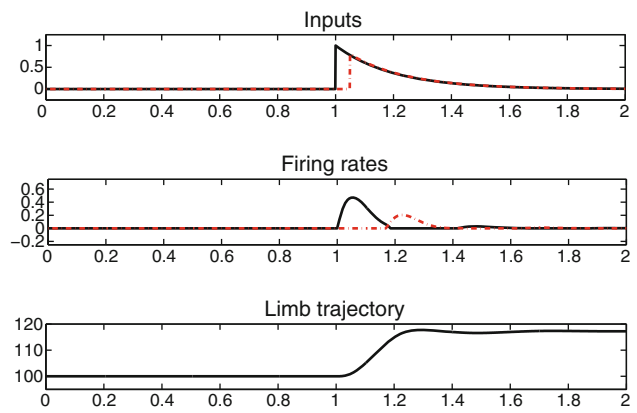

Fig. 14 Model by De Rugy and Sternad. A purely discrete command $S = S_d$ of peak $P_d = 1$ (*top panel*) leads to strongly damped oscillations of the neurons (*middle panel*), resulting in a discrete movement of the limb (*bottom panel*). Here $\gamma = 0.5$, $I = 0.08$, $h = 5$, $\tau = 0.05$, $\tau' = 0.125$, $\tau_s = 0.2$, $\beta = 2.5$, and $\omega = 2.5$
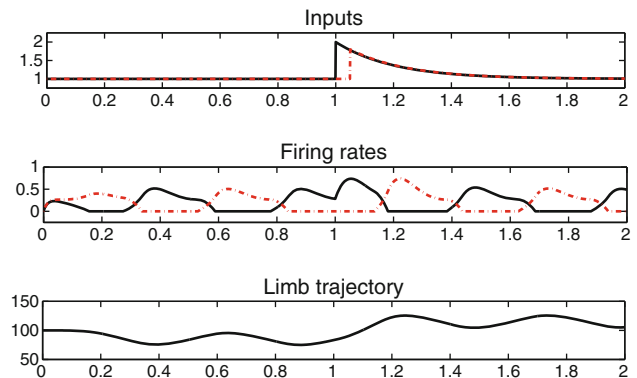

Fig. 15 Model by De Rugy and Sternad. A combined command $S = S_r + S_d$ with $S_r = 1$ and $P_d = 1$ (*top panel*) leads to a perturbed oscillatory behavior of the neurons (*middle panel*), resulting in a rhythmic movement around a varying offset (*bottom panel*). Here $\gamma = 0.5$, $I = 0.08$, $h = 5$, $\tau = 0.05$, $\tau' = 0.125$, $\tau_s = 0.2$, $\beta = 2.5$, and $\omega = 2.5$

Mathematical model. The dynamics of the limb is governed by the following equation:

$$1\ddot{\theta} + \gamma\dot{\theta} - \left(T_i + T_j\right) = 0,$$

where I is the inertia of the limb and γ is its damping.

Figure 13 illustrates the output of the model for a rhythmic command (that is, a constant input). The oscillating firing rates are transformed into a smooth, sinusoidal trajectory through the dynamics of the limb. In Fig. 14, it is shown that a purely discrete movement can be obtained using a peak motor command. Finally, in Fig. 15, the combination of both command signals and the resulting, combined trajectories are shown.

In this model, there is an entrainment effect that emerges from synchronization effects between the two Matsuoka neurons. The distribution of the offset, as well as the phase lag

observed in human subjects, was successfully reproduced by this model [De Rugy and Sternad (2003)]. Note that this model has been extended by Ronsse et al. (2009) to integrate reafferent signals, and thus to capture bimanual features.

7.5 Discussion of the models

We have presented different mathematical models whose principal characteristics are summarized in Table 1. All these models are based on the concept of motor primitives, that is, simple, nonpatterned commands from the brain are turned into complex output trajectories governed by the dynamics of the system. So even though the outputs of the models are not at the same representation level, they can easily be modified to account for another level of representation [for instance, De Rugy and Sternad (2003) apply the model of firing rates of neurons of Matsuoka (1985) to limb control by extending the system to the muscles and the limb dynamics].

All these models are successful in producing more or less complex discrete and rhythmic trajectories (except for the models of Matsuoka and Bullock, which only model one type of movement). However, in order to be plausible, these models should also be able to reproduce the interaction observed in humans between discrete and rhythmic movements mentioned in Sect. 4. As stated earlier, there are two main studies on the subject by Adamovich et al. (1994) and Sternad et al. (2000), and they come to different conclusions. While they both agree that the rhythmic movement is inhibited by the discrete one, the phase of the rhythmic movement is reset after the discrete one, and the frequency tends to be higher after the discrete movement [transient phenomenon according to Sternad et al. (2000)], Adamovich et al. (1994) conclude that (d1) the discrete trajectory is not influenced by the rhythmic movement, which is refuted by Sternad et al. (2000), who observe that (d2) the rhythmic movement influences the discrete one, or, more precisely, lower frequencies of oscillations lead to longer discrete movements.

To rule out either the Two/Two–One/Two or the One/Two–One/One categories, an efficient way to proceed would be to determine whether the mutual influence between discrete and rhythmic movements appears at the spinal or at the muscular level, i.e., if the discrete and the rhythmic dynamics influence each other because there is a unique spinal motor primitive generating them or if it is an artifact due to overlaps during the actual production of the movement. More precisely:

- In both the Two/Two and One/Two hypotheses, the question of the combination of the two movements is left open; more precisely, the interaction has to happen at a lower level of the generation process, that is, at the muscular level, as proposed, for instance, by Adamovich et al. (1994) or by Staude et al. (2002). Adamovich et al. (1994) postulate that discrete and rhythmic movement cannot co-occur, i.e., that any movement can be seen as a sequence of discrete or rhythmic movements. According to them, the mutual influence observed is due to the overlapping of the kinematic outcome of the two movements: they postulate that the kinematic outcome of a movement lasts longer than its generation. Note that this view is not shared by Sternad et al. (2000), as discussed earlier (Sect. 4). Staude et al. (2002), for their part, propose that complex movements arise from the summation of the two movements subject to a threshold-linear mechanism; it is interesting to note that this simple model manages to model the entrainment effect presented in Sect. 4 [see Staude et al. (2002) for more details].

- In the One/One hypothesis, the distinction between discrete and rhythmic movements is assumed to be an artifact of movement categorizations, both movements being in fact generated through the same process. In these models, the notion of interaction of the two movements is an ill-posed problem, as they indeed are produced by the same process. In this model, the mechanisms listed above should thus emerge from the dynamics of the system.

Table 1 Main properties of the different models

Model	Category	Type	Ctrl	Var	Param
Bullock et al.	Two/Two	D	2	2	1
Matsuoka	Two/Two	R	n	$3n$	$3n + n(n-1)$
Schaal et al.	One/Two	D+R	2	26	13
Degallier et al.	One/One	DR	3	5	5
Schöner et al.	One/One	D⊂R	2	7	8
De Rugy et al.	Two/One	DR	1	5	6

Type refers to the type of movements and their relationship: D discrete only, R rhythmic only, $D + R$ discrete and rhythmic as a linear combination of the generator outputs, DR discrete and rhythmic as a unique generator output, $D \subset R$ discrete as truncated rhythmic. *Ctrl* is the number of high-level commands needed to specify the movement, *Var* is the number of variables, and *Param* is the number of parameters of the system. For the Matsuoka model, n refers to the number of neurons involved in the network

- In the Two/One hypothesis, only the representation of the movements is different, the process generating them being the same. In this case, as in the One/One hypothesis, the observed mutual influence should emerge from the dynamics of the motor primitives, as, for instance, the entrainment effect in the model by De Rugy and Sternad (2003).

8 Conclusion

In this review, we have shown that the concept of motor primitives is an interesting approach to the question of the generation of discrete and rhythmic movements and its modeling, notably through the definition of four categories of models for movement generation illustrated by mathematical models found in the literature. Such categories provide a framework for the analysis of different approaches to the generation of discrete and rhythmic movements and thus to discard or corroborate these approaches.

Since we have chosen to take a functional approach, most of the results that we have presented come from animal studies. Even if these results cannot necessarily be generalized to humans in a straightforward way, we believe that they can provide insights into the processes underlying discrete and rhythmic movement generation in humans.

Synergies of muscles have been observed in vertebrates (as reviewed in Sect. 5), which indicates that movement may be built through the combination of spinal building blocks of movements that we call motor primitives. Such an assumption has strong implications for the analysis of discrete and rhythmic movements, in the sense that the intrinsic difference between them may lie at the spinal level rather than in the high-level commands used to encode them. Indeed, evidence has been presented that both discrete and rhythmic movements could result from spinal motor primitives elicited by simple, nonpatterned brain commands, suggesting that the two types of movements may simply emerge from a difference in the topologies (oscillatory or not) of the spinal network underlying them.

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