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Title: Modeling Discrete and Rhythmic Movement through Motor Primitives: A Review

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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, an increasing appeal for a comprehensive model of movement generation requires to bridge the different perspectives arising from the study of those two types of movements.

In this article, we consider discrete and rhythmic movement within the framework of motor primitives, that is of modular generation of movements. Doing so, we hope to get insights on the functional relationships between discrete and rhythmic movements and therefore on suitable representations of both rhythmic and discrete movements.

We start by reviewing some of the existing literature regarding discrete and rhythmic movement, that we study from a functional view point. We then present some mathematical models found in the literature for the generation of discrete and rhythmic movements.

Response to Reviewers: See attachment "response.pdf"

Response to reviewers

First, we would like to thank both reviewers for their useful comments.

Reviewer 2: *This review concerns the paper entitled "Modeling Discrete and Rhythmic Movement through Motor Primitives: A Review", by S. Degallier and A. Ijspeert. The manuscript was submitted to Biological Cybernetics.*

My global comment is that this paper is well written and very clear. It would need minor clarifications/corrections to be accepted. The paper gathers nice concepts about motor control, motor primitives, and mathematical model. I enjoyed reading it.

Here are first two general comments concerning the paper as a whole:

- *You propose Bizzi's view about equilibrium point as the control framework for discrete movement. While Bizzi's group obtained intriguing results to validate this framework, some authors have also questioned this theory (Hinder and Milner, J. Physiol. 549, 2003; or Liu and Todorov, J. Neurosci. 27, 2007), suggesting that discrete movements might be generated from optimization principles. Interestingly, the first paragraph of your introduction refer to the modular organization of movement generation (a correlate of Bizzi's framework) as a nice ground to explain adaptation of movements. Recently, Izawa et al. (J. Neurosci. 28, 2008) have instead suggested that adaptation of discrete movements could result from reoptimization processes. It would be very interesting that you discuss the similarities and dissimilarities between the two approaches, and to what extent the equilibrium approach is really necessary to your contribution. For example, de Rugy et al.'s model is not based on equilibrium-point hypothesis (as far as I understand it).*

  Response. *** The term equilibrium point is here a bit misleading. Indeed, when speaking of force fields we refer to an equilibrium position in space (as used by Bizzi et al in for instance Neuroscientist, 2002), not to muscles rest position (as used by Feldman).

  We do not consider motor primitives at the planning level, but only at the execution level, thus, to our point of view, there is no contradiction with optimization-based approaches. Indeed motor primitives [taken as functional neural and/or muscular units responsible for the generation of a specific movement] are consistent with internal models and optimization-based approaches; motor primitives are indeed believed to be used by the CNS to solve the inverse dynamics problem of finding the motor command corresponding to a planned limb movement (see for instance Mussa-Ivaldi, 1999, Current Opinion in Neurobiology). That is motor primitives provide the CNS with built-in links between muscles and movement direction and hence facilitate the resolution of the inverse problem of finding the muscles commands generating the desired trajectory. We have tried to make this point clearer in the introduction and in the following sections.

- *You should be more cautious when generalizing results and concepts that were obtained with animals (mainly if non-primates) to humans. This is* *clearly stated when you discuss the CPG work (for which only indirect evidences exist for humans) but - in relation to my 1st remark - not when you discuss the generation of discrete movements. It is very likely that the complexity of discrete movements (and the repertoire of possible discrete movements) correlates with the volume of some cortical areas across species, suggesting that the mode of control is certainly more complex in humans than in frogs.*

Response. A paragraph presenting results concerning primates (including humans) has been added; it has notably been shown that a finite set of synergies could account for fast reaching movements in humans (d'Avella et al., Jour. of Neurosci., 2006) providing evidences that the concept of motor primitives mgiht be extendable to higher vertebrates. Note that in the specific section that you are mentioning, we focus mainly on the execution of the movement at the spinal level, not on the planning of the movements in higher areas.

Here are some others remarks, listed as they appear in the text:

- *p.2, left col., line 10: You propose to take a functional perspective. While very central to your contribution, this terminology does look clear to me. Please be more specific. What is a functional perspective? How does it differ from previous work?*

  Response. We have defined more precisely what we mean by a functional perspective:
  By *functional perspective*, we mean that contrarily to other previous approaches, we focus on the processes underlying the generation of the movements rather than on the kinematic outcomes of the movement.

- *p.4, section 4: I wondered why this section should not come first (after introduction). This is very nice material and summary.*

  Response. This section has been moved after the introduction.

- *p.4, right col., line 8: please define "somatosensory information" (extra footnote).*

  Response. The term has now been defined as a footnote as follows:
  The term *somatosensory information* refers to different sensory signals from all major parts of the body, namely proprioception (that is muscles and joints position), touch, pressure, temperature and pain (see Kandel et al., *Principles of Neural Science* (2000) for instance). Note that these different signals do not all use the same pathway.

- *pp.6-7, section 6.1: you nicely summarize the concept of internal models. To what extent is this framework not in opposition with the equilibrium point theory? In a recent paper (Exp Brain Res 194, 2009), Feldman (one of the "popes" of the equilibrium-point theory) argue that efference copies of motor commands in the brain (a necessary element of internal models) are not necessary if one adopts his view on the generation of discrete* *movements. How do you conciliate Internal Models and Equilibrium Point Theory in your paper?*

Response. See Response*** above.

- *p.7, left col., last par. of section 6.1: I do not understand this paragraph. How do you conclude that internal models mean that the CSN represent discrete movements as time-varying equilibrium-points? Please be more explicit.*

  Response. See Response*** above.

- *pp.7-8, section 6.2: even if it gathers nice material, I do not see the interest of this section for your paper. What does it bring to your message? I believe that this section (at least for the part going to line 39 of p.8) can be drastically reduced.*

  Response. This part has been reduced. The pertinence of what has been kept has also been emphasized. Our aim is to link movement encoding with the concept of motor primitives before introducing the existing literature on discrete and rhythmic movements encoding per se.

- *p.15, section 7.4: when citing de Rugy et al.'s model, please also refer to Ronsse et al. (Neural Computation 21, 2009). These authors extended de Rugy's model to cope with reafferent signals, and to capture some bimanual coordination features.*

  Response. Thanks for the reference, it has been added.

Reviewer 3: *Modeling Discrete and Rhythmic Movement through Motor Primitives: A Review - Sarah Degallier and Auke Ijspeert*

The aim of the paper is to review the existing studies and bridge between different perspectives when approaching the studies of discrete versus rhythmic movements using the motor primitives' framework.
In general this is a research topic which is of major interest to Motor Control researchers and generally the authors did quite a good work in compiling the major concepts that are in the scientific forefront when studying discrete versus rhythmic movements. The paper reviews current neurophysiological literature and surveys the many different existing approaches to the problem of controlling such movements by looking at two levels- the level of command and the level of generators, the reviewed models are divided into several groups : the so called Two/Two, Two/One, One/One and One/Two schemes.
Hence, the authors provide quite a useful roadmap to researchers becoming interested in this topic and such readers may find the review as providing an illuminating entry point. Still, the paper should undergo revision since there are several important aspects of the review that should be dealt with as follows.

General comments:

- *It is said in the introduction that experiments have shown that motor primitives seem to be present at the planning and execution levels. Still the paper reviews mainly dynamical systems based models and approaches and the review does not seem to adequately review the topic of the existing of motion primitives for discrete and rhythmic movements at the kinematic level. While given that the paper covers a large number of issues and topic, this confinement to these aspects is quite well understood, the fact that the paper focuses on certain aspects of this general topic and not others should be clearly stated in the introduction.*

  Response. This comment is related to the one of Reviewer 2 who required more explanation on the term *functional* (please see above). Indeed we meant by that the we focus on the generation process more than on the outcome of the movement (even if both are obviously tightly linked), notably because Hogan and Sternad (Exp. Brain Research, 2007) did an excellent work in analyzing the kinematics of discrete and rhythmic movements. The present review thus aims at being a complement to such analyses. To clarify this, the following footnote has been added in the introduction:
  In this review, by *motor primitive* we mean a functional neural and/or muscular unit responsible for the generation of a specific movement. As such a topic is already dense, we do not consider motor primitives in trajectory planning or more generally in the kinematic outcome of the movement. The reader is referred to Hogan and Sternad (Exp. Brain Research, 2007) for a thorough kinematic analysis of discrete and rhythmic movements.

- *A review, I believe, should be as impartial as possible. Whereas a research paper has an agenda to promote, a review paper should not choose sides and should represent the various existing view points on the subject.*
  In that respect, there is still a great debate revolving the existence or even the justification for the need of internal models in the community. Of course, here primitives provide a framework for the current review and the link between primitives and internal models is natural. Nevertheless, the authors should also present in more details other alternative views (e.g. Equilibrium point hypothesis). Thus, while the equilibrium point control is mentioned briefly from the perspective of force fields this is not sufficiently detailed from the perspective of equilibrium trajectory models.

  Response. We do not want to enter the debate as it is not our topic here: the section dealing with internal models has thus been renamed ”Motor primitives in movement planning”. The text on internal models has been reduced so to only keep the part relevant to this review. Moreover we have added a paragraph mentioning that the existence on internal models was still debated and the major objections to their existence. We also now present the approach by Latash et al, Motor Control, 2007, as it presents an alternative view that is also based on muscles synergies.

- *Even though there is a separate discussion of planning versus execution there is not sufficient distinction between representations at different hi-*

erarchical levels, e.g. joint kinematics versus muscle activation. This is especially evident when reviewing the existing models.

Response. The review of existing model has been extensively revised and more details on each model has been given, in particular on the representations. We have tried to clearly specified the type of representation that was discussed throughout the article.

- *The term "Synergy" is used quite often in the manuscript but it is not even once defined. Since, there is some debate revolving this term, it is desirable that the authors briefly define what Synergies are.*

  Response. The term synergy has now been clearly defined in a footnote in the following way:
  By *synergy*, we mean a set of muscles activated in a coordinated way so to execute a specific movement, that is a group of muscles defined relatively to the movement they produced when they are activated together.

- *While the authors review current literature about motor neurophysiology and neural representations they should make greater effort to clearly focus on the literature that is especially pertinent to the distinct neural representations of discrete versus rhythmic movements and not of motor behaviors in general as is currently done. To the best of my understanding the currently available knowledge about such representations at the cortical level is quite limited, perhaps to a few fMRI and/or single cell studies.*

  Response. This part has been reduced. The pertinence of what has been kept has also been emphasized. Our aim is to link movement encoding with the concept of motor primitives before introducing the existing literature on discrete and rhythmic movements encoding per se.

- *In Section 7, the discussion of the mathematical models should be extensively revised. The choice of models is fine. However, each model is very briefly described while the mathematical equations are fully given (and there are 7 models descriptions). This even makes things more complicated since it is impossible to really understand the models as presented by the mathematical equations (moreover, even not all the models' parameters are fully explained). I believe it will be better to give a better intuition of these models and discuss them at a more conceptual level by presenting a more integrated discussion and description of the issues and problems they address and how they fit the different concepts presented in the paper. In the current situation, the interested reader cannot find this part of the review educating enough nor useful and anyway the reader will have to refer to the original paper. Therefore, since it is a review which has to discuss the different approaches, their advantages and shortcomings, as well as open issues, there is no much good in providing too many details which only add clutter and confusion rather than strengthen the concepts behind these models.*

Response. The mathematical section has been revised accordingly to the given suggestions. The parameters and the level of representation are clearly stated and the models are explained in details. The major aspects of the models are now illustrated by figures linking the control parameters and the corresponding output.
The equations have however been kept as we think that for some people equations are clearer than any text. Moreover, we will provide the matlab code we use for generating the figures to the interested readers upon demand, as stated in the text.

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Sarah Degallier · Auke Ijspeert

Modeling Discrete and Rhythmic Movement through Motor Primitives: A Review

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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, an increasing appeal for a comprehensive model for movement generation requires to bridge the different perspectives arising from the study of those two types of movements.

In this article, we consider discrete and rhythmic movement within the framework of motor primitives, that is of modular generation of movements. Doing so, we hope to get insights on the functional relationships between discrete and rhythmic movements and therefore on suitable representations for both of them.

We start by reviewing some of the existing literature regarding discrete and rhythmic movement, that we study from a functional view point. We then present some mathematical models found in the literature for the generation of discrete and rhythmic movements.

1 Introduction

Humans are able to adapt their movements to almost any new situations in a very robust, seemingly effortless way. To explain both this adaptivity and robustness, a very promising perspective is the modular approach to movement generation: Movements results from combinations of a finite set of stable *motor primitives* organized at the spinal level (see Bizzi et al (2008) for a review).

In terms of control, the modularity assumption is attractive because it drastically reduces the dimensionality of the problem: instead of a complex activation of a vast number of muscles across the body, only a couple of synergies of muscles need to be controlled. Here, the term *synergy* designs a set of muscles activated in a coordinated way so to execute a specific movement, that is a group of muscles defined relatively to the movement they produced when they are activated together. Strong evidence, notably through the concepts of central pattern generators and force fields (see resp. reviews by Grillner (2006) and Bizzi et al (2008)), supports the assumption that such functional modules of movements are located at the spinal level.

Indeed, neurological studies have provided evidence that the spinal cord produces many behaviors in a modular way. Bizzi and colleagues have brought to light such synergies of muscles in the frog (Bizzi et al (1991)); they have identified small functional sets of modules related to the direction of movements at the spinal level. Furthermore, it has been shown by Mussa-Ivaldi et al (1994) that by simply combining these modules, a wider range of stable movements could be produced. Finally, Kargo and Giszter (2000) have shown that such synergies could account for the natural whipping reflex in the frog, showing that the CNS could use such primitives to produce behaviors.

In this review, by *motor primitive* we mean a synergy responsible for the generation of a specific movement. As such a topic is already dense, we do not consider motor primitives involved in trajectory planning or more generally present in the kinematic outcome of the movement. The reader is referred to Hogan and Sternad (2007) for a thorough kinematic analysis of discrete and rhythmic movements.

In summary, motor primitives are here taken as neural/motor building blocks of movements that are used by the CNS to execute a particular movement. In this article, we propose to consider discrete and rhythmic movements within this modularity framework; more precisely, we take what we call a *functional perspective* to the generation of these movements. More precisely, here we focus on the processes underlying the generation of the movements rather than on the kinematic outcomes of the movement, as this subject as already been addressed in the past. Indeed, most of the studies on discrete and rhythmic movements are either based on EMG analyzes of the generated movements

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(Hogan and Sternad (2007), van Mourik and Beek (2004)) or on fMRI analysis (Schaal et al (2004)) as it will be reviewed in Section 3. While those studies have provided insightful results on the nature of discrete and rhythmic movements, we think that taking a functional perspective is a useful, complementary step to understand how such movements are generated, and also to provide more understanding on how brain and EMG studies can be bridged.

After a brief recall on some basic notions on movement generation (Section 2), we present several studies on the differences between discrete and rhythmic movements (Section 3). We then introduce some of the literature on the combination of these movements in Section 4. Albeit we are well aware that movement generation is a dynamic process involving the whole motor system, we discuss separately movement execution and movement planning as we believe that in this way properties pertaining to those two phases of movement can be brought to light, as it will be discussed in Sections 5 and 6. We furthermore present in Section 7 some existing mathematical models for the generation of discrete and rhythmic movement, as such models provide discerning information on the generation of these movements.

2 Overview on movement generation

According to textbooks (see for instance Kandel et al (2000)), movement generation is achieved through three motor structures organized hierarchically and corresponding to different levels of abstraction. Namely, those 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 muscles activation to execute the 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 also linked with the spinal cord. Figure 1 represents a schematic view of the motor structures of the central nervous system (CNS). Note that the cerebellum and the basal ganglia act on the cerebral cortex through the thalamus, which is not represented on the figure for clarity reasons.

More precisely, the spinal cord is responsible for the activation of motoneurons through networks of spinal neurons, those circuits being modulated by higher areas. Then, in the middle, the brain stem receives input from the cerebral cortex and projects into the spinal cord. It contributes to the control of posture by integrating visual, vestibular, and somatosensory[1] information. It can also control more distal limb muscles involved in goal directed movements. The cerebral cortex oversees the brain stem and the spinal cord; the primary motor cortex and some other premotor areas project directly to the spinal cord (corticospinal tract) and regulate motor tract from the brain stem.

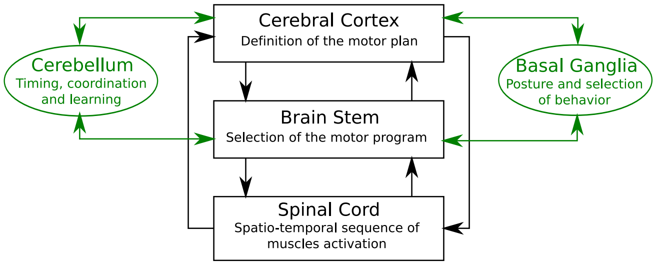

Fig. 1 Hierarchical organization of the three motor structures. At the highest level, the cerebral cortex projects directly to the spinal cord and the brain stem. The spinal cord also receives input from the brain stem. Two independent entities (in green), the cerebellum and the basal ganglia have be proved necessary for smooth movements and postures. They interact with both the cerebral cortex and the brain stem.

Observations on patients with lesions in the cerebellum and basal ganglia have shown that the cerebellum is involved in timing and coordination of movements, as well as in learning of new motor programs, whereas basal ganglia is believed to be involved in the motivation and selection of appropriate behavioral responses.

The *somatosensory information* is crucial for movement execution as it provides the representation of the space in which the task has to be performed and also of the state and posture of the body. A constant update of this information is needed to ensure smooth movements. The somatosensory information is also used to control the movement which is executed. This control can be feedback or feed-forward. Feedback control is used by the spinal cord to maintain a given position and to modulate the force needed to perform the task. A feed-forward control, based on experience, is used for anticipation; it can also modify the feedback response. Schneider and Shiffrin (1977) distinguish the controlled and the automatic processing of information; the controlled process is relatively slow, volitional and attention demanding (as in obstacle avoidance, for instance, where the visual information has to be processed), whereas the automatic one is fast, not volitional (and often unavoidable (Underwood and Everatt (1996))) and demands no attention (as for instance contact information of a foot with the ground which is fed back into the CPGs in locomotion).

Along this three-layered architecture, three types of movement are distinguished relatively to the way there are produced (see, for instance, Kandel et al (2000)): (a) *reflexes*; (b) *rhythmic automatisms*[2]; and (c) *voluntary movements*. Reflexes and rhythmic automatisms are spontaneous, whereas voluntary movements are the result of a (motor) plan. Thus, higher cortical areas are required for voluntary movements. Automatisms are mainly generated at the spinal

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[1] The term *somatosensory information* refers to different sensory signals from all major parts of the body, namely proprioception (that is muscles and joints position), touch, pressure, temperature and pain (see Kandel et al (2000) for instance). Note these different signals do not all use the same pathway.

[2] Rhythmic automatisms (as motor generation processes) are often referred to as rhythmic movements in the literature. However, to avoid confusion with rhythmic movements as kinematic outcomes of the motor system, we will rather use the term automatisms.

cord and the brain stem levels whereas the generation of voluntary movement also involves areas of the cerebral cortex.

Now that some of the basics notion have been defined, we can start reviewing the existing literature on discrete and rhythmic movements.

3 Defining discrete and rhythmic movements

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

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 which occurs between two postures, where postures stand for a non zero interval of time where (almost) no movement occur. 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, those 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 so to become periodic.

Another difficulty comes 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. This distinction is mainly due, from our point of view, 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, for instance central pattern generators (CPGs) in locomotion and sensorimotor transformations in reaching. Second, rhythmic and discrete movements are representative of two different levels of movement generation, i.e. the automatic and voluntary levels. 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 animals, whereas discrete movement is usually studied using brain imaging techniques or kinematic data on awake, behaving animals. Overcoming these differences in perspective is a necessary step to understand movement in general.

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 due to the fact that the methods, the point of view and the physiological level of investigation are different. It is interesting to question if, in terms of motor control, the apparent differences between discrete and rhythmic movement are artifacts due to different scientific approaches or if both movements are in fact produced independently. Indeed, as proposed by Schaal et al (2004) and van Mourik and Beek (2004), three possibilities need to be addressed: (a) rhythmic movements are repeated discrete movements (*concatenation hypothesis*), (b) discrete movements correspond to half a cycle of a rhythmic behavior (*half-cycle hypothesis*) and (c) discrete and rhythmic movements results from different processes (*two primitives hypothesis*).

If hypotheses (b) and (c) are still left open, 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 the movement. It has been ruled out by several studies comparing discrete and rhythmic movements (van Mourik and Beek (2004); Hogan and Sternad (2007)) where the key kinematic features of rhythmic movements are significantly different from those of the discrete movements. Schaal et al (2004) obtained similar results using fMRi techniques: some cortical areas activated during discrete movements where not active during rhythmic ones. In addition, as reported by van Mourik and Beek (2004), Guiard (1993) argued against the concatenation assumption that it 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 however important to point here that those comparisons are always made between a reaching movement and its corresponding back and forth rhythmic movements: Thus the difference observed may be due to the characteristics of reaching itself rather than due 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 experiments 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 it has been pointed out, notably by Miall and Ivry (2004), the discrete movements required more processing, namely choosing where to stop and when to start again, which could also explain the difference observed in the fMRI recordings.

Another non negligible phenomenon is the onset and the ending of a rhythmic movement: indeed, border conditions changes the kinematic properties of the 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 null while it is not the case during in-between cycles. However, in the first and final half-cycles, a similar feature can be observed.

van Mourik and Beek (2004) have studied separately the in between cycles and first and last half-cycles. 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. If their results do not rule out the half-cycle hypothesis, it speaks more for the two primitives hypothesis: the performed cyclical movements could be in fact a sequence of 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 remains thus 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 Discrete and rhythmic movements and their combination

Most of the EMG and movement studies on the combination of rhythmic and discrete movements are built on the same scheme: a particular joint (the finger or the elbow generally) 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 very nice review.

In all these experiments, an entrainment effect was 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 correspond to the peak of momentum of the oscillations in the direction of the discrete movement. Interestingly, it is a well known fact that professional pistol shooters press the trigger in phase with their involuntary tremor, while beginners try to immobilize themselves before shooting.

In terms of EMG, 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 as ”burst synchronization” by De Rugy and Sternad (2003). Performing the same experiment, although at different frequencies, Adamovich et al (1994) and De Rugy and Sternad (2003) came to different conclusion on movement combination.

Indeed, Adamovich et al (1994) observed the three following feature: (a) the oscillations rapidly attenuate during the discrete movement and resume after the peak velocity of the discrete movement; (b) there is a phase resetting of the oscillations after its attenuation; and (c) the frequency tend to be higher after the discrete movement. In addition, they observed that (d) once the discrete movement is initiated, it is performed independently from the rhythmic one, in the sense that the discrete trajectory is not influenced by the rhythmic movement. Basing themselves on the monotonic hypothesis (St-Onge et al (1993)), i.e. an hypothesis according to which the command of the discrete movement stops at the time of its peak velocity, they conclude that discrete and rhythmic movements are excluding each other at the neural level, in the sense that they cannot co-occur. However, their kinematic outcome outlasts them and overlap.

Performing the same experiment at lower frequencies (2-3Hz instead of 5-7Hz), Sternad et al (2000) came to a different conclusion concerning the interdependence of the two movements. Indeed, they observed a significant influence of the rhythmic movement on the discrete movement (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. According to these observations, Sternad et al (2000) propose 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 movement is supported by a study on whisker movements in rats by Haiss and Schwarz (2005), where it has been found that rhythmic and non rhythmic movements can be evoked through two different areas of the primary motor cortex. Indeed, it has been 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 more in details in Section 6.

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

5 Discrete and rhythmic movement in movement execution

We present movement execution through two fundamental concepts, *central pattern generators* and *force fields*, that we develop in the following.

Central pattern generators (CPGs), that is spinal networks involved in many behaviors in vertebrates and invertebrates, is a seminal concept in the generation of (rhythmic) movements (Grillner (1985), Delcomyn (1980)). Although most work on CPGs were originally dedicated to rhythmic movements, Grillner (2006) for instance now enlarges it to discrete movements.

Another primary 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, forces fields provide evidence for a modular organization of the spinal cord circuitry.

In the following we present these two notions more in details, as well as their relationship to discrete and rhythmic movements.

5.1 Central pattern generators

One century ago, two discrepant explanations for the rhythmicity presents in locomotion were competing: one suggesting that sensory feedback was the main trigger of the different phases of locomotion (Sherrington (1910)), and another one suggesting the existence of central neural networks capable of generating rhythms without any sensory input (Brown (1912)), such neural networks being now called central pattern generators (CPGs). Since then, this latter hypothesis has been strengthen by experiments on both vertebrates and invertebrates (see Stein et al (1997) or Ijspeert (2008) for more comprehensive reviews).

Actually, there is now very clear evidence that rhythms are generated centrally without requiring sensory information. 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 its body, electrical or chemical stimulations activate patterns of activity, called fictive locomotion, very similar to the one observed during intact locomotion.

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) report experiments where these units can be divided even further with independent oscillatory centers for flexor and extensor muscles. Furthermore, several experiments show that CPGs are distributed networks made of multiple coupled oscillatory centers (Ijspeert (2008)).

According to Marder and Bucher (2001), two types of CPGs networks can be distinguished: the so-called pacemaker-driven networks and networks with emergent rhythms. Pace maker-driven networks, which are usually networks that are always active, as in breathing, consist of a subnetwork of intrinsically oscillating neurons that drives non-bursting neurons into a cyclic pattern, while in networks with emergent rhythms, the most commonly found, 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 Section 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 the one observed in the immobilized preparation (fictive pattern). The motor pattern generated by the CPGs thus seems to be modulated by the sensory-motor information so that it stays coordinated with body movements.

Sensory feedback is also involved in the mechanisms underlying short-term and long-term adaptation of CPGs according to Pearson (2000). He postulates that the long-term phenomenon are driven by the body and limbs proprioceptors together with central commands and neuromodulators. Kawato (1996) also proposed that persistent errors detected by proprioceptors are used to recalibrate the magnitude of the feed forward command.

The existence of CPGs in the human system is well accepted nowadays, even if the identification of such spinal networks has not been possible yet. Strong evidence is indeed provided by studies on infants (Thelen (2000); Yang et al (1998); Lamb and Yang (2000)). Stepping reflexes, just after birth, have been observed in anencephalic infants, providing evidence that circuits responsible for this behavior are located at the spinal and/or at the brain stem level.

In addition, 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 (see Jeannerod (1988) or Gandevia and Burke (1992)).

Finally, even though it is believed that in humans the role of descending signals is more crucial for movement generation and thus that the spinal cord system may be less able to function after spinal cord injuries (SCI), it was shown that treadmill exercises for patients with SCI improved their walking pattern (Barbeau and Rossignol (1994); Dietz and Harkema (2004); Edgerton et al (2004); Rossignol et al (2007); Wolpaw and Tennissen (2001)). This may be accounted by the fact that CPGs can be trained to function independently from descending signals (Stein (2008)). Dimitrijevic et al (1998) have shown that non rhythmic stimulations of the spinal cord of patients with complete SCI could induce patterned, locomotor-like activity.

In conclusion, the existence of CPGs in animals is now strongly endorsed, while the role of CPGs in humans is not clear yet, notably because movement generation in humans strongly depends on the descending signals (MacKay-Lyons (2002)). However, there are strong evidences that adaptation processes occur in the spinal cord, in particular through promising clinical treatments after SCI that appear to exploit CPGs.

Most of early work on CPGs were focused on rhythmic movements, however the discovery of functional muscles synergies in the frog responsible for discrete movements have lead to an extension of the term, as we will see in the next section.

5.2 Motor primitives and forces fields

Bizzi's 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 end point (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 3-4 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. Since the intensity of stimulation does not change the pattern of force orientation (Giszter et al (1993)), this results provide an efficient way to span the space of possible end-effector target position through the weighted sum of the basic force fields. Similar results were obtained with rats (Tresch et al (1999)) and cats (Krouchev et al (2006); Ting and Macpherson (2005)).

Such findings endorse the hypothesis that movements are produced through the combination of motor primitives produced by spinal functional units, which can be characterized by a force field acting on the end-effector of the limb. This seminal result provides 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 muscles synergies involved in different movements. Indeed, identifying those synergies is a difficult task, mainly because muscles can belong to more than one synergy at the time.

In an experiment using chemical stimulation[3] of interneurons in the frog, Saltiel et al (1998) found out that some regions were eliciting rhythmic behaviors. Force measurements of the limb show a finite number of synergies corresponding to the direction of oscillations. More precisely, in rhythmic activation, the direction of the force field change through time, 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 through connectivity. Interestingly, the different orientations of the oscillation correspond to the directions of the forced fields found using the same method. Furthermore, the rhythmic and tonic areas of activation corresponding to the same orientation were topographically close (Saltiel et al (2005)). This results suggest that rhythms might arise from the temporal combination of simpler tonic modules. According to Saltiel et al (1998), CPGs could be organized such that tonic modules provides the orientation of the oscillations while the timing features comes 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 evidences 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 of the network of motor primitives (CPGs, in the broad sense) rather than to completely distinct pathways. Indeed, discrete networks need to encode a target position and possible a time onset, while rhythmic networks also need to be endowed with a frequency and a phase. As reviewed by Marder and Bucher (2001), such features seem to simply emerge 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. It seems reasonable to postulate that discrete and rhythmic movements are both generated through the specification of respectively target equilibrium points or directions of oscillations through the activation of specific spinal building blocks, while features pertaining to rhythmic movements (such as frequency and phase) may arise from the topological properties of the larger spinal networks eliciting the behavior.

6 Discrete and rhythmic in movement planning

We now question discrete and rhythmic movement during planning. We start by presenting the possible role of motor primitives in movement planning; we 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 motor commands to be sent to the spinal cord to fulfill the desired task.

The question of how the CNS actually computes the inverse model is still open. Indeed, inverse dynamics problems are complex, in particular in systems with high degrees of freedom, that is with high redundancy. In addition, in living systems, the dynamics of the body is changing through time, as well as the external dynamics. According to some authors, the existence of motor primitives might help the CNS

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[3] Chemical activation, here through N-methyl-D-aspartate (NMDA) Iontopheric, is more precise in the sense that it activates only somas and dendrites, whereas in electric stimulation axons and nerve terminals can also be depolarized.

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 muscles commands generating the desired trajectory (Mussa-Ivaldi and Bizzi (2000)).

More precisely, we have seen in Section 5 that motor primitives, at least in frogs, can be combined linearly, bypassing the high nonlinearity of muscles. It can be thus imagined that instead of solving an inverse problem so to control each of the needed muscles to follow the desired trajectory, the CNS choose a combination of motor primitives that best fit this trajectory. In this case the CNS only task is to optimize the activation of each motor primitive so to minimize the error between the desired and the actual trajectories. According to what was postulated in Section 5, such an 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 of oscillation.

Note that the existence and also the need for internal models is still strongly debated. Basically, the opponents of internal models mainly doubt that the brain is able of imitating the natural laws, which seems to be required to solve the inverse problem of finding the motor command that gives the desired natural consequence (for instance the torque needed to accelerate a limb). The reader is referred to articles by Bridgeman (2007) and Feldman (2009) for more details. Note that the concept of motor primitives as we take it here is not in opposition with these models, as for instance proposed by Latash et al (2007). From their perspective, a synergy is a set of muscles that are involved in the control of a variable relevant for the achievement of a particular task and which influence each other so to ensure stability.

We now present some results on the 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 in two areas, the primary motor cortex and the premotor cortex (M1). The latter is formed of the lateral (dorsal and ventral) premotor areas (PMd and PMv) and of the supplementary motor area (SMA) 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, its seems that the parameter that is encoded in the primary cortex is the location in space to 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 out that those simulations were resulting in a complex movement ending in the same location whatever the initial position of the limb was. They conclude from this that instead of encoding regions of the body, the motor cortex was a representation of different complex postures.

Such a finding 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 level of activations of motor cortical neurons control the weights of different motor primitives at the spinal level, that is that cortical neurons elicit combination of preprogrammed basic trajectories rather than encode the complexity of a particular desired trajectory. This could mean that the invariant observed in movement execution are the results of the usage by the CNS of a small set of motor primitives defined at the spinal level rather than to a kinematic plan or to optimization processes in the supra-spinal structures.

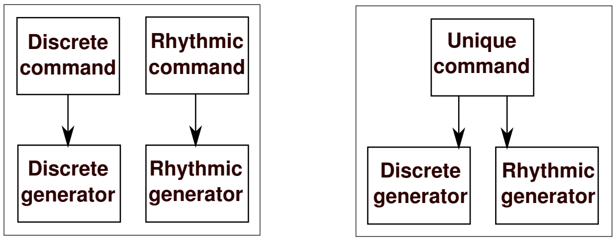
In particular, Haiss and Schwarz (2005) have studied the electric stimulation of different types of whisker movements in the rat, that is rhythmic movement (used for tactile exploration) and whisker retraction (used to sense an object at a specific location). They found that both movements, although performed by the same set of muscles, where elicited by different but adjacent regions of the primary motor cortex. At this point it is difficult to conclude if 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)), however the extension of such an experiment to broader range of movements and animals could possibly provide further insights on the differences in discrete and rhythmic movement generation.

In the same experiment, Haiss and Schwarz (2005) found that eliciting both “discrete” and “rhythmic” areas of the primary motor cortex resulted in a simple combination of the two behaviors: the resulting movements 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 results is important in the sense that it shows that, even if discrete and rhythmic motor primitives result from different processes, which is unknown, the combination of those primitives still results in a coherent, meaningful behavior. We will present two models, by De Rugy and Sternad (2003) and Degallier et al (2008), representing complex movements as oscillations around time-varying offset in the next section.

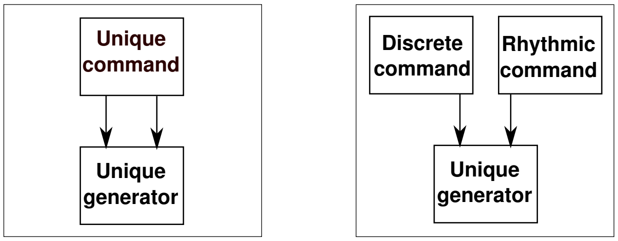
7 Mathematical models for the generation of discrete and rhythmic movements

In this section, we present a set of mathematical models of discrete and rhythmic movements: such modelings provide a functional, qualitative description of movement generation that can be tested against experimental results. We focus on the assumptions underlying them, both at the planning and execution level. We have distinguished four categories of models (Fig.2):

(a) **Two/Two.** Two independent processes exist for movement generation, with both different motor representations and generators (Subsection 7.1);
(b) **One/Two.** A similar motor command is sent to two different generators (Subsection 7.2);
(c) **One/One.** The same motor encoding and the same generator are used to generate both discrete and rhythmic movements (Subsection 7.3);
(d) **Two/One.** Two different motor commands are sent to the same generator (Subsection 7.4).



(a) Two/Two (b) One/Two



(c) One/One (d) Two/One

Fig. 2 Schematic of the four different categories of models.

These four categories of models are discussed more in details in the following; we illustrate them with fitting mathematical models found in the literature[4].

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

Furthermore, dynamical systems are particularly well-suited for modeling of discrete and rhythmic movements, as they have two characteristic types of *stable* solutions - that is solutions robust against perturbations - which correspond to discrete and rhythmic signals. Hence a natural solution for modeling discrete and rhythmic motor primitives is using those 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. Now, 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 (Fig.2(a)), 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 so to finely reproduce the characteristics of both discrete and rhythmic movements. Yet, the question of the combination and of the mutual influence of the movements is left open.

We start by presenting two independent models for discrete and rhythmic generation, developed respectively by Bullock and Grossberg (1988) and by Matsuoka (1985). These seminal models, or extensions of them, have been extensively used in the literature (Schaal et al (2000), De Rugy and Sternad (2003), 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 a desired target position. The final position of the limb is then computed according to the length of the muscles.

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 state. More precisely, here the brain does not encode a trajectory, but a desired state; the actual trajectory emerges from the dynamics of the motor primitive.

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 can also modulate the speed of the movement. There are thus two control parameters, the target length T and the go

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[4] The matlab code for the different models is available upon demand to the authors.

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

[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).

command G, the output of the system being the length of the muscle p.

Mathematical model. The following set of differential equations generate, for each muscle, a trajectory converging to the target position T, at a speed controlled 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.

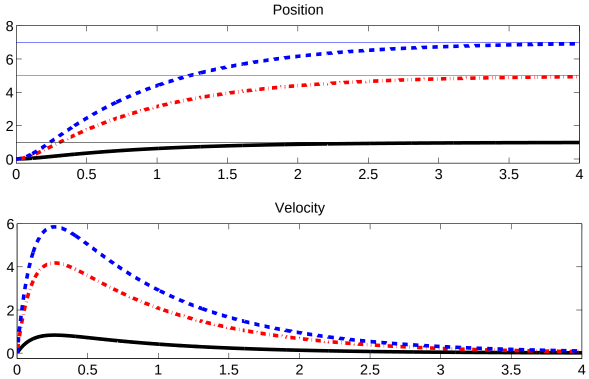

Fig. 3 VITE model. Trajectory for three different targets: G=1, in black, plain line, T=5 in red, dash-dotted line and T=7 in blue, dotted line). It can be seen that the three trajectories converge to their targets (horizontal lines) at the same time (top graph) and that the velocity peak is proportional to the displacement, i.e. to the difference vector (bottom graph). Here, for all the systems, $G=1$ and $\alpha=10$.

As it 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 it is shown in Fig.3. Such a feature is very interesting when doing synchronized movements: indeed all the muscles automatically converges 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 observation that human pointing movements tend to have the same duration, no matter the distance that the hand has to cover (see for instance 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 to start but 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 not only control the target of the movement, but also its speed. These features are illustrated on Fig.4 with go commands modeled by simple step function. Note that more complex functions can be chosen as go command, so to modify (and in particular smoothen) the velocity profile for instance, as it will be shown when presenting the model of Degallier et al (2008).

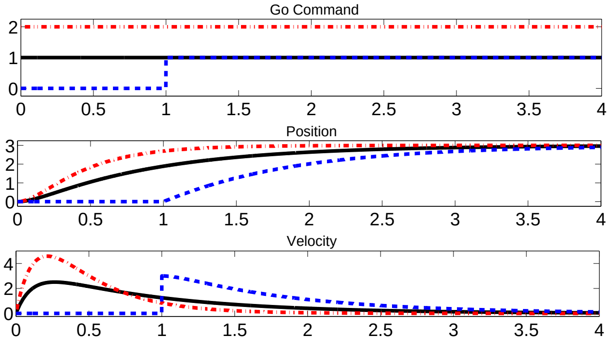

Fig. 4 VITE model. Trajectory with three different go command G: G=1, in black, plain line, G=2 in red, dash-dotted line and G=1 from t=1 s and 0 before in blue, dotted line (top graph). For the three systems, the target is constant ($T=3$). In the middle graph, it is shown that the onset of the movement can be postponed thanks to the go command 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 $\alpha=10$.

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 dofs. 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 spino-muscular 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 *Biol. Cybern*, 1985.

In this article, Matsuoka (1985) proposes a modeling for oscillating network of neurons. As discussed in Sec.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 neurons 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 bigger than the threshold

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[7] Note that we take a single value S_i as the input to the system, but it can be the weighted sum of different inputs.

value of the membrane θ, the neuron starts to fire (with firing rate y_i).

Mathematical model. Here are the equations for one neuron:

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

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

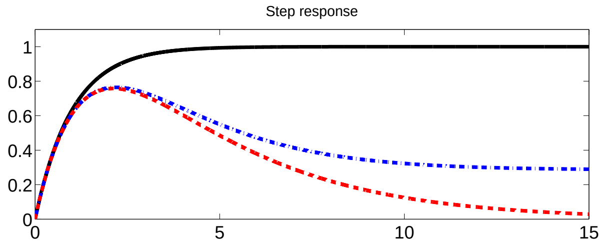

Fig. 5 Matsuoka Oscillator. Three typical step responses of a single neuron (i.e. $S_i = 1$ in each case). In black, plain line, b is set to zero (no adaptation) and the output converges monotonically to the input value. In blue, dash-dotted, line $b = 2.5$, the output raises but decrease after a while, showing a adaptation effect. Finally in red, dotted line, $b = 10$ and it can be seen that the fire rate almost return to zero (which is the case when $b \to \infty$). In all the case, we took $tau = 1$, $\theta = 0$ and $\tau' = 12b/2.5$ (this value being chosen so that no damped oscillation occurs, see Matsuoka (1985))

In this model, the fire rate increases monotonically and converges to a stationary state, which is not the behavior observed in neurons. Matsuoka (1985) thus extends the model to take in account the adaptation x' (also called fatigue) of the neurons, that is the fact that when receiving a step input, the firing rate increases rapidly at first and then gradually decreases, as it is shown in Fig.5. Adaptation has indeed been shown to be essential for the generation of oscillations.

Mathematical model. The model becomes

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

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

The neurons are now coupled so to form a network. Here neither self-inhibition nor excitation are considered.

Mathematical model. For one neuron j, the equations are now

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

where the a_{ij}'s (≥ 0) are the coupling strengths of the inhibitory connections between the neurons i and j and y_j is the output of the neuron j. Note that here, without loss of generality, we take $\theta = 0$ 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.6.

Fig.7 show two possible oscillating networks of three neurons: one where all the neurons mutually inhibit each other and another one where the neurons unilaterally inhibit each other, that is neuron 1 is for instance only inhibited by neuron 2 and only inhibits neuron 3.

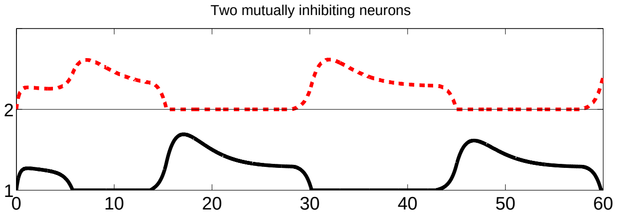

Fig. 6 Mastuoka oscillator. The fire rate for two neurons that inhibits each other for a constant input $S_i = 1$. The parameters here are $a_{12} = a_{21} = 2.5$, $\tau = 1$, $\theta = 0$, $b = 2.5$ and $\tau' = 12b/2.5$

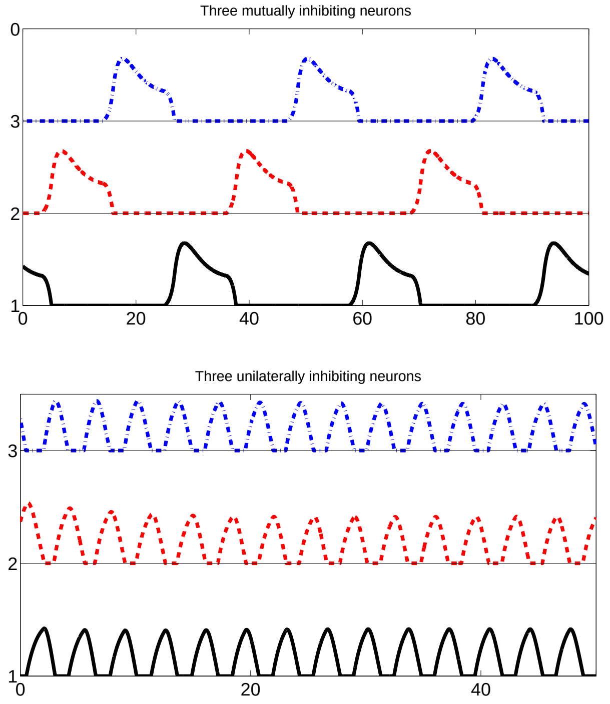

Fig. 7 Matsuoka oscillator. The fire rate for two networks of three neurons for a constant input $S_i = 1$. In the upper graph, the neurons are mutually inhibiting each other, i.e.$a_{ij} = 2.5 \forall i, j = 1,2,3$. In the second case, the neurons are only unilaterally inhibited, i.e. $a_{12} = a_{23} = a_{30} = 2.5$ and $a_{13} = a_{20} = a_{31} = 0.0$. The parameters here are $a_{12} = a_{21} = 2.5$, $tau = 1$, $\theta = 0$, $b = 2.5$ and $\tau' = 12b/2.5$

The model offered by Matsuoka is thus a powerful tool to model oscillatory behaviors under certain conditions. It can moreover account for different types of networks of oscillators. Note that the model can be extended so to have muscles command instead of firing rate as an output; we will see such an example in the following with the model of De Rugy and Sternad (2003).

It is interesting to note that in this model an oscillatory pattern emerges from the dynamic combination of non-cyclic units. Such a model achieves to successfully reproduce the emergent rhythms observed in the spinal cord (see Section 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 movements. Such an hypothesis could reflect the analogy observed by Haiss and Schwarz (2005) between the representation of discrete and rhythmic movements in whisker movements in rats (see Section 6). In this model, mutual influences of movements are supposed to occur at the muscle level rather than at the generation level, as discussed above for the Two/Two hypothesis.

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 proc. 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. the position T and the 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 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 that we have presented before. 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 a activation pattern v_i that resemble what is observed in the primate cortex (see Fig.8, top panel).

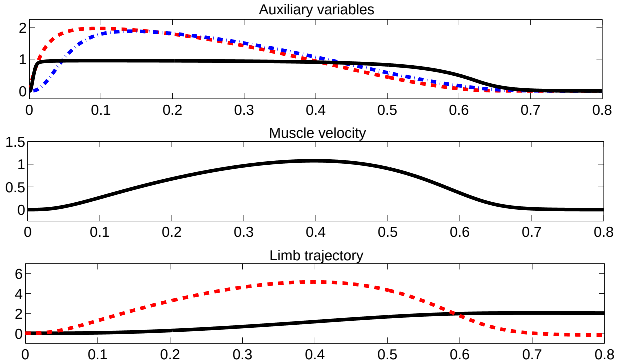

Fig. 8 Model by Schaal et al. A typical discrete trajectory converging to the target T =1. On the top panel, the activation pattern is shown in red, dashed line, as well as its smoothen version (in blue, dash-dotted line). The auxiliary variable r_i, that ensures that velocity profile is roughly a symmetric, bell-shaped curve is shown in black, plain line. The middle panel shows the resulting speed z_i for the muscle and bottom panel the resulting limb trajectory (in 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 $c_o = 60$.

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_0 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 (see Fig.8, middle panel). An auxiliary variable r_i is used to make z_i roughly symmetric and bell-shaped.

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_r and b controls the shape of the signal and are chosen so to obtain a bell-shaped velocity profile. a_z controls the rate of convergence of z_i.

The velocity command of the agonist and antagonist muscles (i and j) are finely integrated to obtain the limb movement p (see Fig.8, bottom panel).

Mathematical model.

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

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 position θ and the desired amplitude A. $\Delta\omega_i$ is turned into an activity signal ξ_i (see Fig.9, top panel).

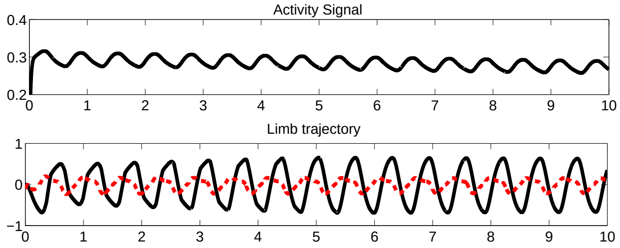

Fig. 9 Model by Schaal et al. A typical rhythmic trajectory converging of amplitude A=0.6. The top panel shows the activation pattern ξ_i. The bottom panel shows the resulting limb trajectory (in black, plain line) and its speed (red, dashed line). Here $a_\xi = 50.0$, $a_\psi = 1.0$, $\beta = 2.5$, $w = 2.5$ and $c_r = 20$.

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 in account the fact that ψ_i is a velocity and not a position.

Mathematical model.

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

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 (see Fig.8, bottom panel).

Mathematical model.

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

where c_r controls the frequency of the oscillations.

The movement of each dof 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 dof during coordinated movement (see Schaal et al (2000) for more details).

It has many variables that allows for the tuning of desired basic building blocks of movements, but that also makes the system quite complex. The model achieves to reproduce movements containing many human-like features, as a bell-shaped velocity profile for instance.

7.3 One/One hypothesis

The One/One hypothesis, that assumes that a unique motor representation and generator are used to produce movements, implies either that one of the movement 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 case of a larger class of movements. The difficulty here is that the model should be designed so 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 movement 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 bio-inspired architecture for movement generation for the infant-like robot iCub.**
  S. Degallier, L. Righetti, L. Natale, F. Nori, G. Metta, A.J. Ijspeert ,
  in the proc. of *the second 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 a periodic movements around time-varying offsets.

Here the input is a command specifying the target T_i of the discrete movement, and the amplitude M_i and the frequency ω_i of the rhythmic movement. A null (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.

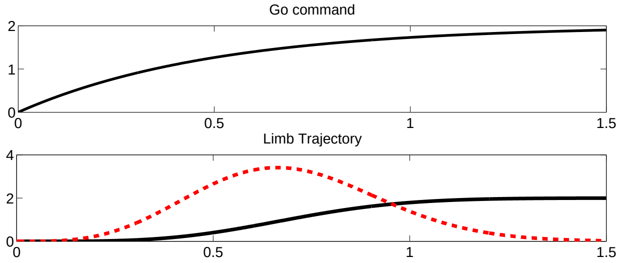

Fig. 10 Model by Degallier and al. The top panel shows the go function used in this implementation, that is a trajectory asymptotically converging to p_i(=2 here), instead of the step functions presented with the VITE model. Such a go command turns the velocity command into a symmetric, bell-shaped curve (red, dashed line), as it can be seen on the bottom graph, as well as the resulting limb trajectory (black, plain line) converging to the target $T_i = 2$. Here $d = 2$ and $b = 2.5$.

The first set of equation controls the discrete movement and is inspired from the VITE model that was presented above. The trajectory converges towards a goal T_i and the go command G_i is chosen so to ensure a bell-shaped velocity profile, as it it illustrated in Fig.10. As for 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

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

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

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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 $\sqrt{m_i}$ and frequency ω_i. These oscillations can be switched on and off easily through the parameters controlling the amplitude (more 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 so to allow an independent control of duration of the ascending (ω_{up}) and of the descending (ω_{down}) part of the sinusoidal, as illustrated on Fig.11. This feature is particularly useful for the control of the swing and the stance phase in locomotion.

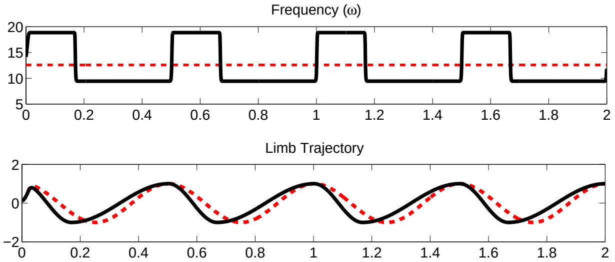

Fig. 11 Model by Degallier and al. The top panel shows the value of the frequency ω_i that is modulated through the parameters ω_{up} and ω_{down}. In red, dashed line, $\omega_{up} = \omega_{down}$ and the resulting movement (bottom panel) is a normal sinusoidal movement. In black, plain line, $\omega_{down} > \omega_{up}$ 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, $a = 100$, $m = 1$ and $f = 100$.

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

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

where $r_i = \sqrt{x_i^2 + z_i^2}$. a controls the rate of convergence to the limit cycle, f the rapidity of the switching between the swing and the 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 movements around a time-varying offset.

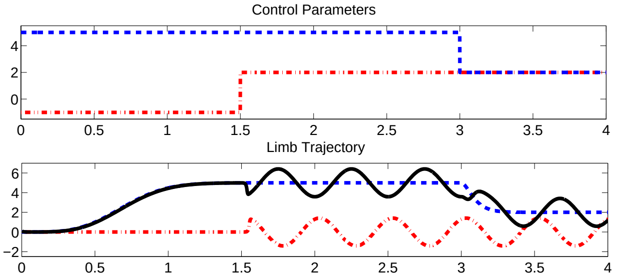

Fig. 12 Model by Degallier and al. The top panel shows the target T_i for the discrete movement and the resulting trajectory is shown in the bottom panel (in blue, dashed line). In red, dash-dotted line is shown the amplitude control parameter M_i (top panel) and the resulting trajectory (bottom panel). In the bottom panel, in black, plain line, the combined trajectory is also shown. It can be noted that is not a simple linear combination of the discrete and the rhythmic trajectory. showing 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 $f_i = 100$.

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 on Fig. 12.

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

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

We present here the model developed by Schöner and Santos (2001). This model is built to generate discrete movements, but 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. A two-layered system is used, consisting of a layer able to generate both oscillations and stationary states (”timing layer”) and another layer controlling the switching between those states (”neural dynamics control”).

The timing layer consist in three terms: the first one is an attractor towards the initial state x_i, the second one is a Hopf oscillator of amplitude 1 and the third one is an attractor towards the target position X_f. All these terms a multiplied by three ”neurons” that are never fully active at the same time.

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

$$\begin{cases} \dot{x} = -a|u_{\mathrm{i}}|(x - x_{\mathrm{i}}) + |u_{\mathrm{h}}|(b(1-r^2)x - \omega y) - a|u_{\mathrm{f}}|(x - X_{\mathrm{f}}) \\ \dot{y} = -a|u_{\mathrm{i}}|y + |u_{\mathrm{h}}|(b(1-r^2)y - \omega x) - a|u_{\mathrm{f}}|y \end{cases}$$

where x is the output of the system and y an auxiliary variable, a and b are constant controlling the speed of convergence of the system. Gaussian white noise is added to the system. In this system, $|u_i|$ (i=i, h, f) represents neurons which are never active (i.e. equal to one) at the same time.

The sequence of movement is controlled by the neural layer, and more precisely through three ”neurons” u_i, u_h and u_f activating respectively the first attractor, the Hopf oscillator and the target attractor. At rest position only the first attractor is active ($u_i = 1, u_h = 0, u_f = 0$), so that even if perturbations occurs 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 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” 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 action is illustrated in Fig.13.

Note that a trajectory converging to the target point could be obtained simply by using the final attractor only, however here the trajectory is governed by time-varying attractor along the limit cycle, reducing the transient, i.e the uncontrolled phases.

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

$$\begin{cases} \alpha\dot{u}_{\mathrm{i}} = \mu_{\mathrm{i}} u_{\mathrm{i}} - |\mu_{\mathrm{i}}| u_{\mathrm{i}}^3 - c(u_{\mathrm{h}}^2 + u_{\mathrm{f}}^2) u_{\mathrm{i}} \\ \alpha\dot{u}_{\mathrm{h}} = \mu_{\mathrm{h}} u_{\mathrm{h}} - |\mu_{\mathrm{h}}| u_{\mathrm{h}}^3 - c(u_{\mathrm{i}}^2 + u_{\mathrm{f}}^2) u_{\mathrm{h}} \\ \alpha\dot{u}_{\mathrm{f}} = \mu_{\mathrm{f}} u_{\mathrm{f}} - |\mu_{\mathrm{f}}| u_{\mathrm{f}}^3 - c(u_{\mathrm{i}}^2 + u_{\mathrm{h}}^2) u_{\mathrm{f}} \end{cases}$$

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

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

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

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

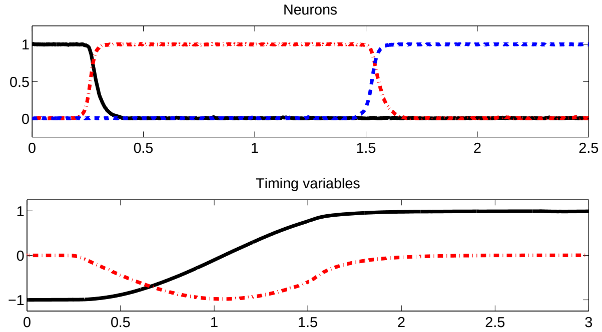

Fig. 13 Model by Schoner and Santos. In the top panel, the activity of the three neurons (u_i in black, plain line, u_h in red, dash-dotted line and u_f in blue, dashed line) during a typical discrete movement can be observed. Only one neuron is active a the time, corresponding to three stages of the movement: rest at initial position, move to the target and converge and rest at the target position. In the bottom panel, the obtained trajectory x_i is shown (in black, plain line) as well as the auxiliary variable y_i. Here $a = 5$, $b = 1$, $\omega = 2$, $c = 2.1$ and $\alpha = 0.02$.

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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.

Movements can thus be shaped through the neuronal dynamics that qualitatively changes the space of solutions of the timing layer. The three sequences of this movement (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 multi dofs system, coordination can be obtain through the coupling of rhythmic parts of the system (see Schöner and Santos (2001) for more details). Synchronized discrete movements can be obtained trough 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 together. 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 has originally been developed to explain the phase entrainment effect observed in humans (please refer to De Rugy and Sternad (2003) or to Sec.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-neurons Matsuoka oscillator to generates two firing rates (x_i, x_j). These firing rates are then transformed into muscle commands (T_i, 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 which, with well-tuned parameters, will later generate a discrete movement. The rhythmic command is simply a constant signal.

Mathematical model. The command input is given by

$$S = S_r + S_d$$

where S_r =const and

$$\dot{S}_d = \tau_s(-S_d + p_d)$$

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 i):

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

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' 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 (T_i, T_j) exerted by a pair of agonist/antagonist muscles.

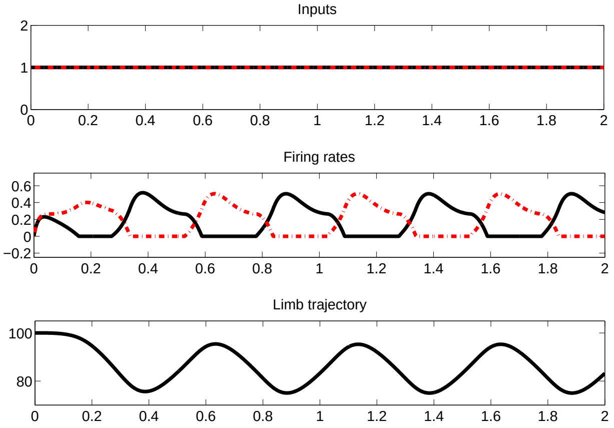

Fig. 14 Model by De Rugy and Sternad. A purely rhythmic command $S = S_R = 1$ (top panel) entrains the coupled neurons to oscillates (middle panel), leading to an oscillatory trajectory of the limb (bottom panel). Here $\gamma = 0.5$, $I = 0.08$, $h = 5$, $\tau = 0.05$, $\tau' = 0.125$, $tau_s = 0.2$, $\beta = 2.5$ and $\omega = 2.5$.

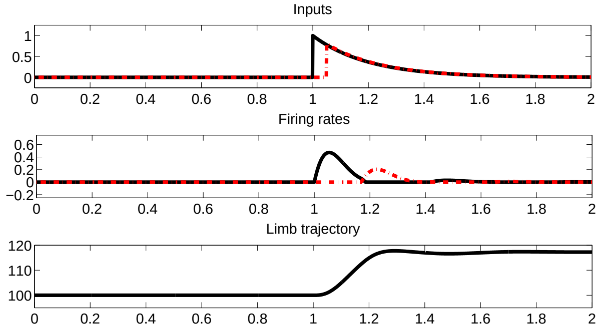

Fig. 15 Model by De Rugy and Sternad. A purely discrete command $S = S_D$ of peak $p_D = 1$ (top panel) leads to strongly damped oscillations of the neurons (middle panel), resulting in a discrete movement of the limb (bottom panel). Here $\gamma = 0.5$, $I = 0.08$, $h = 5$, $\tau = 0.05$, $\tau' = 0.125$, $tau_s = 0.2$, $\beta = 2.5$ and $\omega = 2.5$.

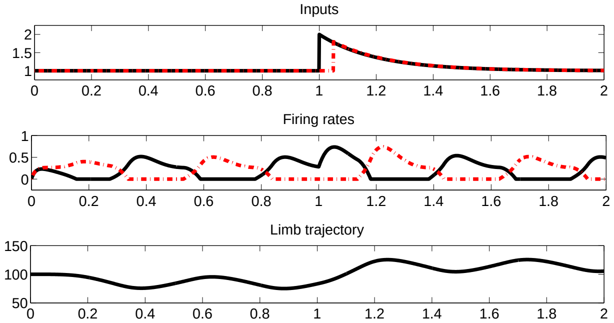

Fig. 16 Model by De Rugy and Sternad. A combined command $S = S_R + S_D$ with $S_R = 1$ and $p_D = 1$ (top panel) leads to a perturbed oscillators behavior of the neurons (middle panel), resulting in a rhythmic movement around a varying offset (bottom panel). Here $\gamma = 0.5$, $I = 0.08$, $h = 5$, $\tau = 0.05$, $\tau' = 0.125$, $tau_s = 0.2$, $\beta = 2.5$ and $\omega = 2.5$.

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

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

where h_T is the gain for the torques.

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

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

$$I\ddot{\theta} + \gamma\dot{\theta} - (T_i + T_j) = 0$$

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

Fig.14 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.15, it is shown that a purely discrete movement can be obtained using a peak motor command. Finally, in Fig.16, the combination of both command signal and the resulting, combined trajectories are shown.

In this model, there is an the 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) so to integrate reafferent signals and so to capture bimanual features.

7.5 Discussion on the models

We have presented here several models based the concept of motor primitives. Indeed the important common feature of these models is that simple, non patterned commands from the brain are turned into complex outputs governed by the dynamics of the system. So even though the outputs of the models are not at the same representation level, they can quite easily be be modified to account for another level of representation: as for instance De Rugy and Sternad (2003) extended the model of firing rates of neurons of Matsuoka (1985) to limb control by extending the system to the muscles and the limbs dynamics.

A viable model should be able to reproduce the interaction observed in humans between discrete and rhythmic movements that we have mentioned in Sec.4. As it was said before, 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

(a) the rhythmic movement is inhibited by the discrete one;
(b) the phase of the rhythmic movement is reseted after the discrete one;
(c) 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), as they have observed that

(d2) the rhythmic movement influence the discrete one, more precisely lower frequencies of oscillations lead to longer discrete movements.

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 sequencing 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: indeed they postulate that the kinematic outcome of a movement lasts longer that its generation. Note that this view is not shared by Sternad et al (2000), as was discussed before (see Section 4) . Staude et al (2002), for their part, propose that complex movement arise from the summation of the two movements subject to a threshold-linear mechanism; it is interesting to note that this simple model achieves to model the entrainment effect presented in Sec.4 (please refer to Staude et al (2002) for more details).

In the One/One and Two/One hypotheses, 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 emerge from the same process. Note that a viable model should be able to reproduce the observations presented above, these being consequences of the dynamics of the motor primitives, as for instance the phase entrainment in the model by De Rugy and Sternad (2003).

In conclusion, we have presented different dynamical systems that can successfully produce discrete and rhythmic movements, even though the interaction of the two movements is usually not addressed (with the exception of the model by De Rugy and Sternad (2003)). We believe that such systems can be used to better understand the complex problem of movement generation and to possibly determine the possible control architecture underlying the production of both discrete and rhythmic movements.

8 Conclusion

In this review, we have presented concepts relevant for the modeling of the generation of discrete and rhythmic movements. The purpose of such a modeling is twofold: first, to bridge two different approaches in motor control, originally dedicated uniquely to either discrete or rhythmic movements, and second, to define a global model of the motor structure applicable to robotics.

Because we choose to take a functional approach, most of the results that we have presented come from animal studies. If this results can not necessarily be generalized to humans in a straight forward way, we believe that they can provide insights on the processes underlying discrete and rhythmic movements generation in humans.

Indeed synergies of muscles have been observed in humans (as reviewed in Sec.5), which indicates that movement may be built through the combination of spinal building block of movements that we call motor primitives. Such an assumption has great implications in 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, evidences have been presented that both discrete and rhythmic movements could results from spinal motor primitives elicited by simple, non patterned brain commands, suggesting that the two types of movements may simply emerge from difference in the topologies (oscillating or not) of the spinal network underlying them.

We have concluded this review with some possible modelings of rhythmic and discrete movement within this framework of modular movement generation. We have proposed four categories of models with respect to the representation of discrete and rhythmic movements at both the planning and the execution levels. For each of this models, existing mathematical formulations were presented that were capable of generating both discrete and rhythmic movements.

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