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Early switching between movement types: Indication of predictive control?

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1. Introduction

Olympic runners in hurdles races need to switch between performing a rhythmic movement (running) and a discrete movement (jumping the hurdles). Over the past half-century, researchers have studied the similarities and the differences between rhythmic and discrete movements. This comparative analysis has been performed on kinematic data [11,12,39], on theoretical models of movement [36], as well as on brain-activation patterns [37,40 vs. 44]. Recent evidence demonstrates that within periodic movement alone, there exist movements with pronounced harmonic features, and ones with elements that resemble discrete movements (e.g., [5-7,10,26], see Fig. 1). It has been suggested that the employment of one vs. the other movement type depends on the task's index of difficulty [5-7] or on the specific combination of amplitude and frequency of the movement [26]. High-frequency, small-amplitude movements are highly harmonic, whereas lowfrequency, large-amplitude movements resemble a concatenated string of discrete submovements [26]. That is, the a priori requirements of the task determine the type of movement that will be used.

Categorical, rather than gradual, changes characterize the movements of both upper and lower limbs, and across species. A switch

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ABSTRACT

In everyday life, we frequently alternate between performing discrete and rhythmic movements. When performing a periodic movement, two distinct movement types can be distinguished: highly harmonic vs. discrete-like. The harmonicity of the movement is used to classify it as one or the other. We asked: (1) whether the frequency at which a periodic movement is performed affects the harmonicity of the resultant movement; and (2) what underlies switching between these movement types. To answer these questions, we studied horizontal flexion/extension forearm movements in 13 young adults over a wide range of frequencies. Movements were performed either at a fixed frequency, or at gradually increasing or decreasing target frequencies. We found movement harmonicity to depend on the frequency of the movement. Furthermore, we found a reverse hysteresis behavior, where participants switched movement type in anticipation of the future-required frequency. These findings suggest that predictive control is employed in switching between movement types.

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between movement types which is dependent on movement rate has been described in quadrupeds (e.g., [18]), human lower limbs [20] and human upper limbs [23]. More specifically, a switch, rather than a gradual change, between harmonic and inharmonic movements was discussed in [6,7,17].

How exactly task requirements determine the type of movement and what is the switching mechanism are the open questions which motivate the current study.

Our goals in the current experiment were: (1) to study the effect of the forearm's movement frequency (when amplitude is kept constant) on the choice of movement type, and (2) to find the "switch frequency" (Fs), at which the switch between movement types occurs. We kept the target amplitude of the movement constant, while changing the required movement frequency, in order to study how this variation affects the choice of movement type. We employed two experimental paradigms: in the first, static paradigm, we asked participants to perform movements at six constant frequency ranges; in the second, dynamic paradigm, participants were asked to perform movements whose target-frequency requirement changed continuously throughout the trial, either increasing or decreasing.

There exist three main alternatives with regard to the value of the switching frequency Fs: (1) it may take on a single frequency value, and this frequency would be the same in the static and dynamic trials; (2) it may take more than a single value, where these values (different for the increasing and for the decreasing trials), form the shape of a classical hysteresis curve; or (3) it may take more than a single value, where these values form the shape of a reverse hysteresis curve.

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Fig. 1. Examples of a highly harmonic (A) and a discrete-like (B) movement. These velocity traces are from one of this study's participants performing movements in block F and block A, respectively (see Section 2).

2. Methods

2.1. Participants

13 adult right-handed participants were tested using their right arm (Age: 25.4 ± 3.8 years; 6 females, 7 males). All participants gave their informed consent to participate, as stipulated by the local Helsinki Committee.

2.2. Equipment

A forearm support, consisting of a wrist brace strapped to an arm rest, was hinged to a stationary support, mounted on a table in front of the seated participant. The forearm support was connected to the shaft of a rotary incremental encoder with a position resolution of 0.002 degrees per count. Data were recorded at 200 Hz. Both the position and the velocity of the forearm were displayed in real time on a computer screen situated in front of the participants. A large, opaque plastic cover was placed parallel to the table, and above the apparatus, such that during the experiment, the participant's forearm was occluded from view (see Fig. 2).

2.3. Protocol

Participants were asked to perform 1-dimensional horizontal flexion/extension movements with their forearm, at frequencies dictated by a closed shape on a phaseplane display, showing angular velocity vs. angular position; no explicit timing cues were given [10,26]. The phase plane has been widely used to study dynamical systems, especially those that typically underlie the production of rhythmic behavior (e.g. limit-cycle oscillators [23]). The target forearm behavior was indicated by a region of the phase plane; this region was a doughnut shape formed from two ellipses displayed on the screen (see Fig. 2). Each ellipse corresponds to a sinusoidal motion about the elbow, with the nonzero width of the doughnut shape allowing for a range of amplitudes and frequencies. The protocol consisted of two parts: static and dynamic.



Fig. 2. Experimental setup. The participant's forearm is occluded from view, and a trace of its movement in the phase plane is displayed on the screen, where the target amplitude and frequency is dictated by a doughnut shape.

2.3.1. Static blocks

In part I, participants performed six blocks of five trials each, with each trial lasting 15 s. The six blocks were differentiated by the required frequency range (see Table 1), and therefore by the vertical extent of the target ellipses on the visual display; the higher the required frequency, the taller were the displayed ellipses. Table 1 lists the frequency values for movement along the center of the annulus, as well as the allowed ranges, in each of the six experimental blocks. Participants were instructed to perform flexion/extension movements of their forearm, such that the displayed trace of their movement remains within the area on the screen delimited by the two ellipses, defining a target annulus. All ellipses defined a target amplitude of $20 \pm 3^{\circ}$. The order of presentation of the blocks was altered and balanced across participants. Before each block of five trials, participants were allowed to practice the movement until they felt comfortable with the task.

2.3.2. Dynamic blocks

In part II of the experiment, participants were again asked to perform flexion/extension movements with their forearm, while aiming to stay within the target closed region on the phase plane. However, in this part of the experiment, the target movement frequency was gradually increasing or decreasing during each 63.5-s trial, between the lowest and the highest frequency ranges required in the static part of the experiment. Two consecutive variable-frequency trials required a gradual increase (INC) in frequency, and two a gradual decrease (DEC), with the order of presentation of INC and DEC trials counter-balanced across participants.

2.4. Data analysis

Position was recorded as the angular displacement about the elbow joint and filtered using a first order Butterworth filter with a cutoff frequency of 20 Hz. Trend was removed from the position data, so as to reduce the effects of drift. This was achieved by removing the best straight-line fit from the angular position data. Data were analyzed using MATLAB[®] (7.8, The MathWorks, Natick, MA).

2.4.1. Harmonicity

For every movement half-cycle, between two zero-crossings in the position record, the unitless harmonicity index was calculated as follows: when a single peak in acceleration occurred in the half cycle, the harmonicity value was set to one; when an inflection occurred in the half-cycle acceleration trace, movement harmonicity was computed as the ratio of the minimum to the maximum absolute value of the acceleration within the given half cycle; finally, if the acceleration trace within the half cycle changed its sign, the harmonicity value was set to zero [7,16].

In the static trials, harmonicity values were then averaged across the entirety of each 15-s trial. In the dynamic trials, harmonicity values were used to determine the point at which a switch occurred between movement types, as explained below.

The harmonicity index has previously been demonstrated to be a robust indicator of movement type (see, for example, [26]).

2.4.2. Identification of Fs

In each of the variable trials, harmonicity of each half cycle was calculated as explained above. In the INC trials, the harmonicity values were scanned until the first instance of a harmonicity value above 0.5^1 was encountered. If the following 4 instances of H > 0.5 occurred within 4 movement cycles of each other, that point was considered as the switch point. Otherwise, the next instance of H > 0.5 was similarly

¹ The cutoff value H=0.5 was chosen to comply with convention (see [5–7,17]). However, analysis of the data with cutoff H values as low as 0.1 and as high as 0.9 demonstrates that the reverse-hysteresis result reported below is robust, and not dependent on this specific choice of cutoff value.

Table 1

Target frequency values for each of the six experimental blocks.

Frequency (in Hz)	Block					
	А	В	С	D	E	F
Center	0.17	0.56	1.02	1.6	2.3	3.1
Range	0.042-0.34	0.39-0.79	0.72-1.4	1.2-2.2	1.8-3.1	2.4-3.9



Fig. 3. Hooke's plots of movements performed in the static blocks by a single participant (one trial from each block). The letters on the top right-hand corner of each panel denote the block from which the traces are taken (see Table 1).

examined, and so on. The same method was applied for the DEC trials, but with H < 0.5. Multiple movement cycles were examined in order to ensure that a switch point was indeed encountered, rather than a momentary change in the nature of the movement.

2.4.3. Statistical analysis

A non-parametric paired test, the sign test, was used to test the significance of differences between data sets. This nonparametric test was chosen to eliminate the need for assumptions regarding population distributions required in parametric tests. The Holm–Bonferroni correction was applied where necessary, to account for multiple comparisons and avoid type-I error.

3. Results

3.1. Static blocks: low-frequency movements are discrete-like, high-frequency movements are harmonic

Hooke's plots for the 6 static blocks are shown in Fig. 3. Movements in blocks A and B show the "N-shaped" Hooke plot characteristic of movements with a discrete nature, whereas movements in blocks C–F trace a straight line through the Hooke plot, as is seen in highly harmonic movements [29].

Harmonicity values for the 6 static blocks are shown in Fig. 4. Blocks A–C were each significantly different from the other five blocks (p < 0.0005). Harmonicity values in blocks A and B are below 0.5, and in blocks C–F above 0.5, indicating fragmentation of the movement around movement reversals in the former two blocks, not present in the latter four blocks. This indicates a change in movement type, which is dependent on frequency, as we expected to see, and places Fs between 0.6 Hz and 1 Hz, corresponding to the central frequencies in blocks B and C.

3.2. Dynamic blocks: reverse hysteresis in Fs

Hooke's plots from the INC and the DEC blocks are shown in Fig. 5. Movements at low frequencies in either the INC or the DEC trials create an "N-shaped" Hooke's plot, whereas those at



Fig. 4. Harmonicity values (mean \pm SE) for the six static blocks. The *x*-axis denotes the central frequency in each of the blocks. An asterisk denotes a block is significantly different from all other blocks.



Fig. 5. Hooke's plots of movements performed in the dynamic blocks by a single participant (one trial from each block INC/DEC). Traces from the beginning of the trial are colored in light gray and become darker as the trial progresses.



Fig. 6. FsINC and FsDEC for all 13 participants. As can readily be seen from the figure, the switch in the increasing-frequency trials occurred at a lower frequency than in the decreasing-frequency trials for all 13 participants.

high frequencies form a straight line through the Hooke's plot, corresponding to highly harmonic movements.

A significant difference was found between the Fs in the INC (FsINC) trials and that in the DEC trials (FsDEC), with the switch in the INC trials occurring at a lower frequency (0.82 ± 0.16 Hz) than the switch in the DEC trials (1.1 ± 0.16 Hz; p < 0.00025), indicating a "reverse hysteresis" behavior.² Importantly, for all participants, FsINC was lower than FsDEC (see Fig. 6).

4. Discussion

We found a reverse-hysteresis behavior in the frequency Fs at which participants switched from performing a discrete-like movement to performing a harmonic movement. That is, during the dynamic trials, where target frequency was continuously increasing or decreasing, Fs depended on whether the frequency of the movement was increasing or decreasing. Moreover, in both INC and DEC trials, the switch occurred early on, creating an overlap zone, where movements were performed in either a highly smooth or in a fragmented manner. Future studies should examine whether the switch point in the static trials more closely matches the INC or DEC switch point.

There exist two main alternatives with regard to the location of Fs: either it is the result of the physical plant, or it is the result of a variation in the control scheme. The overlap region in the frequency spectrum which we identified, where movements can be performed as either discrete-like or highly harmonic, suggests that even if physical properties of the muscles play a part in the switching, they are not the sole reason for the switch.

Multistability, where two motor schemes coexist at the same movement speed, can occur as classical hysteresis, where there is a lag in return to a previous state, depending on the direction of change of speed, or as reverse hysteresis, manifested as an enhanced return to a previous state, depending on the direction of change of speed [13].

The hysteresis phenomenon is commonly found in nature. It can be described as a limited tendency to stay at a given state, despite a changing environment. It has the benefit of avoiding rapid oscillations between states around the switch point between these states, which may have an associated cost [2].

Reverse hysteresis is less common, and we asked what may underlie this observed behavior. A plausible explanation is that predictive control may guide the early switching between movement types, in anticipation of the future. Predictive control is a form of control which incorporates a prediction of the future behavior of the system. It is most useful for systems whose future behavior may vary from what is currently perceived [43]. The ability to identify a change in the environment and adapt to it in feed-forward manner, rather than rely on the inherently delayed feedback-based response, is important. It can serve as a means to avoid injury (as in the case of retracting an arm from a heat source prior to sensing pain), or even life-threatening situations [14,33]. Feed-forward adaptation has been demonstrated to exist in various motor contexts, including adaptation to force perturbations [41], bimanual adaptation [24], and locomotion [28]. In feed-forward adaptation, the nervous system learns about the environment, and predicts the required motor command using motor memory, which is sometimes referred to as an internal model. A mechanism for switching among internal models is needed for flexible adaptation under frequent environmental changes [21]. In the context of episodic memory, amnesiacs, who have trouble with memory of past events, tend to have trouble with prediction of future events as well [14]. In fact, it has been proposed that the main function of forming memories is to allow us to anticipate what may happen in the future [38].

It has been demonstrated that anticipatory changes take place in the motor system. For example, healthy individuals were found

² This significant reverse hysteresis result was also validated using an alternative method for switch-point detection, whereby a sigmoid function was fit to harmonicity as a function of frequency, and used to determine the point of transition.

to systematically divert their gaze and head toward the future direction of a curved trajectory [15]. Head-direction cells in the antedorsal nucleus of the rat thalamus were found to systematically display anticipatory shifts toward the future direction of the head in space [4].

There is evidence to support a role for the cerebellum in predictive control of movement. It has been theorized [27] that the cerebellum acts as a Smith predictor. That is, a forward model provides a rapid prediction of the motor command outcome, while a second copy of this prediction is fed back after a delay which matches the amount of time that the actual feedback from the system is delayed, such that the two can be directly compared. Individuals with cerebellar damage were found to be impaired in their ability to generate movements that required predictive, as opposed to reactive, control [3], such as grip-force modulation [32]. Importantly, brain-imaging data supports a role for the cerebellum in switching between internal models when faced with a changing motor context [22]. Under certain circumstances, however, individuals with cerebellar damage showed predictive motor ability [3], such as when required to make predictive saccades to targets appearing at regular intervals [25]. In addition, deficient anticipatory motor control in individuals with Parkinson's disease [30] and in individuals who suffered a hemiparetic stroke [35] suggests that multiple brain regions participate in predictive control. Various cerebral regions were identified as related to switching between internal models [22]. Sub-cortical structures, such as the basal ganglia, are suggested to be involved in switching between motor plans in a changing environment [45].

Whereas the current study explored movements of the upper limb, examining the extensive body of research performed on the walk-to-run (WR) and run-to-walk (RW) transitions can be instructive. Humans are found to change gait when the dimensionless Froude number is around 0.5 [1]. There is no agreement as to what brings about this switch. Early studies asserted that humans transition between gaits at the energetically optimal speed; however, this theory was later refuted [46]. Similarly, a minimum in the metabolic cost of gait was shown by some researchers to correspond to the transition speed, while others determined that the transitions occur at speeds slower than those predicted by the minimum-metabolic cost hypothesis [31,34]. It was suggested that the ability of the ankle plantar flexors to produce force diminishes as walking speed approaches the transition speed; the transition to a running gait may allow them to generate greater force as it would improve their contractile conditions, thus rendering them more effective in satisfying increasing energetic demands of faster movement speeds [31]. Finally, EMG data support the hypothesis that switching between gaits is done to minimize muscle activation, with different sets of muscles activated depending on the gait type [34]. Theoretical considerations have led researchers to suggest a classical hysteresis should exist when switching between gait patterns [2,9], for example, as the result of a finite delay in response to a changing environment. Experimental evidence either provided support for this hypothesis (e.g., [19]), revealed no difference between the WR and RW transitions speed [34], simply averaged them (see [20]), or showed reverse hysteresis [13]. Diedrich and Warren [8,9] reported individual behavior ranged from a significant classical hysteresis to a significant reverse hysteresis. Evidence for reverse hysteresis is found in Thorstensson and Roberthson [42] as well, but significance values are not reported. Getchell and Whitall [13] suggested that the reverse hysteresis phenomenon is the result of the effect of participants' intention on the coordination dynamics

Thus, data from both the upper and the lower limb are consistent with an interpretation that people engage in predictive control, and change their control strategy in preparation for a change in the environment, rather than perform this change only in feedback form, after the environmental change has taken place. This behavior can be advantageous, as it bypasses the inherent delays in feedback-based reactions to a changed environmental context.

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References

- [1] R. Alexander, Walking and running, American Scientist 72 (1984) 348-354.
- R. Alexander, Optimization and gaits in the locomotion of vertebrates, Physiological Reviews 69 (1989) 29–64.
- [3] A. Bastian, Learning to predict the future: the cerebellum adapts feedforward movement control, Current Opinion in Neurobiology 16 (2006) 645–649.
- [4] H. Blair, P. Sharp, Anticipatory head direction signals in anterior thalamus: evidence for a thalamocortical circuit that integrates angular head motion to compute head direction, Journal of Neuroscience 15 (1995) 6260–6270.
- [5] J. Buchanan, J. Park, Y. Ryu, C. Shea, Discrete and cyclical units of action in a mixed target pair aiming task, Experimental Brain Research 150 (2003) 473–489.
- [6] J. Buchanan, J. Park, C. Shea, Systematic scaling of target width: dynamics, planning, and feedback, Neuroscience Letters 367 (2004) 317–322.
- [7] J. Buchanan, J. Park, C. Shea, Target width scaling in a repetitive aiming task: switching between cyclical and discrete units of action, Experimental Brain Research 175 (2006) 710–725.
- [8] F. Diedrich, W. Warren, Why change gaits? Dynamics of the walk-run transition, Journal of Experimental Psychology: Human Perception and Performance 21 (1995) 183–202.
- [9] F. Diedrich, W. Warren, The dynamics of gait transitions: effects of grade and load, Journal of Motor Behavior 30 (1998) 60–78.
- [10] J. Doeringer, N. Hogan, Intermittency in preplanned elbow movements persists in the absence of visual feedback, Journal of Neurophysiology 80 (1998) 1787-1799.
- [11] P. Fitts, The information capacity of the human motor system in controlling the amplitude of movement, Journal of Experimental Psychology 47 (1954) 381–391.
- [12] P. Fitts, J. Peterson, Information capacity of discrete motor responses, Journal of Experimental Psychology 67 (1964) 103–112.
- [13] N. Getchell, J. Whitall, Transitions to and from asymmetrical gait patterns, Journal of Motor Behavior 36 (2004) 13–27.
- [14] D. Gilbert, T. Wilson, Prospection: experiencing the future, Science 317 (2007) 1351–1354.
- [15] R. Grasso, P. Prevost, Y. Ivanenko, A. Berthoz, Eye-head coordination for the steering of locomotion in humans: an anticipatory synergy, Neuroscience Letters 253 (1998) 115–118.
- [16] Y. Guiard, On Fitts's and Hooke's laws: simple harmonic movement in upperlimb cyclical aiming, Acta Psychologica 82 (1993) 139–159.
- [17] Y. Guiard, Fitts' law in the discrete vs. cyclical paradigm, Human Movement Science 16 (1997) 97-131.
- [18] D. Hoyt, C. Taylor, Gait and the energetics of locomotion in horses, Nature 292 (1981) 229–240.
- [19] A. Hreljac, Determinants of the gait transition speed during human locomotion: kinematic factors, Journal of Biomechanics 28 (1995) 669–677.
- [20] A. Hreljac, R. Imamura, R. Escamilla, W. Edwards, Effects of changing protocol, grade, and direction on the preferred gait transition speed during human locomotion, Gait & Posture 25 (2007) 419–424.
- [21] H. Imamizu, M. Kawato, Brain mechanisms for predictive control by switching internal models: implications for higher-order cognitive functions, Psychological Research 73 (2009) 527–544.
- [22] H. Imamizu, T. Yoshioka, M. Kawato, Contribution of cerebro-cerebellar communication loop to switching of internal models: fMRI studies, Japanese Journal of Physiology 54 (2004) S51.
- [23] J. Kelso, Phase transitions and critical behavior in human bimanual coordination, American Journal of Physiology. Regulatory, Integrative and Comparative Physiology 246 (1984) 1000–1004.
- [24] E. Klaiman, A. Karniel, Bimanual adaptation: internal representations of bimanual rhythmic movements, Experimental Brain Research 171 (2006) 204–214.
- [25] A. Lasker, E. Isotalo, D. Zee, Predictive saccades to a regularly alternating target in cerebellar patients, Annals of the New York Academy of Sciences 1039 (2005) 544–547.
- [26] S. Levy-Tzedek, H. Krebs, D. Song, N. Hogan, H. Poizner, Non-monotonicity on a spatio-temporally defined cyclic task: evidence of two movement types? Experimental Brain Research 202 (2010) 733–746.
- [27] R. Miall, D. Weir, D. Wolpert, J. Stein, Is the cerebellum a Smith predictor? Journal of Motor Behavior 25 (1993) 203–1203.
- [28] S. Morton, A. Bastian, Cerebellar contributions to locomotor adaptations during splitbelt treadmill walking, Journal of Neuroscience 26 (2006) 9107.

- [29] D. Mottet, R. Bootsma, The dynamics of goal-directed rhythmical aiming, Biological Cybernetics 80 (1999) 235–245.
- [30] L. Muratori, T. McIsaac, A. Gordon, M. Santello, Impaired anticipatory control of force sharing patterns during whole-hand grasping in Parkinson's disease, Experimental Brain Research 185 (2008) 41–52.
- [31] R. Neptune, K. Sasaki, Ankle plantar flexor force production is an important determinant of the preferred walk-to-run transition speed, Journal of Experimental Biology 208 (2005) 799–808.
- [32] D. Nowak, H. Topka, D. Timmann, H. Boecker, J. Hermsdörfer, The role of the cerebellum for predictive control of grasping, The Cerebellum 6 (2007) 7–17.
- [33] B. Porr, F. Worgotter, Learning a forward model of a reflex, Advances in Neural Information Processing Systems (2003) 1555–1562.
- [34] B. Prilutsky, R. Gregor, Swing and support-related muscle actions differentially trigger human walk-run and run-walk transitions, Journal of Experimental Biology 204 (2001) 2277–2287.
- [35] P. Raghavan, E. Petra, J. Krakauer, A. Gordon, Patterns of impairment in digit independence after subcortical stroke, Journal of Neurophysiology 95 (2006) 369–378.
- [36] R. Ronsse, D. Sternad, P. Lef vre, A computational model for rhythmic and discrete movements in bimanual coordination, Neural Computation 21 (2009) 1335–1370.
- [37] S. Schaal, D. Sternad, R. Osu, M. Kawato, Rhythmic arm movement is not discrete, Nature Neuroscience 7 (2004) 1136–1143.

- [38] D. Schacter, D. Addis, The ghosts of past and future, Nature 445 (2007) 27.
- [39] R. Schmidt, H. Zelaznik, B. Hawkins, J. Frank, J. Quinn, Motor-output variability: a theory for the accuracy of rapid motor acts, Psychological Review 86 (1979) 415-451.
- [40] R. Seidler, D. Noll, G. Thiers, Feedforward and feedback processes in motor control, Neuroimage 22 (2004) 1775–1783.
- [41] R. Shadmehr, F. Mussa-Ivaldi, Adaptive representation of dynamics during learning of a motor task, Journal of Neuroscience 14 (1994) 3208.
- [42] A. Thorstensson, H. Roberthson, Adaptations to changing speed in human locomotion: speed of transition between walking and running, Acta Physiologica Scandinavica 131 (1987) 211–214.
- [43] C. Tin, C. Poon, Internal models in sensorimotor integration: perspectives from adaptive control theory, Journal of Neural Engineering 2 (2005) 147–163.
- [44] C. Winstein, S. Grafton, P. Pohl, Motor task difficulty and brain activity: investigation of goal-directed reciprocal aiming using positron emission tomography, Journal of Neurophysiology 77 (1997) 1581.
- [45] E. Yehene, N. Meiran, N. Soroker, Basal ganglia play a unique role in task switching within the frontal-subcortical circuits: evidence from patients with focal lesions, Journal of Cognitive Neuroscience 20 (2008) 1079–1093.
- [46] G. Ziv, A. Rotstein, Physiological characteristics of the preferred transition speed in racewalkers, Medicine & Science in Sports & Exercise 41 (2009) 797–804.