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This dissertation is in part based on the following peer-reviewed articles, which are referred to as I to IX in the text.

I. **Hansen EA**, Jensen K, Pedersen PK. Performance following prolonged sub-maximal cycling at optimal versus freely chosen pedal rate. *Eur J Appl Physiol* 98: 227-233, 2006.
II. **Hansen EA**, Raastad T, Hallén J. Strength training reduces freely chosen pedal rate during submaximal cycling. *Eur J Appl Physiol* 101: 419-426, 2007.
III. **Hansen EA**, Ohnstad AE. Evidence for freely chosen pedalling rate during submaximal cycling to be a robust innate voluntary motor rhythm. *Exp Brain Res* 186: 365-373, 2008.
IV. **Hansen EA**, Waldeland H. Seated versus standing position for maximisation of performance during intense uphill cycling. *J Sports Sci* 26: 977-984, 2008.
V. **Hansen EA**, Jensen K, Hallén J, Rasmussen J, Pedersen PK. Effect of chain wheel shape on crank torque, freely chosen pedal rate, and physiological responses during submaximal cycling. *J Physiol Anthropol* 28: 261-267, 2009.
VI. Rønnestad BR, **Hansen EA**, Raastad T. Strength training affects tendon cross-sectional area and freely chosen cadence differently in noncyclists and well-trained cyclists. *J Strength Cond Res* 26: 158-166, 2012.
VII. **Hansen EA**, Rønnestad BR, Vegge G, Raastad T. Cyclists' improvement of pedaling efficacy and performance after heavy strength training. *Int J Sports Physiol Perform* 7: 313-321, 2012.
VIII. **Hansen EA**, Voigt M, Kersting UW, Madeleine P. Frequency and pattern of rhythmic leg movement in humans after fatiguing exercises. *Motor Control* 18: 297-319, 2014.
IX. Sardroodian M, Madeleine P, Voigt M, **Hansen EA**. Frequency and pattern of voluntary pedalling is influenced after one week of heavy strength training. *Hum Mov Sci* 36: 58-69, 2014.

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To Jitka, Birk, and Johan for their great support and love

Preface

The present dissertation is based on experimental studies carried out at Institute of Sports Science and Clinical Biomechanics, University of Southern Denmark, Department of Physical Performance, Norwegian School of Sport Sciences, and Center for Sensory-Motor Interaction, Department of Health Science and Technology, Aalborg University, Denmark. I would like to express my appreciation for the support from these institutions and all the people who have been involved in the studies.

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Curiosity and wonderment has been major driving forces for the present work.

Ernst Albin Hansen

Aalborg, August, 2014

List of abbreviations

CI_{95}	95% confidence interval
CPG	central pattern generator
ICC	intra-class correlation coefficient
IN	interneuron
MN	motor neuron
MVC	maximal voluntary contraction
r	correlation coefficient
RM	repetition maximum
RPE	rate of perceived exertion
rpm	revolutions per min
VO	oxygen uptake
VO_{2max}	maximal oxygen uptake
VO_{2peak}	peak oxygen uptake
W_{max}	maximal aerobic power output

1 Introduction

Cycling, running, and walking are examples of common voluntary human rhythmic movements. A better understanding of the behaviour and control of such movements is useful in the work to improve performance, function, and rehabilitation of exercising, healthy, and injured humans. Walking is the most common human exercise model for studying rhythmic leg movement [see e.g. (Dietz et al., 1994; Zehr and Haridas, 2003; Cappellini et al., 2006)]. Cycling constitutes another suitable exercise model [see e.g. (Balter and Zehr, 2007; Sakamoto et al., 2007; Hartley and Cheung, 2013)] that has the characteristics that it offers a more constrained movement plus a gearing system.

It has been suggested that neural networks, now termed central pattern generators, in the spinal cord can generate the rhythm and shape the pattern of the bursts of motor neurons and in that way generate rhythmic movements [see for review (Zehr and Duysens, 2004; Prochazka and Yakovenko, 2007; Guertin, 2009; Grillner, 2011)]. Whereas most investigations of central pattern generators have been, and still is, conducted on animals (Orlovsky et al., 1999), in more recent years experiments have been conducted on humans (Shima et al., 2011; Lacquaniti et al., 2012; Maclellan et al., 2013a) with an overall main purpose of improving the incorporation of rhythmic movements in post-neurotrauma rehabilitation strategies (Dimitrijevic et al., 1998; Minassian et al., 2007). Some research has in particular focused on the importance of central pattern generators for control of voluntary rhythmic movement behaviour during exercise (Zehr, 2005). Studies of central pattern generator-generated voluntary rhythmic movement in healthy humans are challenged by researchers' restricted access to the spinal cord. Still, analysis of motor behaviour is used to increase our understanding of how the nervous system is organized and function (Goulding, 2009).

The overall purpose of the present dissertation was to contribute to the understanding of voluntary human rhythmic leg movement behaviour and control. Pedalling was used as exercise model for studying the movement. The present dissertation has been defined to primarily focus on individuals performing submaximal movement. Healthy and recreationally active individuals as well as trained cyclists participated and were exposed to for example cardiopulmonary and mechanical loading, fatiguing exercise, and heavy strength training. A variety of experimental hypotheses were tested in a number of studies (I-IX). This was done in an attempt to further elucidate and develop the overall working hypothesis that freely chosen pedalling frequency to a large extent is a result of central pattern generator output.

1.1 Dissertation overview

In section 2, an overview is given of the effect of pedalling frequency on selected biomechanical, physiological, and psychophysiological variables of pedal force, brain activity, electromyographic activity, $\dot{V}O_2$, energy turnover, efficiency, as well as perceived exertion during prolonged cycling. Section 3 constitutes a brief review of the effect of pedalling frequency on cycling performance. Section 4 is a presentation of the tenacious myth that minimisation of rate of energy turnover strongly affects the choice of pedalling frequency. In section 5, a working hypothesis of central pattern generator to strongly affect freely chosen pedalling rhythm is presented. In section 6, factors that in the present work were selected to be tested for their effect on the pedalling rhythm are presented. These factors included power output, mechanical and cardiopulmonary loading, fatiguing exercise, as well as heavy strength training. Sections 7 and 8 constitute summaries in English and Danish, respectively.

Table 1 provides an overview of the articles that the present dissertation is in part based on. In the table, information is presented on the equipment that was applied and the interventions that were performed. In addition, the table contains brief descriptions of the knowledge that was obtained and has contributed to the understanding of voluntary rhythmic leg movement behaviour and control during pedalling.

Insert Table 1 around here

2 Effect of pedalling frequency on selected variables

2.1 Pedal force

The product of pedal force and pedal velocity determines the power output. Pedal velocity is reflected by the pedalling frequency. It follows, that if pedalling frequency is changed during cycling at a constant power output, the pedal force will also change. Pedal force has been investigated during pedalling at different frequencies.

In one study (Patterson and Moreno, 1990), effective pedal force (i.e. force applied perpendicular to the crank arm) was measured in 11 men with recreationally bicycling experience during ergometer cycling at 100 and 200 W at 40 to 120 rpm. The results showed a clear decrease of the effective pedal force with increasing pedalling frequency.

In another study (Candotti et al., 2007), investigating 17 cyclists and triathletes during ergometer cycling at about 5% below the second ventilatory threshold at 60 to 105 rpm, a similar result was observed.

2.2 Brain activity

The intensity and volume of brain activity is influenced both by generation of movements and by sensory feedback evoked by movements. Brain activity has been investigated during pedalling movements at different frequencies.

In one study (Christensen et al., 2000), the cerebral activation during bicycling movements was investigated by oxygen-15-labelled H2O positron emission tomography (PET) in 7 healthy individuals. Compared to rest, active bicycling movements at a “loading” of the ergometer of 1 to 12 kg (corresponding to not stated power outputs) significantly activated sites bilaterally in the primary sensory cortex, primary motor cortex, supplementary motor cortex, and anterior part of cerebellum. Comparing passive bicycling movements with rest, an almost equal activation was observed. Subtracting passive from active bicycling movements, significant activation was only observed in the leg area of the primary motor cortex and the precuneus, while not in the primary sensory cortex. The primary motor cortex activation was positively correlated with the frequency of the active bicycling movements. However, with regard to that particular result is should be noted that power output was most likely increased with increasing bicycling movement frequency since load rather than power output was maintained constant. Imagination of bicycling movements, compared to rest, activated bilaterally sites in the supplementary motor cortex. The authors suggested that higher motor centres, including the primary and supplementary motor cortices as well as the cerebellum, take an active part in the generation and control of rhythmic motor tasks such as bicycling. Still, it was also noted by the authors that perhaps the main part of the cerebral activation observed during the passive bicycling was in fact caused by the sensory

feedback evoked by the moving limbs and that a similar mechanism also explains a very significant part of the cerebral activation during active bicycling.

In another study (Mehta et al., 2012), functional magnetic resonance imaging (fMRI) was used to record human brain activity during slow (30 rpm), fast (60 rpm), and passive (30 rpm) pedalling as well as during pedalling at a variable frequency. Ten healthy adults participated and exercised at, again, a not stated power output. After identifying regions of interest, the intensity and volume of brain activity in each region was calculated and compared across conditions. The results showed that the primary sensory and motor cortices, supplementary motor area, and cerebellum were active during pedalling. The intensity of activity in these areas increased with increasing pedalling frequency and complexity. The cerebellum was the only brain region that showed significantly lower activity during passive as compared to active pedalling. The authors concluded that primary sensory and motor cortices, supplementary motor area, and cerebellum have a role in modifying continuous, bilateral, multijoint lower extremity movements. Further, that much of this brain activity may be driven by sensory signals from the moving limbs.

2.3 Electromyographic activity

Muscle activation can be investigated by recordings of electromyographic activity from surface electrodes placed on the skin over muscles. Electromyographic activity has been investigated during pedalling at different frequencies.

In one study (Ericson et al., 1985), linear envelope electromyographic activity normalised to electromyographic activity during isometric MVC was investigated in 11 healthy individuals during ergometer cycling at 0 to 240 W at 40 to 100 rpm. The results showed that an increase of the pedalling frequency increased the electromyographic activity over the gluteus maximus, gluteus medius, vastus medialis, medial hamstring, gastrocnemius medialis, and soleus muscles.

In another study (Macintosh et al., 2000), root-mean-square electromyographic activity was investigated from 7 leg muscles in 8 active male individuals during ergometer cycling at 100 to 400 W at 50 to 120 rpm. The results showed that a second-order polynomial equation fitted the average root-mean-square electromyographic activity data of all muscles vs. pedalling frequency (r^2 ranging from 0.87 to 0.996) for each power output. The pedalling frequency with the lowest amplitude of electromyographic activity (denoted the optimal cadence) for a given power output increased with increases in power output from on average 57 rpm at 100 W to on average 99 rpm at 400 W.

2.4 Oxygen uptake, energy turnover, and efficiency

Measurements of rate of $\dot{V}O_2$ can be converted to estimates of rate of energy turnover, alternatively denoted metabolic power output, by taking into account respiratory exchange ratio. Further, when mechanical power output is known from for example cycle ergometer measurement, the gross efficiency of cycling can be calculated (Coyle et al., 1992; Hansen et al., 2002a). In addition, alternative forms of efficiency can be calculated. These can for example account for estimates of ‘‘internal power’’, generated by muscles to overcome energy changes of moving body segments, and/or account for resting rate of $\dot{V}O_2$ (Hansen et al., 2004; Hansen and Sjøgaard, 2007).

When rate of $\dot{V}O_2$ is depicted as a function of pedalling frequency, the relationship is U-shaped (Coast and Welch, 1985)(I). For comparison, the relationship is inverted U-shaped when gross efficiency is depicted as a function of pedalling frequency (Böning et al., 1984; Hansen et al.,

2002a) as illustrated in Figure 1. The pedalling frequency with the lowest rate of VO_2 or highest gross efficiency can be denoted the energetically optimal pedalling frequency and occurs at around 50 to 80 rpm depending on power output or exercise intensity in a way that the energetically optimal pedalling frequency increases with increasing exercise intensity (Nielsen et al., 2004).

Insert Figure 1 around here.

2.5 Perceived exertion

The subjective RPE is for example determined by having individuals indicating their perceived effort on a 6 to 18 point scale during exercise (Borg, 1970). RPE has been investigated during pedalling at different frequencies.

In one study (Löllgen et al., 1980), overall RPE was investigated in 6 healthy male individuals during ergometer cycling at power outputs corresponding to 70% and 100% of VO_{2max} at 40 to 100 rpm. Fitting a parabolic curve to the group average RPE data revealed U-shaped relationships with minimum RPE values occurring at 65 and 73 rpm at 70% and 100% of VO_{2max}, respectively.

In another study (Hansen et al., 2002a), overall RPE was investigated in twenty healthy males during treadmill cycling at 61 to 115 rpm at 40% and 70% of the power output at which VO_{2max} was attained. Fitting a second-degree polynomial to the group average RPE data revealed a parabolic relationship with minimum RPE values occurring at 63 and 72 rpm at the low and high power output, respectively.

3 Effect of pedalling frequency on cycling performance

Performance during prolonged submaximal cycling may for example be directly determined in a constant duration test where duration is pre-set and covered distance or average power output constitutes the performance measure. An alternative is a time trial test where distance or work is pre-set and time or average power output constitutes the performance measurement (Currell and Jeukendrup, 2008). Indirectly, cycling performance may be indicated by physiological and psychophysiological responses such as energy turnover, VO_{2max}, and RPE. The exact reason for performance deterioration during prolonged submaximal cycling is difficult to determine and beyond the subject of the present dissertation. It depends on for example, but is not limited to, cycling intensity and duration, as well as training status and environmental conditions. Often, the reason for performance deterioration is considered to be multifactorial. For an exhaustive review of different models of cycling performance deterioration, the reader is referred to a previous publication (Abbiss and Laursen, 2005). There has only been published a couple of studies in which the effect of pedalling frequency on performance during prolonged (>30 min) submaximal cycling has been investigated.

In one study (I), it was tested whether 9 trained male cyclists performed better during all-out ergometer cycling following prolonged ergometer cycling at the energetically optimal pedalling frequency rather than at the freely chosen pedalling frequency. First, the energetically optimal and the freely chosen pedalling frequencies were determined during ergometer cycling at 180 W, which constituted a moderate power output for the participating cyclists. In addition, baseline performance was determined by measuring both average power output and rate of VO_{2peak} during

5-min all-out ergometer cycling at freely chosen pedalling frequency. Subsequently, on two separate days, the cyclists cycled 150 min at 180 W at the energetically optimal frequency (on average 73 rpm) and at the freely chosen pedalling frequency (on average 95 rpm), respectively. Each bout was followed by a 5-min all-out trial. During the prolonged ergometer cycling, heart rate, rate of VO_2, and RPE were 7% to 9% higher at the freely chosen than at the energetically optimal pedalling frequency. It was further estimated that glycogen utilization was 22% higher during cycling at the freely chosen than at the energetically optimal pedalling frequency. In addition, rate of VO_{2peak} was lower than at baseline only after the prolonged cycling bout at freely chosen pedalling frequency. During the 5-min all-out trial following prolonged cycling at the energetically optimal and the freely chosen pedalling frequency, average power output was 8% and 10% lower than at baseline, respectively. The reduction was not different between pedalling frequencies. It was concluded that during prolonged submaximal cycling, the relatively low energetically optimal pedalling frequency was at least as advantageous as the relatively high freely chosen pedalling frequency for performance optimization in subsequent all-out cycling.

In a subsequent publication (Stebbins et al., 2014), a similar aim and design was reported. A main difference was, though, that intensities during the prolonged ergometer cycling varied between 50% and 80% of rate of VO_{2max}. This was to better reflect the varying work demands of competitive road cycling. Moreover, the pedalling frequencies during the prolonged (180 min) cycling were pre-set at 80 and 100 rpm, assuming 80 rpm to be closer to the energetically optimal pedalling frequency than 100 rpm. Lastly, rather than an all-out trial for determination of performance, an incremental ramp test at freely chosen pedalling frequency was performed following the prolonged cycling, to determine maximal power output. Eight competitive male road cyclists participated. Physiological variables such as heart rate, rate of VO_2, and blood lactate concentration were higher during the prolonged cycling at 100 rpm than at 80 rpm. The total rate of energy turnover during cycling at the 65% and 80% VO_{2max} intervals at 100 rpm (on average 15 and 19 kcal min^{-1}, respectively) were higher than at 80 rpm (on average 14 and 18 kcal min^{-1}, respectively). Gross efficiency was lower at 100 rpm than at 80 rpm during both the 65% (on average 21.3% vs. 22.8%) and the 80% (on average 22.1% vs. 23.1%) intervals. Maximal power output in the ramp test was lower after cycling at 100 rpm (on average 327 W) than after cycling at 80 rpm (on average 362 W). It was concluded, that in conditions simulating prolonged competitive cycling, a relatively low pedalling frequency as compared to a relatively high (i.e., 80 vs. 100 rpm) was more efficient and resulted in better performance during intensive cycling.

4 Myth of energy turnover minimisation to strongly affect freely chosen pedalling frequency

During walking and running, a U-shaped relationship between stride frequency and rate of energy turnover can be observed when data are averaged for groups of individuals. That has previously been summarised (Martin et al., 2000). Furthermore, the average freely chosen stride frequency in groups of individuals coincides with the average energetically optimal stride frequency (Martin et al., 2000). The latter has reinforced the widespread proposition that humans choose their stride frequency with the purpose of minimising rate of energy turnover (Martin et al., 2000; Alexander, 2002). However, this proposition has be questioned (Dean, 2013) by for example referring to the finding that when walking downhill, humans seem to prefer a more cautious and costly form of gait than the energetically optimal (Hunter et al., 2010). Further, when data are considered on an individual level, the entire literature within the field apparently only provides a single, fair (r=0.68),

correlation between energetically optimal stride frequency and freely chosen stride frequency during running, for a group of individuals (recreational runners)(Cavanagh and Williams, 1982).

An alternative is to consider the freely chosen stride frequency as a resultant rhythmic movement output from the nervous system including central pattern generators (Zehr, 2005). Further, coincide of the freely chosen stride frequency and the energetically optimal stride frequency could be a result of human evolution where stride frequency has preceded the metabolic response – not *vice versa* (Hirasaki et al., 2004). Consider that man has walked and been running from the very beginning of human evolution (Lovejoy, 1988). And add, that minimisation of rate of energy turnover during unrestricted walking possibly has been a criterion for natural selection in human evolution since spared energy could then be used for other purposes, such as growth or reproduction, or for walking longer distances (Nakatsukasa et al., 2006).

During cycling, groups of children (Klausen et al., 1985), recreationally active adults (Hansen et al., 2002a), trained runners (Marsh and Martin, 1997), and competitive cyclists (Marsh and Martin, 1997; Foss and Hallén, 2005)(I), all freely choose a relatively high pedalling frequency, which is accompanied by higher rates of $\dot{V}O_2$ and energy turnover as well as a lower gross efficiency than what could have been attained by simply pedalling slower with a larger gearing. An example of this is illustrated in Figure 1. In fact, the phenomenon was observed in a professional cyclist and discussed for the first time as early as a century ago (Benedict and Cathcart, 1913). This phenomenon suggests that humans do not choose their pedalling frequency with the purpose of minimising energy turnover, and the phenomenon has been designated the "cadence paradox" (Kohler and Boutellier, 2005). Given that an actual paradox is considered, it indicates that coincide of freely chosen and energetically optimal pedalling frequency should be expected. And actually it has, somewhat surprisingly, been indicated occasionally in the literature that humans choose to pedal in a particular way (e.g. at a particular frequency) with the purpose of minimising rate of energy turnover (Sparrow and Newell, 1998; Umberger et al., 2006; Sparrow et al., 2007) despite the considerable amount of contrasting evidence referred to in the beginning of this paragraph.

The common understanding of existence of a "cadence paradox" has perhaps to do with the fact that despite completion of plentiful investigations involving numerous physiological and biomechanical variables, researchers have had difficulty in finding certain characteristics that are optimized at the freely chosen pedalling frequency or strongly correlated with the freely chosen pedalling frequency. Thus, as late as in 2007 - almost a century after the first documentation and wonder of the "cadence paradox" by Benedict and Cathcart (1913) - it was stated that "the underlying reasons leading to the choice of a particular pedaling cadence in cyclists have yet not been clearly established" (Bieuzen et al., 2007). Nevertheless, as the present dissertation will suggest, novel insight has emerged through recent research of the old mystery of pedalling frequency choice during submaximal cycling.

5 Working hypothesis of central pattern generator to strongly affect freely chosen pedalling rhythm

Coordination of rhythmic movement has been suggested to be controlled by neural networks located in the spinal cord and termed central pattern generators (Duysens and Van de Crommert, 1998; Zehr and Duysens, 2004; Zehr, 2005). A suggested model for this control is that oscillating neural circuitry (half-centres) is resided in the lumbar spinal cord (Brown, 1911; Brown, 1914). Further, this half-centre (one half for flexor activation, another half for extensor activation) model suggests that discrete rhythm or pattern generating networks are responsible for producing the

basic locomotor rhythm and muscle activity seen in locomotion (Zehr, 2005). It has been advocated that both descending supraspinal drive and sensory feedback assist in fine-tuning the output from the central pattern generators, even though the details of these mechanisms are not known. For review of this, the reader is referred to previous publications (Van de Crommert et al., 1998; MacKay-Lyons, 2002; Zehr and Duysens, 2004).

Walking has been used as an exercise model in studies of human rhythmic movement (Dietz et al., 1994; Zehr and Haridas, 2003; Maclellan et al., 2013b). Cycling is another model (Balter and Zehr, 2007; Sakamoto et al., 2007; De Marchis et al., 2013), which not only offers a more constrained movement but also a gearing system that allows relatively low and high pedalling frequencies to be chosen as compared to stride frequencies during walking. In this context, it is worth noting that freely chosen pedalling frequency is largely individual, showing a considerable inter-individual range from about 50 to 100 rpm (Hansen et al., 2002a; Sarre et al., 2003)(III).

It has been suggested that freely chosen pedalling frequency during submaximal cycling represents an innate voluntary rhythmic leg movement frequency, under the primary influence of central pattern generators (III)(Hartley & Cheung, 2013). In other words, freely chosen pedalling frequency may be a good reflection of central pattern generator-generated movement frequency output. Freely chosen pedalling frequency has been reported to have a high within-session reliability with a between-bout correlation coefficient of r=0.84 (Hansen et al., 2002a). Moreover, freely chosen pedalling frequency has also been reported to have almost perfect between-day reliability with a between-day *ICC* of 0.91 (VIII). Lastly, freely chosen pedalling frequency has been reported to be steady in a 12-week longitudinal perspective with an average within-individual CI_{95} of 8 rpm across individuals (range of CI_{95} from 5 to 13 rpm)(III).

For completeness, it should be noted that existence of central pattern generators in humans is difficult to conclusively prove. Indirect evidence of their existence comes from for example spinal cord injured individuals (Calancie et al., 1994; Dimitrijevic et al., 1998) and infants (Yang et al., 1998).

Figure 2 summarises the main message from this section. That is that the freely chosen pedalling frequency during submaximal cycling has a highly individual and at the same time steady base, which is perhaps largely influenced by central pattern generator characteristics. This does, however, not at all exclude the influence that other factors internal and external to the cyclist under certain circumstances can have on the freely chosen pedalling frequency.

Insert Figure 2 around here.

5.1 Division of pedalling rhythm into frequency and pattern

For the present dissertation, it was considered that (*i*) the freely chosen pedalling frequency reflects the rhythmic movement frequency of the voluntary rhythmic leg movement of pedalling and that (*ii*) the tangential pedal force profile reflects the rhythmic movement pattern of pedalling (VIII; IX). This division was inspired by the fact that the internal organisation of the central pattern generator is considered to be functionally separated into two components, in which, one is responsible for rhythmic movement frequency and another is responsible for rhythmic movement pattern (Perret and Cabelguen, 1980; Kriellaars et al., 1994; McCrea and Rybak, 2008; Dominici et al., 2011).

Figure 3 illustrates a hypothetical multilevel arrangement from supraspinal level over central pattern generator to rhythmic movement that can be considered in the elucidation of behaviour and control of voluntary pedalling rhythm. Figure 4 illustrates selected key pedal force profile characteristics consisting of maximum tangential pedal force (F_{max}) and minimum tangential pedal force (F_{min}), as well as phase with negative tangential pedal force (Ph_{neg}).

Insert Figure 3 around here.

6 Factors tested for their effect on pedalling rhythm

6.1 Power output

It has been reported that male cyclists during intensive treadmill cycling increased the freely chosen pedalling frequency by on average 15 to 17 rpm when power output was increased from values corresponding to 86% to 165% of W_{max} (IV). An approximately 6 rpm increase (average value) of the freely chosen pedalling frequency with approximately 100 W increase of the power output had beforehand been reported for healthy males during submaximal treadmill cycling (Hansen et al., 2002a; Hansen et al., 2002b). In addition, it is known from investigations of road cycling that freely chosen pedalling frequency is increased with increased cycling speed in trained cyclists (Sargeant, 1994) and with increased power output in male road cyclists (Ebert et al., 2006). These results indicated that during treadmill and road cycling, an increase of the power output affects individuals' voluntary rhythmic leg movement behaviour in a way that they choose to pedal faster. Furthermore, the results indicated that the behaviour of the voluntary pedalling rhythm, at least the movement frequency, during road cycling is well replicated during treadmill cycling. This is an important consideration for laboratory studies that must closely simulate outdoor cycling. For comparison, it has been observed that the freely chosen pedalling frequency is unaffected by increased power output during cycling on electromagnetically braked ergometers (Marsh and Martin, 1998; Marsh et al., 2000). Accordingly, it indicates that perhaps cycling on electromagnetically braked ergometers does not fully simulate road and treadmill cycling. A reason for this might be that crank inertial load, which can be comparable between road and treadmill cycling, is lower on most cycle ergometers (Fregly et al., 2000; Hansen et al., 2002b). Crank inertial load is the effective rotational inertia about the crank axis due to the moment of inertia of the flywheel or rear wheel. It has the effect of resisting changes in the velocity of the cranks (Fregly et al., 2000). For example, if a cyclist with a body mass of 70 kg performs cycling at 90 rpm at the same power output on a very steep uphill road at 10 km h^{-1} and subsequently on a level road at 50 km h^{-1} with gear ratios of 26/28 (chain wheel/free wheel) and 52/12, respectively, the change in gear ratio from 26/28 to 52/12 results in a change in crank inertial load from approximately 8 to 180 kg m^2 (Hansen and Smith, 2009).

6.2 Mechanical loading

When cycling speed or power output is increased during treadmill or road cycling at a set pedalling frequency, both mechanical loading (e.g. peak and average pedal force in each pedal thrust) and cardiopulmonary loading (e.g. heart rate, ventilation rate, and rate of VO_2) are increased. The report from Sargeant (1994) of increased pedalling frequency with increased cycling speed, as described in section 6.1, inspired to conduct studies of pedalling frequency choice in which the

mechanical loading was modified separately without changing the cardiopulmonary loading. The purpose was to elucidate an overall working hypothesis, which was, that altered mechanical loading could cause a change of the freely chosen pedalling frequency.

In one study (Hansen et al., 2002b), freely chosen pedalling frequency was investigated in 9 healthy male individuals during horizontal treadmill cycling at low (on average 16 to 20 kg m^2) and high (on average 103 to 120 kg m^2) crank inertial load at two power outputs of approximately 150 and 250 W. Higher crank inertial load resulted in on average 3% to 5% higher peak crank torque (reflecting peak effective pedal force) during cycling at a constant pedalling frequency. In addition, results showed that freely chosen pedalling frequency was systematically on average 6 to 8 rpm higher during cycling at high as compared to low crank inertial load. One interpretation was that the higher peak crank torque during cycling at high crank inertial load, via increased mechanoreceptor stimulation, possibly induced an increase in perceived exertion. This in turn possibly caused the individuals to increase their pedalling frequency, since both average and peak crank torque, and perceived exertion, could thereby be reduced. Still, a challenge with that interpretation is that 100 W increased power output caused an increase in freely chosen pedalling frequency that was similar to the increase that was observed from the change in crank inertial load. And that occurred despite that such a change in power output causes a considerable larger increase in peak and average pedal force. An alternative interpretation could involve the fact that delta crank torque, representing the difference between peak and minimum crank torque, on average was 10% higher during cycling at high than at low crank inertial load. And, suggestively, that called for increased rate of force development to be performed by the active muscles at high crank inertial load. This could require increased muscle activation, including increased common drive from supraspinal centres (De Luca and Erim, 1994) to the central pattern generator (Minassian et al., 2007), and contribute to larger net excitability of the central pattern generator. A later study (Bertucci et al., 2012) supported the findings by Hansen et al. (2002b) of an increasing effect of crank inertial load on freely chosen pedalling frequency by showing a tendency (p=0.06) for a positive correlation between crank inertial load during road cycling at consistent power output (on average approx. 245 W) and freely chosen pedalling frequency in 9 male cyclists.

In a second study (V), 10 trained cyclists performed ergometer cycling at 180 W with a traditional circular and a non-circular (Biopace II, CR-BP20, Shimano, Osaka, Japan) chain wheel at pre-set target and freely chosen pedalling frequencies. The purpose was to test the hypotheses *i*) that peak crank torque during cycling at two pre-set target pedalling frequencies of 65 and 90 rpm would be higher when using the circular as compared to the non-circular chain wheel, and *ii*) that the freely chosen pedalling frequency, as a consequence of the higher peak crank torque, would be higher with the circular chain wheel, to reduce the peak and average crank torque. The results showed that crank torque profiles were similar between the two chain wheels during cycling at pre-set target pedalling frequencies. This was probably a result of the fact that the non-circular chain wheel that was used, was not skewed enough to cause detectable differences in the crank torque profiles. In line with this, although in contrast to the initial hypothesis, the freely chosen pedalling frequency remained similar during cycling with the two different chain wheels.

In a third study (III), 8 healthy and recreationally active individuals first performed ergometer cycling at the power output corresponding to 65% of VO_{2max} at 40, 55, 70, 85, and 100 rpm for determination of the relationship between pedalling frequency and rate of VO_2. Subsequently, they performed ergometer cycling at freely chosen pedalling frequency at the following three conditions: (*i*) power output corresponding to 65% of VO_{2max} at 200 m altitude (laboratory

location); (*ii*) power output as in *i*, but at 3,000 m simulated altitude that resulted in an exercise intensity of 80% of VO_{2max}, and; (*iii*) power output corresponding to 80% of VO_{2max} at 200 m altitude. In that way, percentage of VO_{2max} (reflecting cardiopulmonary loading) was similar in condition *ii* and *iii* whereas power output (reflecting mechanical loading) was higher in condition *iii* than in condition *ii*. The results showed that the freely chosen pedalling frequency was unaffected by increased power output during cycling at a consistent cardiopulmonary loading. This caused the authors to reject an experimental hypothesis of the study, which was, that during submaximal ergometer cycling at a constant cardiopulmonary loading, an increase in power output or mechanical loading would cause individuals to pedal faster to reduce the force in each pedal thrust. Furthermore, the rejection of this experimental hypothesis was interpreted to support the working hypothesis of the study, which was, that the freely chosen pedalling frequency is characterized as a robust innate voluntary motor rhythm under primary influence of central pattern generators.

6.3 Cardiopulmonary loading

In the last-mentioned study (III), the three conditions also allowed another comparison to be made. Thus, power output was identical in condition *i* and *ii* whereas the cardiopulmonary loading was higher in condition *ii* than in condition *i*. The results showed that the freely chosen pedalling frequency was unaffected by increased cardiopulmonary loading during ergometer cycling at constant power output. This caused the authors to reject another experimental hypothesis of the study, which was, that during submaximal ergometer cycling at identical power output, an increase in percentage of VO_{2max} would cause individuals to reduce their pedalling frequency towards a lower and approx. 5% less energy-demanding pedalling frequency, thereby decreasing the load on the cardiopulmonary system. Furthermore, the rejection of this experimental hypothesis was interpreted to support the working hypothesis of the study, which was, that the freely chosen pedalling frequency is characterized as a robust innate voluntary motor rhythm under primary influence of central pattern generators. A subsequent study (Hartley and Cheung, 2013), supported that interpretation. Hartley and Cheung (2013) had 20 healthy individuals performing three successive 20 min bouts of ergometer cycling at constant RPE at ambient temperatures of 20 °C, 35 °C, and 20 °C, respectively. Results showed that the thermal stress of heart rate and rectal temperature increased at the high ambient temperature. Still, the freely chosen pedalling frequency was unaffected by the thermal stress even that a reduction of the pedalling frequency could have reduced the thermal stress through a reduced cardiopulmonary loading.

6.4 Fatiguing exercise

Fatigue may be defined as decreased functional capacity of the muscles (Côté et al., 2008). This definition implies the inability to maintain a required voluntary muscle force and to provide accurate performance. Often, the reason why fatigue occurs is considered to be multifactorial. The effects of fatigue are well documented in isometric conditions including for example changes in position sense. For extensive review, the reader is referred to previous publications (Gandevia, 2001; enoka and Duchateau, 2008). Fewer studies, however, have addressed the effects of fatigue on muscles and joints of adjacent or remote body parts (Côté et al., 2008). Fatigue affects the coordination of fingers' and upper extremities' rhythmic movement (Côté et al., 2008; Singh et al.,

2010). However, it is largely unknown whether fatigue will also affect rhythmic leg movement behaviour in terms of movement frequency and movement pattern.

In one study (VIII), 9 healthy individuals performed ergometer cycling at 100 W at freely chosen pedalling frequency as well as at a pre-set target pedalling frequency of 60 rpm before and after fatiguing hip flexion and hip extension exercises. The results showed that an alteration of key characteristics of the tangential pedal force profile (reflecting the rhythmic movement pattern) was found during cycling at 60 rpm, after hip flexion exercise. Thus, minimum tangential pedal force decreased by on average 12%, while maximum tangential pedal force increased by on average 5%, and the length of the phase with negative tangential pedal force increased by 3%. In other words, the alteration comprised a longer phase with negative tangential pedal force in the upstroke phase. In addition, the minimum tangential pedal force in the upstroke phase became more negative. Thus, the legs were "actively lifted" to a lesser extent. These alterations were most likely a result of fatigue in the hip flexors. For comparison, fatiguing hip extension exercise did not affect the rhythmic movement pattern. Further, the freely chosen pedalling frequency (reflecting the rhythmic movement frequency) was not affected after the two different types of fatiguing exercise. Of note is that an alteration of the rhythmic movement pattern concomitant with a preservation of the rhythmic movement frequency is indeed conceivable. The reason is that rhythmic movement may be generated by a central pattern generator organised in two components, in which, one is responsible for rhythmic movement frequency and another is responsible for rhythmic movement pattern (Perret and Cabelguen, 1980; Kriellaars et al., 1994; McCrea and Rybak, 2008; Dominici et al., 2011) as described in section 5.1.

The effect of fatiguing exercise on rhythmic movement pattern in pedalling has not been investigated in a similar way in other studies. And that part of the results from study VIII can thus not be compared with other results. With regard to the effect of fatiguing exercise on rhythmic movement frequency in general, it has previously been reported that the duration of hammering movement remained unchanged in presence of fatigue in healthy individuals asked to hammer repetitively (Côté et al., 2008). In addition, well-trained individuals were reported to maintain their freely chosen pedalling frequency during 1 h of ergometer cycling at 65% of W_{max} (Sarre et al., 2005). On the other hand, the freely chosen pedalling frequency in well-trained individuals, triathletes, endurance trained men, and well-trained male cyclists decreased by on average 7 to 18 rpm across 1 to 5 h of ergometer cycling (Lepers et al., 2000; Vercruyssen et al., 2001; Jeukendrup et al., 2006; Johnson et al., 2006; Argentin et al., 2006). The latter indicates that fatigue, which is assumed to be developed at least in some cases of prolonged cycling, might cause a reduction of the freely chosen pedalling frequency.

6.5 Heavy strength training

It has been reported that healthy individuals decreased their freely chosen pedalling frequency by on average 8 and 10 rpm during ergometer cycling at 37% and 57% of W_{max}, respectively, after 12 weeks of heavy strength training (II). The training was progressive, applying 12RM to 2RM loading, performed 4 days per week, and included 2 days per week with leg-extensor and knee-flexor exercises. Hip flexion exercise in form of sit-ups on an incline abdominal board and abdominal crunch in a machine was also performed as part of the training regimen. The training group consisted of 14 individuals whereas a control group consisted of 7 individuals. The results showed that the training group increased strength (1RM) in both squat (on average 20%) and leg curl (on average 12%) from the beginning to the end of the study period. The observed reduction of the

freely chosen pedalling frequency is considered substantial. If an individual for example pedals at a freely chosen pedalling frequency of 70 rpm and is asked to instantly reduce it to 60 rpm, the individual in most cases will perceive it as a considerable change. The study did not point at a causal relationship between maximal leg strength *per se* and choice of pedalling frequency. The reason was that absolute values of maximal leg strength and freely chosen pedalling frequency were not correlated, regardless of a large variation in both variables (e.g., 40 to 200 kg in squat and 55 to 97 rpm at 57% of W_{max}). In line with that, an absence of a relationship between maximal voluntary isometric knee extension torque and freely chosen pedalling frequency has been reported before (Hansen et al., 2002a). In addition, it was found that improvement in maximal leg strength not was correlated to reduction in freely chosen pedalling frequency (II). This would further support that strength *per se* does not influence pedalling frequency. Since strength *per se* did, thus, does not appear to determine the choice of pedalling frequency, it was considered that other outcomes of the strength training were focused on, as possible reasons for the considerably changed pedalling behaviour.

Changes within the neuromuscular system (including tendons) were considered to be involved. Strength training may down-regulate Ib afferent feedback (autogenous inhibitory feedback) from the force-sensitive Golgi tendon organs at a given constant level of stimulation (Aagaard et al., 2000). Such a down-regulation could for example be due to less tendon organ deformation as a result of increased tendon stiffness following strength training (Kubo et al., 2002). It was speculated that if this is so, then perhaps strength training reduces the part of the sensed effort that is related to the muscle/tendon load, and thereby causes subjects to decrease the freely chosen pedalling frequency and thereby reduce energy turnover, despite the fact that this increases the force in each pedal thrust (II).

In a subsequent study (VI), 7 recreationally active individuals decreased their freely chosen pedalling frequency by on average 11 rpm during ergometer cycling at 125 W after 12 weeks of heavy strength training. The training was progressive, applying 10RM to 4RM loading, and performed 2 days per week. The performed training exercises were half squat, leg press with one leg at a time, standing one-legged hip flexion, and ankle plantar flexion. The results showed that the individuals increased 1RM in half squat by on average 31% following the training period. In addition, the cross sectional area of the patellar tendon was increased after the 12 weeks of training (from 165 to 177 mm^2). Thus, one could speculate that the reduction of the freely chosen pedalling frequency could be associated with the patellar tendon development. On the other hand, the reduction of the pedalling frequency was observed already after 4 weeks of strength training, which is relatively fast with respect to tendon development during strength training. That could imply that some factors being unrelated with tendon characteristics (e.g. neural factors) might be involved in the changed pedalling behaviour. Patellar tendon cross sectional area was unfortunately not measured at 4 weeks, so we do not know whether adaptations in the tendon had occurred already at that time point.

In yet a succeeding study (IX), the temporal effects of four weeks of separate heavy hip extension and heavy hip flexion strength training interventions on freely chosen pedalling frequency and tangential pedal force profile (at freely chosen and at a 60-rpm pre-set target pedalling frequency) were investigated during ergometer cycling at 100 W. The purpose was to determine how early in a strength training period the voluntary rhythmic leg movement frequency and pattern were modified and whether hip extension and hip flexion training had the same effect. In the previously mentioned studies II and VI, strength training exercises involved both hip

extension and hip flexion. For study IX, 27 recreationally active individuals were randomised into three groups. One group performed progressive heavy hip extension strength training. Another group performed progressive heavy hip flexion strength training. A third group constituted control individuals. Training sets were alternately made with right and left legs so that both legs were trained. The hip extension and hip flexion exercises are illustrated in Figure 5. The targeted muscle groups in the hip extension exercise and the hip flexion exercise included the gluteus maximus and the iliopsoas muscles, respectively. These muscles have an important role in the generation of pedalling (So et al., 2005; Gondoh et al., 2009) and they are both single joint muscles acting across the hip joint that may be considered the leading joint during pedalling (Dounskaia, 2005). Training applied 10RM to 5RM loading and was performed 2 days per week. The results showed that strength (1RM) increased by on average 25% and 33% in the groups that trained hip extension and hip flexion, respectively. Yet, the freely chosen pedalling frequency was only changed in the group that trained hip extension. More specifically, the change consisted of a decrease that commenced already after a single week of training. The decrease of the freely chosen pedalling frequency in the group that trained hip extension training amounted to a maximum average of 14 rpm across four tests performed one, two, and three weeks into the training period, as well as after the complete training period. This decrease was larger than the corresponding changes in the control group.

The early change in movement behaviour in study IX indicated that neural factors presumably play a major role since morphological changes are considered to take farther time. The tangential pedal force profile was not influenced during cycling at the pre-set target pedalling frequency of 60 rpm, which may suggest that the hip extension strength training primarily influenced the output from the component of the central pattern generator that is considered to be responsible for rhythmic movement frequency. Decreased frequency output from the central pattern generator after heavy strength training could be caused by reduced net excitability of the central pattern generator itself. It could also be caused by reduced common drive from supraspinal centres (De Luca and Erim, 1994) to the central pattern generator (Minassian et al., 2007). After strength training, individual motor units can produce more force, and fewer motor neurons are thus required for undertaking a given exercise task. Presumably, a reduction in recruitment of motor neurons would be reflected in diminished cortical activation (Carroll et al., 2011). Indeed, less muscle has been reported to be required to lift the same load after short-term strength training (Ploutz et al., 1994). Further, it has been reported that following three weeks of leg extensor strength training, movement tasks were performed with attenuated cortical demand, which was interpreted as evidence for enhanced neural efficiency (Falvo et al., 2010). According to the suggested model by Brown (1911)(see section 5), the oscillating neural circuitry in form of half-centres (one half for flexor activation and one half for extensor activation) resided in the lumbar spinal cord is responsible for producing the basic locomotor rhythm and muscle activity. Interactions within and between flexor and extensor half-centres of a given limb underlie the fine coordination of muscle activity during locomotion (Orlovsky et al., 1999). The reduction in the freely chosen pedalling frequency after a period of hip extension strength training, while not after hip flexion strength training, may indicate that the half-centre for extensor activation is particularly susceptible regarding generation of rhythmic movement frequency.

A phenomenon that has revealed itself in the present work is that when individuals are exposed to heavy strength training, movement behaviour responses appear to be influenced by the type of the individuals. For example, well-trained cyclists did not change their freely chosen

pedalling frequency after the same heavy strength training regimen that affected recreationally active individuals to markedly decrease their pedalling frequency (VI). This should be taken into account when designing future studies and interpreting results. The reason is not clear. It could be that well-trained cyclists, because of natural selection, represent individuals with some special characteristics of pedalling behaviour and control. It could also be that countless repetitions of a particular movement (in this case pedalling) during daily training, often throughout years, affect the movement behaviour and control in a particular way. Both aspects could, by the way, play a role for the occasional observation that trained cyclists pedal faster than more inexperienced cyclists (Takaishi et al., 1998; Hopker et al., 2007). In the majority of the present research, trained cyclists were involved as participants when research questions were focussed on performance whereas healthy recreationally active individuals were involved when research questions were focussed on basic understanding of movement behaviour and control. As an example of focus on performance, it was shown with 18 well-trained cyclists, that the crank torque profile during ergometer cycling was affected by adding heavy strength training to their usual endurance training regimen (VII). The strength training was as in (VI). In a 5-min all-out trial completed at freely chosen pedalling frequency following 185 min of submaximal ergometer cycling at 44% of W_{max}, the particular phase in the upstroke phase of the crank revolution where negative or retarding crank torque occurs was shortened by on average 16°, corresponding to on average 14%. In addition, the peak positive or propulsive crank torque increased by on average 3%. The interpretation of this was that strength training improved the pedalling efficacy concomitantly with improved performance in terms of on average 7% higher power output in the all-out trial after the strength training period.

7 Summary

The overall purpose of the present dissertation was to contribute to the understanding of voluntary human rhythmic leg movement behaviour and control. This was achieved by applying pedalling as a movement model and exposing healthy and recreationally active individuals as well as trained cyclists to for example cardiopulmonary and mechanical loading, fatiguing exercise, and heavy strength training. As a part of the background, the effect of pedalling frequency on diverse relevant biomechanical, physiological, and psychophysiological variables as well as on performance was initially explored.

Freely chosen pedalling frequency is considerably higher than the energetically optimal pedalling frequency. This has been shown by others and was confirmed in the present work. As a result, pedal force is relatively low while rates of VO_2 and energy turnover are relatively high during freely chosen pedalling as compared to a condition where a lower and more efficient pedalling frequency is imposed. The freely chosen pedalling frequency was in the present work, and by others, found to most likely be less advantageous than the lower energetically optimal pedalling frequency with respect to performance during intensive cycling following prolonged submaximal cycling. This stimulates the motivation to understand the behaviour and control of the freely chosen pedalling frequency during cycling.

Freely chosen pedalling frequency was in the present work shown to be highly individual. In addition, the pedalling frequency was shown to be steady in a longitudinal perspective across 12 weeks. Further, it was shown to be unaffected by both fatiguing hip extension exercise and hip flexion exercise as well as by increased loading on the cardiopulmonary system at constant mechanical loading, and *vice versa*. Based on this, the freely chosen pedalling frequency is

considered to be characterised as a highly individual, steady, and robust innate voluntary motor rhythm under primary influence of central pattern generators. The last part of the characterisation is largely based on, and supported by, work of other researchers in the field.

Despite the robustness of the freely chosen pedalling frequency, it may be affected by some particular factors. As an example from the present work, freely chosen pedalling frequency during treadmill cycling increased by on average 15 to 17 rpm when power output was increased from a value corresponding to 86% and up to 165% of W_{max}. This phenomenon is supported by other studies. As another example from the present work, freely chosen pedalling frequency decreased by on average 9 to 14 rpm following heavy strength training that involved both hip extension and hip flexion. Further, the present work suggested that the latter phenomenon occurred within the first week of training and was caused by in particular the hip extension strength training rather than the hip flexion strength training. The fast response to the strength training indicated that neural adaptations presumably caused the observed changes in movement behaviour.

The internal organisation of the central pattern generator is by some other researchers in the field considered to be functionally separated into two components, in which, one is responsible for movement frequency and another is responsible for movement pattern. For the present dissertation, the freely chosen pedalling frequency was considered to reflect the rhythmic movement frequency of the voluntary rhythmic leg movement of pedalling. The tangential pedal force profile was considered to reflect the rhythmic movement pattern. The present work showed that fatiguing hip flexion exercise in healthy and recreationally active individuals modified the tangential pedal force profile during cycling at a pre-set target pedalling frequency in a way that the minimum tangential pedal force became more negative, the maximum tangential pedal force increased, and the phase with negative tangential pedal force increased. In other words, the legs were “actively lifted” to a lesser extent in the upstroke phase. Fatiguing hip extension exercise did not have that effect. And none of the fatiguing exercises affected the freely chosen pedalling frequency. The present work furthermore showed that the primary effect of hip extension strength training was that it decreased the freely chosen pedalling frequency. An interpretation of this could be that the hip extension strength training, in particular, influenced the output from the component of the central pattern generator that may be responsible for rhythmic movement frequency.

8 Dansk resumé

Hovedformålet med nærværende afhandling var at bidrage til forståelsen af adfærden og kontrollen af voluntær rytmisk bevægelse udført med benene hos mennesket. Rekreativt aktive personer samt trænede cyklister deltog som forsøgspersoner. Formålet blev forsøgt opfyldt ved at anvende cykling som bevægelsesmodel og undersøge frekvensen og mønstret af benenes cykelbevægelse før og efter eksponering i form af eksempelvis kardiopulmonær og mekanisk belastning, trættende arbejde samt tung styrketræning. Som en del af baggrunden undersøgtes effekten af pedalfrekvens på diverse relevante biomekaniske, fysiologiske og psykofysiologiske variable, samt på præstation.

Selvvalgt pedalfrekvens er betydeligt højere end den energetisk optimale pedalfrekvens. Dette har været vist af andre og blev bekræftet i nærværende arbejde. Som en konsekvens af dette er pedalkraften relativ lav mens iltoptagelses- og energiomsætningshastigheden er relativ høj under cykling med selvvalgt pedalfrekvens sammenlignet med cykling hvor en lavere og mere energetisk effektiv pedalfrekvens benyttes. Nærværende, samt andres, arbejde viste at den

selvvalgte pedalfrekvens tilsyneladende er mindre fordelagtig end den lavere energetisk optimale pedalfrekvens med hensyn til at præstere under intensiv cykling foretaget i forlængelse af længerevarende submaksimal cykling. Dette fænomen stimulerer motivationen til at forstå adfærden og kontrollen af den selvvalgte pedalfrekvens under cykling.

Selvvalgt pedalfrekvens viste sig i nærværende arbejde at være meget individuel. Det blev også vist at selvvalgt pedalfrekvens var stabil over en periode på 12 uger. Derudover blev det vist at selvvalgt pedalfrekvens var upåvirket både af øget kardiopulmonær belastning ved konstant mekanisk belastning, og omvendt. Baseret på dette foreslås det at karakterisere den selvvalgte pedalfrekvens som en i høj grad individuel, stabil og robust indre voluntær rytmisk bevægelse som er under primær indflydelse af centrale mønstergeneratorer. Den sidste del af karakteristikken er i høj grad baseret på, og understøttet af, arbejde foretaget af andre indenfor dette område.

På trods af den selvvalgte pedalfrekvens robuste karakter er den påvirkelig af nogle faktorer. Nærværende arbejde viste for eksempel at den selvvalgte pedalfrekvens under cykling på løbebånd blev forøget med i gennemsnit 15 til 17 rpm når arbejdseffekten blev forøget fra en værdi svarende til 86 % og op til 165 % af W_{max}. Dette fænomen understøttes af andre undersøgelser. Som et andet eksempel fra det nærværende arbejde reduceredes den selvvalgte pedalfrekvens med i gennemsnit 9 til 14 rpm efter tung styrketræning som involverede både hofteekstension og hoftefleksion. Endvidere kan det på baggrund af nærværende arbejde foreslås at sidstnævnte fænomen indtraf indenfor den første uges træning, og i særdeleshed var forårsaget af træning med hofteekstension. Det hurtige respons på styrketræningen indikerer at neurale tilpasninger formentligt er årsag til de observerede ændringer i bevægelsesadfærden.

Den interne organisering af en central mønstergenerator er af nogle arbejdere indenfor området foreslået at være funktionelt opdelt i to komponenter hvor den ene komponent genererer bevægelsesfrekvensen mens den anden genererer bevægelsesmønstret. I nærværende arbejde blev den selvvalgte pedalfrekvens betragtet som en afspejling af den rytmiske bevægelsesfrekvens under den voluntære rytmiske ben-bevægelse som cykling udgør. Den tangentielle pedalkraft-profil blev betragtet som en afspejling af det rytmiske bevægelsesmønster. Nærværende arbejde viste at trættende hoftefleksionsarbejde hos rekreativt aktive personer forårsagede en ændring af den tangentielle pedalkraft-profil under cykling med en forudbestemt pedalfrekvens. Således blev den minimale tangentielle pedalkraft mere negativ mens den maksimale tangentielle pedalkraft blev forøget. Endelig blev fasen med negativ tangentiel pedalkraft forlænget. Med andre ord blev benene i mindre grad aktivt løftet i den opadgående fase af cykelbevægelsen. Trættende hofteekstensionsarbejde forårsagede ikke det samme. Og ingen af de to trættende arbejdsformer påvirkede den selvvalgte pedalfrekvens. Nærværende arbejde viste endvidere at den primære effekt af tung styrketræning med hofteekstension var at det reducerede den selvvalgte pedalfrekvens. En fortolkning af dette kunne være at træning med hofteekstension i særlig grad påvirkede signalet fra den komponent af den centrale mønstergenerator som kan tænkes at generere bevægelsesrytmen.

Table

Table 1. Overview of the articles that the dissertation is based upon. The table contains key information on type of individuals participating, equipment used, intervention performed, and findings that contributed to the understanding of voluntary rhythmic leg movement behaviour and control during pedalling.

Article	Individuals and equipment	Intervention	Key findings
I	Trained male cyclists (*n*=9). Monark[1] and SRM ergometer[2]. AMIS metabolic cart[3].	Prolonged submaximal (2.5 h at 180 W) cycling at freely chosen and energetically optimal pedalling frequency followed by 5 min all-out cycling for performance measurement.	Freely chosen pedalling frequency was on average 22 rpm higher than the energetically optimal pedalling frequency. The optimal pedalling frequency was at least as advantageous as the freely chosen pedalling frequency with respect to 5 min all-out cycling performance.
II	Healthy males and females (*n*=29) who rarely cycled. Lode cycle ergometer[4]. SensorMedics metablic cart[5].	Submaximal (37% and 57% of W_{max}) cycling at freely chosen pedalling frequency before and after 12 weeks of heavy strength training. Training exercises were performed 2 days per week and consisted of squat, knee extension, sitting leg curl, standing calf raise, and two core exercises (sit-ups on an incline abdominal board and abdominal crunch in a machine).	Freely chosen pedalling frequency was decreased by on average 9 rpm following strength training. This was accompanied by an on average 3% lower rate of energy turnover.
III	Healthy and recreationally active males and females (*n*=8). Hypobaric chamber[6]. Lode cycle ergometer[4]. Douglas bag system.	Submaximal cycling at freely chosen pedalling frequency at (*i*) power output corresponding to 65% of VO_{2max} at 200 m altitude (laboratory location); (ii) power output as in (*i*) but at 3,000 m simulated altitude, and; (*iii*) power output corresponding to 80% of VO_{2max} at 200 m altitude. Conditions (*i*) and (*ii*) provided constant mechanical loading on the legs and varied loading on the cardiopulmonary system. Conditions (*ii*) and (*iii*) provided constant loading of the cardiopulmonary system and varied mechanical loading of the legs.	Freely chosen pedalling frequency was highly individual and at the same time steady in a longitudinal perspective across 12 weeks. Further, freely chosen pedalling frequency was unaffected by increased loading on the cardiopulmonary system at constant mechanical loading, and *vice versa*.
IV	Male competitive cyclists (*n*=10). Road racing bicycle mounted with SRM dynamometer[7]. Woodway treadmill[8].	Intensive uphill cycling (10% incline, and 86% to 165% of W_{max}) at freely chosen pedalling frequency.	Freely chosen pedalling frequency increased by on average 15 to 17 rpm when power output increased from 86% to 165% of W_{max}.
V	Trained male cyclists (*n*=10). SRM ergometer[2]. AMIS metabolic cart[3].	Submaximal (180 W) cycling at freely chosen and pre-set target (65 and 90 rpm) pedalling frequencies with either a 52-tooth noncircular chain wheel[9] or a 52-tooth circular chain wheel.	Neither peak crank torque (during cycling at pre-set target pedalling frequencies), nor freely chosen pedalling frequency were reduced during cycling with the noncircular chain wheel.

Table 1 (*continued*)**.**

VI	Recreationally active males (*n*=7) and well-trained male and female cyclists (*n*=23). Lode ergometer[4]. Oxycon metabolic cart[10]. Magnetic resonance tomography[11].	Submaximal (125 W) cycling at freely chosen pedalling frequency before and after 12 weeks of heavy strength training. Training exercises were performed 2 days per week and consisted of half squat, leg press with one leg at a time, standing one-legged hip flexion, and ankle plantar flexion.	The recreationally active individuals chose an on average 11 rpm lower pedalling frequency after four weeks of strength training. The reduced pedalling frequency was accompanied by a reduction in physiological responses. The well-trained cyclists did not change their freely chosen pedalling frequency.
VII	Well-trained male and female cyclists (*n*=20). Lode ergometer[4].	Prolonged submaximal (185 min at 44% of W_{max}) cycling followed by a 5-min all-out trial. Cycling was performed at freely chosen pedalling frequency before and after 12 weeks of heavy strength training.	Crank torque profile was affected by the strength training. Thus, in the all-out trial, the particular phase in the upstroke phase of the crank revolution where negative or retarding crank torque occurs was shortened by on average 16°, corresponding to 14%. In addition, the peak positive or propulsive crank torque increased by on average 3%.
VI	Healthy and recreationally active men and a woman (*n*=9). SRM ergometer[2]. Force pedals[12].	Submaximal (100 W) cycling at freely chosen and a pre-set target (60 rpm) pedalling frequency before and after fatiguing hip flexion or hip extension exercises.	Freely chosen pedalling frequency was not affected after fatiguing exercises. Fatiguing hip flexion exercises caused the following average changes in the tangential pedal force profile during cycling at a pre-set target pedalling frequency: Minimum tangential pedal force decreased by 12%. Maximum tangential pedal force increased by 5%. The phase with negative tangential pedal force increased by 3%.
IX	Recreationally active men and women (*n*=27). SRM ergometer[2]. Force pedals[12].	Submaximal (100 W) cycling at freely chosen and a pre-set target (60 rpm) pedalling frequency before, during, and after 4 weeks of heavy hip extension or hip flexion strength training.	Freely chosen pedalling frequency was only decreased after hip extension strength training. The decrease amounted maximally to an average of 14 rpm across the measurements and commenced already after a single week of training. The tangential pedal force profile during cycling at the pre-set target pedalling frequency was not changed following the two training interventions.

[1](Monark AB, Varberg, Sweden). [2](Schoberer Rad Messtechnik, Jülich, Germany). [3]AMIS 2001 metabolic cart (Innovision, Odense, Denmark). [4]Lode Excalibur Sport (Lode, Groningen, The Netherlands). [5]SensorMedics Vmax 29 (AKU MED A/S, Oslo, Norway). [6](Norwegian Universal Technology AS, Haugesund, Norway). [7]SRM model Science crank dynamometer (Schoberer Rad Messtechnik, Jülich, Germany). [8]Woodway ELG 2 (Woodway GmbH, Weil am Rhein, Germany). [9]Biopace II (CR-BP20, Shimano, Osaka, Japan). [10]Oxycon Pro (Erich Jaeger, Hoechberg, Germany). [11]Magnetom Avanto 1.5 T (Siemens AG, Munich, Germany). [12]Powerforce system force pedals (Radlabor GmbH, Freiburg, Germany).

Figures

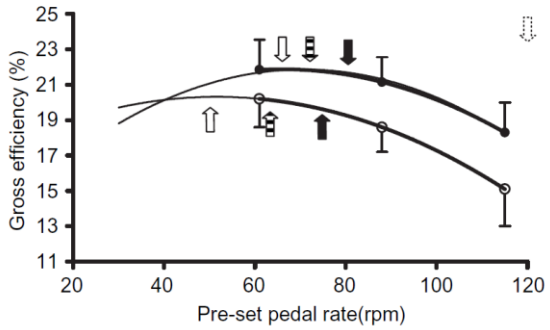

Figure 1

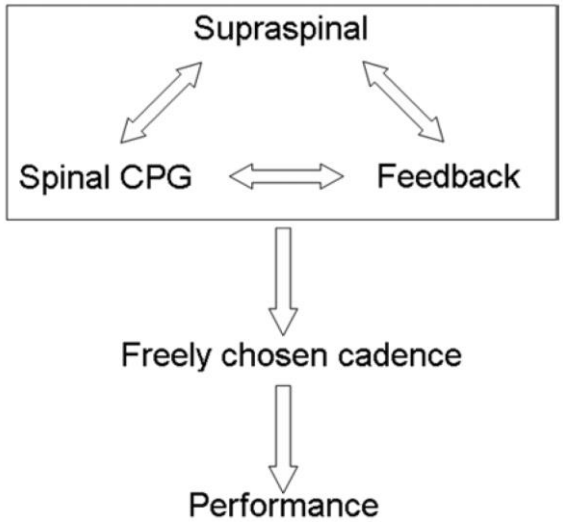
Supraspinal
Spinal CPG
Feedback
Freely chosen cadence
Performance

Figure 2

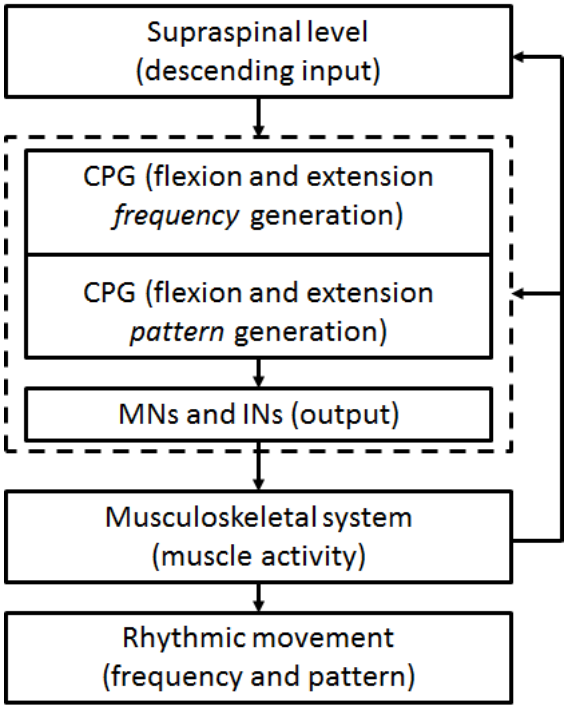
Supraspinal level
(descending input)
CPG (flexion and extension
frequency generation)
CPG (flexion and extension
pattern generation)
MNs and INs (output)
Musculoskeletal system
(muscle activity)
Rhythmic movement
(frequency and pattern)

Figure 3

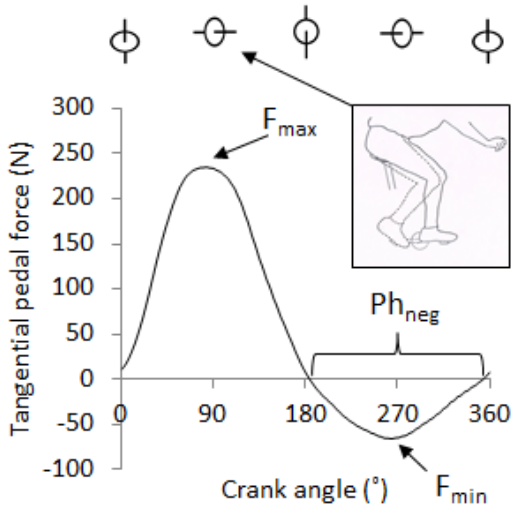
Tangential pedal force (N)
300
250
200
150
100
50
0
-50
-100
0
90
180
270
360
Crank angle (˚)
F_{max}
Ph_{neg}
F_{min}

Figure 4

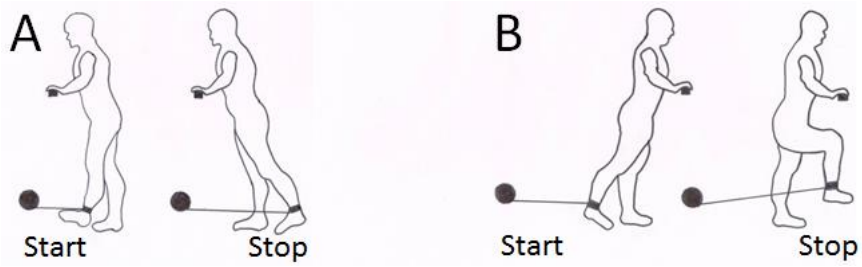

Figure 5

Figure captions

Figure 1 Inverted U-shaped relationships between pedalling frequency and gross efficiency. Data (group average±SD) are obtained during cycling at low (open circles) and high (solid circles) submaximal power output. The parts of the curves that have thin lines represent extrapolations. Average pedalling frequencies at maximum gross efficiency (open arrows), minimum RPE (arrows with horizontal lines), freely chosen pedalling frequency (solid arrows), and maximum peak crank power during maximal cycling (broken arrow) are indicated. The figure is reprinted, by permission, from a previous publication (Hansen et al., 2002a).

Figure 2 General outline of the interrelationships between spinal central pattern generator (CPG) activity, supraspinal input, and sensory feedback arising during pedalling in creating the freely chosen frequency. Performance during submaximal cycling is influenced by pedalling frequency, as reviewed in section 3. This is also illustrated in the figure. The figure is based on previous work (Zehr and Duysens, 2004) and is reprinted, by permission, from a previous publication (Hansen and Smith, 2009).

Figure 3 A hypothetical multilevel arrangement to be considered for elucidation of behaviour and control of voluntary pedalling rhythm. The figure is based on previous work (Zehr, 2005; Prochazka and Yakovenko, 2007). MNs, motor neurons. INs, interneurons.

Figure 4 A data example (*n*=1) showing a tangential pedal force profile for the right pedal during cycling at 100 W. Characteristics of the profile are illustrated. The figure is reprinted, by permission, from IX.

Figure 5 An illustration of the heavy strength training exercises performed in study IX. A) Hip extension training. B) Hip flexion training. The same exercises were applied to induce fatigue in study VIII. The figure is reprinted, by permission, from IX.

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