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Published in: Journal of Motor Behavior

DOI (link to publication from Publisher): 10.1080/00222895.2019.1592101

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Publication date: 2020

Document Version Accepted author manuscript, peer reviewed version

Link to publication from Aalborg University

Citation for published version (APA):
Hansen, E. A., Bak, S., Knudsen, L., Seiferheld, B., Stevenson, A. J. T., & Emanuelsen, A. (2020). Contralateral Transfer of the Phenomenon of Repeated Bout Rate Enhancement in Unilateral Index Finger Tapping. *Journal* of Motor Behavior, 52(1), 89-96. https://doi.org/10.1080/00222895.2019.1592101

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Contralateral transfer	of the phenomenon of	repeated bout rate	enhancement in	unilateral
index finger tapping				

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Published in Journal of Motor Behavior (2020, 52(1):89-96)

This is the accepted version of the article.

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ABSTRACT

These hypotheses were tested: 1) Freely chosen frequency in unilateral index finger

tapping is correlated between the two index fingers, and 2) A 3-min bout of unilateral index

finger tapping followed by 10 min rest results in an increase of the freely chosen tapping

frequency performed by the contralateral index finger in a second bout. Thirty-two adults

participated. Freely chosen tapping frequencies from first bouts were 167.2±79.0 and

161.5 \pm 69.4 taps/min for the dominant and non-dominant hand, respectively (p=.434).

These variables correlated (R=.86, p<.001). When bout one and two were performed with

the dominant and non-dominant hand, respectively, the frequency increased by

 $8.1\%\pm17.2\%$ in bout two (p=.011). In opposite order, the frequency increased by

14.1% \pm 17.5% (p<.001), which was not different from the ~8% (p=.157).

Keywords: Cross-limb transfer, Inter-limb transfer, Motor control,

Introduction

A better understanding of the behaviour and control of human voluntary stereotyped

rhythmic movements is beneficial in the work to improve performance, function, and

rehabilitation of for example exercising and injured individuals. Index finger tapping is

frequently applied as a motor task for investigations of voluntary rhythmic movements in

healthy individuals (Hammond & Gunasekera, 2008; Mora-Jensen, Madeleine, & Hansen,

2017; Wing & Kristoffersen, 1973; Zentgraf, et al., 2009) as well as in patients (Pitcher,

Piek, & Barrett, 2002; Roche, Viswanathan, Clark, & Whitall, 2016; Teo, Rodrigues,

2

Mastaglia, & Thickbroom, 2013). Index finger tapping consists of repeated alternating extension and flexion of the metacarpal phalangeal joint caused primarily by repeated alternating activation of the extensor digitorum muscle and the flexor digitorum profundus muscle.

Index finger tapping has been suggested to be controlled by spinal neural networks, termed central pattern generators (CPGs), in collaboration with supraspinal descending drive and sensory feedback (Hansen & Ohnstad, 2008; Shima, Tamura, Tsuji, Kandori, & Sakoda, 2011). The majority of the knowledge regarding CPG-mediated movement has been obtained by studies performed on animals since such studies allow direct access to the neurons in the spinal cord. For reviews on the topic, the reader is referred to previous publications (Grillner, 2003, 2009). Behavioural studies are also recommended within the research field since they can add unique information from intact individuals performing voluntary movement (Goulding, 2009; Schlinger, 2015). As an example, a study was performed to investigate how common the rhythmogenesis (i.e. genesis and maintenance of a rhythmic movement) was for the two legs in humans (Stang, Wiig, Hermansen, & Hansen, 2016). In the study, single-leg as well as two-legged-alternating knee extension tasks were performed at freely chosen frequencies. It was observed that freely chosen knee extension frequencies ranged from 15 to 68 repetitions per min across all participants and all three knee extension tasks. Further, there was a high correlation (R = .99) between frequencies generated with the dominant leg and the non-dominant leg. It was also observed that there were high correlations between frequencies performed in single-leg knee extension with each of the two legs, separately, and the frequency performed in the two-legged knee extension task (R = .94 and R = .95). Based on the results, it was suggested that involved CPGs of the two legs share a common frequency generator, or

that separate frequency generators of each leg are attuned via interneuronal connections (Stang, et al., 2016). For a model of a hypothetical multi-layered organization of rhythm and pattern generators in the spinal cord, under influence of descending and sensory input, the reader is referred to figure 2 in the paper by Stang et al. (2016). It has previously been assumed that the freely chosen tapping frequency is directly related to the frequency of the internal clock (Dosseville et al., 2002). The internal clock is assumed to be located in the brain (Ivry and Keele, 1989), as described in a review paper on the subject (Allman et al., 2014). However, it has been mentioned that it constitutes a challenge that knowledge about the location and about physiological details of the internal clock are sparse (Baer et al., 2015). Finally, it should also be noted that the degree of steadiness of the freely chosen tapping frequency has previously been investigated. Thus, across seven tests performed over a 12-week period, an intra-individual 95% confidence interval of the tapping frequency of 13 taps per min was reported, as an average across seven individuals (Hansen and Ohnstad, 2008).

Based on the characteristics of the present tapping task, it may be estimated that the spinal component of the motor control is considerable, as compared to the supraspinal component. This estimation is, for example, based on the findings that freely chosen tapping results in less brain activity (Kawashima, et al., 1999) and less muscle activation (Emanuelsen, et al., 2018) as compared to frequency-paced tapping. Furthermore, that training, and thereby presumed increased automation, of complicated multiple-finger tapping results in less brain activity (Wu, Kansaku, & Hallett, 2004). These aspects are relevant to consider when comparing the present results with results from the literature and when interpreting the present results.

Another behavioural observation is the phenomenon of repeated bout rate enhancement. Briefly, the phenomenon covers an increase of the freely chosen index finger tapping frequency during the second of two consecutive tapping bouts, which are separated by 10 min rest (Emanuelsen, et al., 2018; Hansen, Ebbesen, Dalsgaard, Mora-Jensen, & Rasmussen, 2015; Mora-Jensen, et al., 2017). It has been suggested by Hansen et al. (2015) that the repeated bout rate enhancement might be a result of a net excitation of the spinal CPG itself, caused by neuromodulators (El Manira & Kyriakatos, 2010; Frigon, 2017; Marder, 2012). However, it is unknown whether tapping with the index finger on one hand can elicit excitation of the CPG involved in the generation of tapping with the contralateral index finger, and result in repeated bout rate enhancement during tapping with the index finger on the other hand. In other words, whether a contralateral transfer of the phenomenon can be elicited.

The aim of the present study was to test the following two hypotheses. First, that the freely chosen frequency in unilateral index finger tapping is highly correlated between the two index fingers. Second, that a single 3-min bout of unilateral index finger tapping followed by a 10-min rest period results in a rate enhancement of the freely chosen tapping frequency performed by the contralateral index finger in a subsequent 3-min unilateral tapping bout. The knowledge provided by the present study adds to our understanding of the behaviour and control of human voluntary stereotyped rhythmic movement as well as it complements the existing knowledge of CPG-mediated movements obtained from animal studies.

Methods

Participants

Thirty-two healthy adults (20 men and 12 women, 1.79 ± 0.09 m, 80.5 ± 15.8 kg, and 26.1 ± 5.0 years) volunteered for participation in the present study. The handedness of the participants was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971), which resulted in 29 right-handed (L.Q. = 78.33 ± 22.52) and 3 left-handed (L.Q. = -35.82 ± 14.57) participants. None of the participants had any history of neural disorders or diseases. Furthermore, none of the participants used their index fingers to play any sort of computer games or musical instruments for more than one hour each week. All participants received written and oral information about the procedures and the overall aim of the study before participating. Furthermore, participants were not informed about the specific hypotheses of the study in an attempt to prevent any deliberate control of their finger tapping rate. All participants were told not to consume coffee 3 hours before testing as well as not to consume alcohol or any kind of euphoric drugs 24 hours before testing. The study conformed to the standards set by the Declaration of Helsinki and was approved by the North Denmark Region Committee on Health Research Ethics (N-20170017).

Experimental design

For the present study, a repeated measures crossover design was applied. To begin with, participants were randomly assigned into two groups. Group 1 (n = 16, 10 men and 6 women) performed unilateral index finger tapping with the dominant hand first (Bout 1) and subsequently (Bout 2) with the non-dominant hand in the first test session. In a second test session, this group reversed the order of tapping. Group 2 (n = 16, 10 men and 6 women) performed index finger tapping with the non-dominant hand first (Bout 1) and subsequently (Bout 2) with the dominant hand in the first test session. In a second test session, this group also reversed the order of tapping. The first and the second test session were

separated by 21 ± 1 days as 16 days have previously been reported to secure wash-out (Hansen, et al., 2015). Participants were tested at approximately the same time of day (i.e., with a maximal difference of 2 hours) during the first and second test sessions to prevent any influence of circadian rhythm on finger tapping frequency (Moussay, et al., 2002).

Test sessions

The participant was seated in an adjustable chair and encouraged to find a comfortable position where index finger tapping could be performed continuously for 3 min. An LED-tracker was attached to the finger nail of the index finger to be used in the first tapping bout. The signal from the LED-tracker was used by a motion capture system (VisualeyezTM system, Phoenix Technologies Inc., Burnaby, BC, Canada) for calculation of the vertical displacement of the index finger during tapping. Before the first tapping bout started, it was stressed that tapping was neither supposed to be performed as fast as possible nor with as high a force as possible. Rather, the participant should tap in a relaxed and natural way and apply a "preferred rhythm". Tapping was performed on a FS6-250 force transducer (Advanced Mechanical Technology Inc., Watertown, MA, USA) to allow for the determination of the impact force during tapping.

The first tapping bout in a test session consisted of 3 min of unilateral index finger tapping at a freely chosen tapping frequency. Hereafter, a 10-min rest period followed. During the rest period, the LED-tracker was moved to the index finger of the contralateral hand to be used in the second tapping bout. Subsequently, a second 3-min tapping bout of freely chosen unilateral index finger tapping was performed.

Data collection

With regards to the kinematic measurements, the motion capture system was calibrated before data recordings to define a local 3D-scaled coordinate system. The index finger movement in the vertical direction (in the sagittal plane) was measured using the motion capture system and sampled at 100 Hz. With regards to the kinetic measurements, the force transducer was calibrated using three known masses to secure linearity and accuracy of the measurements. Force data were amplified 4,000 times, analogue low-pass filtered at 1,050 Hz, and digitalized by a 12 bits NI BNC-2090A A/D-board (National Instruments, Austin, TX, USA). The sampling was performed at 5,000 Hz using a Lab-VIEW-based (National Instruments Co., Austin, TX, USA) custom-programmed software (Mr. Kick III, Knud Larsen, Aalborg University, Denmark). During data analysis, force recordings were digitally low-pass filtered at 200 Hz. Kinematic and kinetic recordings were synchronized using an external trigger function in "Mr. Kick III".

Data analysis

The data analysis was performed using MATLAB version 2015a (MathWorks Inc., Natick, MA, USA). A custom-written script developed for a recently performed study (Emanuelsen, et al., 2018) was used. For each participant, variables of tapping frequency, peak force, and vertical displacement were quantified for each single tap and subsequently averaged across each 3-min tapping bout. Briefly, a reference force value was defined as the mean force across 1 s, before tapping started. A single tap was then considered to begin when the initial finger impact on the force transducer resulted in a force that exceeded an upper pre-set force limit. The force then had to fall below another pre-set lower force limit before the next tap could be identified. The force limits were based on the

reference force value and were adjusted for each data file to account for differences between the participants' different tapping characteristics. The tapping frequency for each tap, reported in taps per min, was determined as 60 s divided by the time (in s) between two consecutive initial finger impacts. The peak force for each tap, reported in N, was determined as the difference between the maximal force value detected during the contact time and the reference force value. The vertical finger displacement, reported in mm, was determined as the vertical distance between minima and maxima displacement values found for each tap.

Statistical analyses

The Shapiro-Wilks test was performed in SPSS 25.0 (SPSS Inc., Chicago, IL, USA) to evaluate whether the data were normally distributed. For normally distributed data, the Student's paired two-tailed t-test was applied for comparisons and a Pearson product-moment correlation coefficient was calculated. Those tests were performed in Excel 2016 (Microsoft Corporation, Bellevue, WA, USA). For interpretation of the correlation coefficient, < .25 was considered weak, .25 to .50 was considered moderate, .51 to .75 was considered fair, and > .75 was considered high (Berg & Latin, 2008). In case of data that were not normally distributed, comparisons were done with a Related-samples Wilcoxon Signed Rank Test performed in SPSS. When the latter was done, it is indicated in the Results section. Data are presented as mean \pm standard deviation (SD) unless otherwise indicated. The significance level was set at p < .05.

Results

Tapping frequency

Freely chosen unilateral tapping frequencies amounted to 167.2 ± 79.0 taps per min and 161.5 ± 69.4 taps per min for the index finger of the dominant and the non-dominant hand, respectively (t=0.79, p = .434). For calculation of these values, tapping frequencies from the first tapping bouts, i.e. at two different days, were applied. Furthermore, there was a high correlation (R = .86, p < .001) between the tapping frequencies recorded for the dominant and the non-dominant hand (Fig.1).

When the first tapping bout was performed with the index finger of the dominant hand and the second bout was performed with the index finger of the non-dominant hand, the tapping frequency increased by $8.1\% \pm 17.2\%$ in the second bout (Related-samples Wilcoxon Signed Rank Test: p = .011). For comparison, when the first tapping bout was performed with the index finger of the non-dominant hand and the second bout was performed with the index finger of the dominant hand, the tapping frequency increased by $14.1\% \pm 17.5\%$ in the second bout (Related-samples Wilcoxon Signed Rank Test: p < .001). The $\sim 8\%$ and the $\sim 14\%$ within-session increases in tapping frequency were not statistically significantly different, as evaluated by a t-test (p = .157). For absolute values, the reader is referred to Fig. 2.

Peak force and vertical displacement

Values of peak force and vertical displacement are presented in Table 1. The only observed difference in these data was a $7.9\% \pm 32.6\%$ lower peak force in the second bout when the index finger of the dominant hand had been used for tapping in the first bout and the index finger of the non-dominant hand was used for tapping in the second bout (p = .003).

Discussion

The present study showed a high correlation between the freely chosen index finger tapping frequency performed by the index finger of the dominant hand in the first bout and the corresponding tapping frequency performed with the index finger of the non-dominant hand (measured another day). This finding is in line with a previous report of high correlations of unilateral freely chosen movement frequencies performed by the two legs separately during rhythmic leg exercise tasks (Stang, et al., 2016). Based on their result, Stang et al. (2016) suggested that involved CPGs of the two legs might share a common frequency generator, or that separate frequency generators of each leg are attuned via interneuronal connections. Furthermore, the present study showed that a single bout of freely chosen tapping with the index finger of one hand enhanced the freely chosen tapping frequency performed in a second tapping bout with the index finger of the other hand by an average of 8%-14%. The latter result suggests that a contralateral transfer of repeated bout rate enhancement in unilateral index finger tapping can occur, which is a novel finding.

The present magnitude of repeated bout rate enhancement can be numerically compared to previously reported values. Mora-Jensen et al. (2017) and Emanuelsen et al. (2018) reported, respectively, on average 6% and 8% rate enhancements in the second of two consecutive tapping bouts. Previous to those studies, an accumulated rate enhancement of 8% had been reported to occur across four consecutive tapping bouts (Hansen, et al., 2015). With regards to the present absolute values of the peak force, similar values have been collected in comparable experiments previously (Mora-Jensen, et al., 2017; Sardroodian, Madeleine, Mora-Jensen, & Hansen, 2016). Regarding the present absolute values of vertical displacement, slightly larger values have been observed in

comparable experiments previously (Mora-Jensen, et al., 2017; Sardroodian, et al., 2016). We cannot explain the difference with anything other than the fact that participant samples were not the same in the present and the previous studies.

Interlimb transfer of performance of unilateral index finger movement has been reported previously. Carroll et al. (2008) had participants complete practice trials of ballistic abduction movements of the right index finger. The goal of the training was to improve the peak acceleration of the movement. Carroll et al. (2008) reported that training improved performance by 140% in the right hand and by 82% in the untrained left hand. Further, bilateral corticospinal excitability was increased following the unilateral training. A control group was included in the study for comparison, and that group showed no changes (Carroll, Lee, Hsu, & Sayde, 2008). In a study performed by another research group, participants practiced tapping at maximal speed six days per week for two weeks with the left or right middle finger in a between-subject design (Koeneke, Battista, Jancke, & Peters, 2009). The primary goal of the training was to increase tapping speed. The trained middle finger showed improvements of on average 10%-17% while the unpractised middle finger showed statistically significant improvements of on average 7%-8%. For comparison, a control group showed no changes (Koeneke, et al., 2009). However, it should be noted that the tapping task in the present study can be characterized as being submaximal, simple, stereotyped, and performed at a freely chosen rate. Furthermore, the present study focused on acute transfer effects rather than on effects of long-term training. Thus, aspects such as maximal performance, long-term training, and learning may be of minor relevance for the present study.

With regards to interpreting the present results, it has previously been argued that analysis of motor behavior may be used to increase our understanding of the organization

and function of the nervous system (Goulding, 2009). Along that line, the present study applied an operational approach that links experimental observations to theory, as suggested previously (Kelso & Schöner, 1988). The same kind of approach has been carried out previously (Jeka, Kelso, & Kiemel, 1993; Sardroodian, Madeleine, Voigt, & Hansen, 2015).

The physiological mechanisms underlying the present behavioural findings can obviously only be speculated upon because of the nature of the present study. It is possible that the present repeated bout rate enhancement effect should be considered a kind of repetition priming as described recently (Cropper, Jing, Perkins, & Weiss, 2017; Siniscalchi, Cropper, Jing, & Weiss, 2016). The present findings may be interpreted to support the working hypothesis proposed by Stang et al. (2016), that the involved CPGs either share a common frequency generator or that separated frequency generators are attuned via interneurons. Further, it is possible that neuromodulators released during neural activity in the first bout excited the rhythm generating part of the CPG controlling the contralateral index finger, and that this was responsible for the generation of a higher tapping frequency in the second bout. The possibility that CPGs are excited by released neuromodulators has been discussed by others recently (Cropper, et al., 2017; Gad, et al., 2017; Perrier & Cotel, 2015). For completeness, it should also be mentioned that the excitability of corticospinal projections to a passive limb has been reported to be increased during preparation for action with the contralateral limb (Chye, Riek, de Rugy, Carson, & Carroll, 2018). Thus, it is possible that the present transfer of repeated bout rate enhancement was a result of neuromodulation on both supraspinal and spinal levels. Finally, it is possible that the present repeated bout rate enhancement effect was a result of a repetition priming of an internal clock.

With regards to the conflicting finding of a lower peak force in the second bout, when the first bout was performed with the index finger of the dominant hand, compared to no such finding for the opposite order of the hands, there is no straightforward explanation.

Mora-Jensen et al. (2017) previously reported unchanged peak force during a repeated bout rate enhanced tapping rate.

The present finding that repeated bout rate enhancement shows interlimb transfer is not only of academic interest. It may also have important clinical implications for movement rehabilitation. Thus, the present study supports the idea that it is possible to train the unaffected limb of a patient and thereby increase the excitability of the part of the nervous system involved in generation of movement of a contralateral affected limb. Such a strategy could be considered a supplement to strategies of passive movement of affected limbs, electrical stimulation, and pharmacological stimulation, which were mentioned in a recent review (Hofstoetter, Knikou, Guertin, & Minassian, 2017).

Conclusion

The present study showed that there was a high correlation between the freely chosen unilateral index finger tapping frequency performed with the dominant and the non-dominant hand, respectively. Furthermore, there was a contralateral transfer of the repeated bout rate enhancement. Thus, a single 3-min bout of freely chosen unilateral index finger tapping followed by a 10-min rest period resulted in a rate enhancement of on average 8%-14% of the freely chosen unilateral tapping frequency performed with the contralateral index finger in a second tapping bout.

Acknowledgements

The volunteers are thanked for their participation. The present research was supported by The Ministry of Culture Committee on Sports Research in Denmark.

Figure legends

Fig. 1. Scatterplot of freely chosen unilateral index finger tapping frequency recorded for the index finger of the dominant hand versus frequency recorded for the index finger of the non-dominant hand (measured another day). Data are from the first bouts. A line of identity is included. n = 32.

Fig. 2. Freely chosen unilateral index finger tapping frequencies. Individual data are grey. Mean data are black. SD values are omitted for clarity. n = 32. *Different from the first bout (p < .05).

Table 1 Descriptive data of peak force and vertical displacement from the bouts of unilateral freely chosen index finger tapping. Data are presented at mean \pm SD.

	Peak force (N)	Vertical displacement (mm)			
Dominant hand in Bout 1,					
non-dominant hand in Bout 2					
Bout 1	.87 ± .50	18.2 ± 7.5			
Bout 2	.76 ± .48*	18.9 ± 10.8			
Non-dominant hand in Bout 1,					
dominant hand in Bout 2					
Bout 1	.80 ± .49	18.3 ± 8.2			
Bout 2	.83 ± .46	18.6 ± 7.5			

For force data: n = 32. For displacement data: n = 30 (due to missing data). *Different from Bout 1 (p = .003).

REFERENCES

- Allman, M. J., Teki, S., Griffiths, T. D., & Meck, W. H. (2014). Properties of the internal clock: first- and second-order principles of subjective time. *Annu. Rev. Psychol.*, **65**, 743-771.
- Baer, L. H., Park, M. T. M., Bailey, J. A., Chakravarty, M. M., Li, K. Z. H., & Penhune, V. B. (2015). Regional cerebellar volumes are related to early musical training and finger tapping performance. *Neuroimage* **109**, 130-139.
- Berg, K. E., & Latin, R. W. (2008). Essentials of research methods in health, physical education, exercise science, and recreation (3 ed.): Wolters Kluwer.
- Carroll, T. J., Lee, M., Hsu, M., & Sayde, J. (2008). Unilateral practice of a ballistic movement causes bilateral increases in performance and corticospinal excitability. *J. Appl. Physiol.*, 104, 1656-1664.
- Chye, L., Riek, S., de Rugy, A., Carson, R. G., & Carroll, T. J. (2018). Unilateral movement preparation causes task-specific modulation of TMS responses in the passive, opposite limb. *J. Physiol.*, *596*, 3725-3738.
- Cropper, E. C., Jing, J., Perkins, M. H., & Weiss, K. R. (2017). Use of the Aplysia feeding network to study repetition priming of an episodic behavior. *J. Neurophysiol.*, *118*, 1861-1870.
- Dosseville, F., Moussay, S., Larue, J., Gauthier, A., & Davenne, D. (2002). Physical exercise and time of day: influences on spontaneous motor tempo. *Percept. Mot. Skills* **95**, 965-972.
- El Manira, A., & Kyriakatos, A. (2010). The role of endocannabinoid signaling in motor control. *Physiology*, *25*, 230-238.

- Emanuelsen, A., Voigt, M., Madeleine, P., Kjær, P., Dam, S., Koefoed, N., & Hansen, E. A. (2018). Repeated Bout Rate Enhancement Is Elicited by Various Forms of Finger Tapping. *Front. Neurosci.*, 12:526.
- Frigon, A. (2017). The neural control of interlimb coordination during mammalian locomotion. *J. Neurophysiol.*, *117*, 2224-2241.
- Gad, P., Gerasimenko, Y., Zdunowski, S., Turner, A., Sayenko, D., Lu, D. C., & Edgerton, V. R. (2017). Weight Bearing Over-ground Stepping in an Exoskeleton with Non-invasive Spinal Cord Neuromodulation after Motor Complete Paraplegia. *Front. Neurosci.*, 11:333.
- Goulding, M. (2009). Circuits controlling vertebrate locomotion: moving in a new direction.

 Nat. Rev. Neurosci., 10, 507-518.
- Grillner, S. (2003). The motor infrastructure: from ion channels to neuronal networks. *Nat. Rev. Neurosci.*, *4*, 573-586.
- Grillner, S. (2009). Pattern generation. *Encyclopedia of Neuroscience*, 487-494.
- Hammond, G., & Gunasekera, S. (2008). Production of successive force impulses by the left and right hands. *J. Mot. Behav., 40*, 409-416.
- Hansen, E. A., Ebbesen, B. D., Dalsgaard, A., Mora-Jensen, M. H., & Rasmussen, J. (2015). Freely chosen index finger tapping frequency is increased in repeated bouts of tapping. *J. Mot. Behav.*, 47, 490-496.
- Hansen, E. A., & Ohnstad, A. E. (2008). Evidence for freely chosen pedalling rate during submaximal cycling to be a robust innate voluntary motor rhythm. *Exp. Brain Res.*, 186, 365-373.
- Hofstoetter, U. S., Knikou, M., Guertin, P. A., & Minassian, K. (2017). Probing the Human Spinal Locomotor Circuits by Phasic Step-Induced Feedback and by Tonic

- Electrical and Pharmacological Neuromodulation. *Curr. Pharm. Des., 23*, 1805-1820.
- Ivry, R. B., & Keele, S. W. (1989). Timing functions of the cerebellum. *J. Cogn. Neurosci.*1, 136-152.
- Jeka, J. J., Kelso, J. A. S., & Kiemel, T. (1993). Spontaneous transitions and symmetry: Pattern dynamics in human four-limb coordination. *Hum. Mov. Sci.*, *12*, 627-651.
- Kawashima, R., Inoue, K., Sugiura, M., Okada, K., Ogawa, A., & Fukuda, H. (1999). A positron emission tomography study of self-paced finger movements at different frequencies. *Neuroscience*, *92*, 107-112.
- Kelso, J. A. S., & Schöner, G. (1988). Self-organization of coordinative movement patterns. *Hum. Mov. Sci*, *7*, 27-46.
- Koeneke, S., Battista, C., Jancke, L., & Peters, M. (2009). Transfer effects of practice for simple alternating movements. *J. Mot. Behav.*, *41*, 347-355.
- Marder, E. (2012). Neuromodulation of neuronal circuits: back to the future. *Neuron*, *76*, 1-11.
- Mora-Jensen, M. H., Madeleine, P., & Hansen, E. A. (2017). Vertical finger displacement is reduced in index finger tapping during repeated bout rate enhancement. *Motor Control*, *21*, 457-467.
- Moussay, S., Dosseville, F., Gauthier, A., Larue, J., Sesboüe, B., & Davenne, D. (2002).

 Circadian rhythms during cycling exercise and finger-tapping task. *Chronobiol. Int.,*19, 1137-1149.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9, 97-113.

- Perrier, J. F., & Cotel, F. (2015). Serotonergic modulation of spinal motor control. *Curr. Opin. Neurobiol.*, 33, 1-7.
- Pitcher, T. M., Piek, J. P., & Barrett, N. C. (2002). Timing and force control in boys with attention deficit hyperactivity disorder: subtype differences and the effect of comorbid developmental coordination disorder. *Hum. Mov. Sci.*, *21*, 919-945.
- Roche, R., Viswanathan, P., Clark, J. E., & Whitall, J. (2016). Children with developmental coordination disorder (DCD) can adapt to perceptible and subliminal rhythm changes but are more variable. *Hum. Mov. Sci., 50*, 19-29.
- Sardroodian, M., Madeleine, P., Mora-Jensen, M. H., & Hansen, E. A. (2016).

 Characteristics of Finger Tapping Are Not Affected by Heavy Strength Training. *J. Mot. Behav.*, *48*, 256-263.
- Sardroodian, M., Madeleine, P., Voigt, M., & Hansen, E. A. (2015). Freely chosen stride frequencies during walking and running are not correlated with freely chosen pedalling frequency and are insensitive to strength training. *Gait. Posture, 42*, 60-64.
- Schlinger, H. D. (2015). Behavior analysis and behavioral neuroscience. *Front. Hum. Neurosci.*, 9:210.
- Shima, K., Tamura, Y., Tsuji, T., Kandori, A., & Sakoda, S. (2011). A CPG synergy model for evaluation of human finger tapping movements. *Conf. Proc. IEEE Eng. Med. Biol. Soc.*, 2011, 4443-4448.
- Siniscalchi, M. J., Cropper, E. C., Jing, J., & Weiss, K. R. (2016). Repetition priming of motor activity mediated by a central pattern generator: the importance of extrinsic vs. intrinsic program initiators. *J. Neurophysiol.*, *116*, 1821-1830.

- Stang, J., Wiig, H., Hermansen, M., & Hansen, E. A. (2016). Voluntary movement frequencies in submaximal one- and two-legged Knee extension exercise and pedaling. *Front. Hum. Neurosci.*, *10*:36.
- Teo, W. P., Rodrigues, J. P., Mastaglia, F. L., & Thickbroom, G. W. (2013). Comparing kinematic changes between a finger-tapping task and unconstrained finger flexion-extension task in patients with Parkinson's disease. *Exp. Brain Res.*, 227, 323-331.
- Wing, A. M., & Kristoffersen, A. B. (1973). The timing of interresponse intervals. *Percept. Psychophys.*, *13*, 455-460.
- Wu, T., Kansaku, K., & Hallett, M. (2004). How self-initiated memorized movements become automatic: a functional MRI study. *J. Neurophysiol.*, *91*, 1690-1698.
- Zentgraf, K., Lorey, B., Bischoff, M., Zimmermann, K., Stark, R., & Munzert, J. (2009).

 Neural correlates of attentional focusing during finger movements: A fMRI study. *J. Mot. Behav.*, *41*, 535-541.

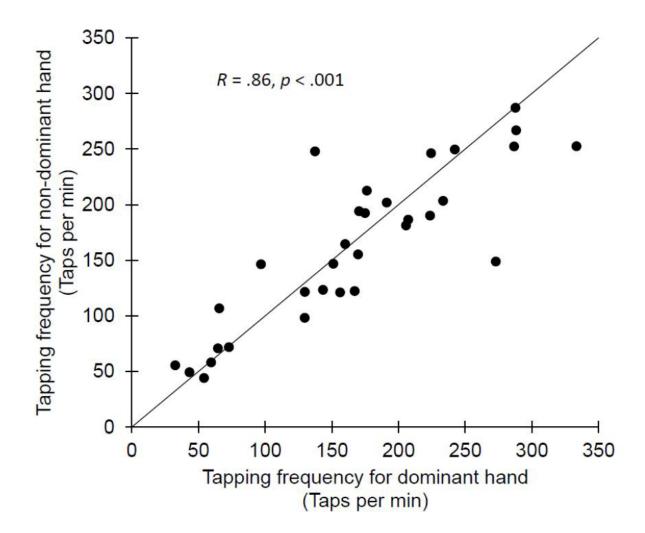


Fig. 1.

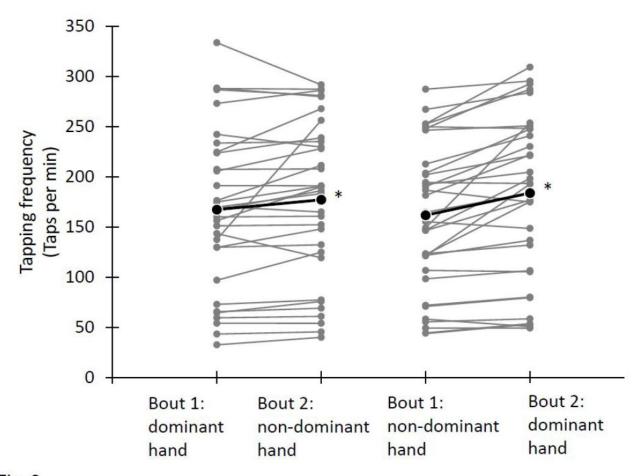


Fig. 2.