



Running on uneven ground: leg adjustments to altered ground level

Roy Müller, Reinhard Blickhan

► To cite this version:

Roy Müller, Reinhard Blickhan. Running on uneven ground: leg adjustments to altered ground level. Human Movement Science, 2010, 29 (4), pp.578. 10.1016/j.humov.2010.04.007 . hal-00659889

HAL Id: hal-00659889

<https://hal.science/hal-00659889>

Submitted on 14 Jan 2012

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Accepted Manuscript

Running on uneven ground: leg adjustments to altered ground level

Roy Müller, Reinhard Blickhan

PII: S0167-9457(10)00063-1
DOI: [10.1016/j.humov.2010.04.007](https://doi.org/10.1016/j.humov.2010.04.007)
Reference: HUMOV 1233

To appear in: *Human Movement Science*



Please cite this article as: Müller, R., Blickhan, R., Running on uneven ground: leg adjustments to altered ground level, *Human Movement Science* (2010), doi: [10.1016/j.humov.2010.04.007](https://doi.org/10.1016/j.humov.2010.04.007)

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

Title

Running on uneven ground: leg adjustments to altered ground level

Authors

Roy Müller^{a,*}, Reinhard Blickhan^a

^a Motionscience, Institute of Sport Sciences, Friedrich-Schiller-University Jena, Seidelstraße
20, 07740 Jena, Germany

Corresponding Author

*Phone: +49 3641 945724, Fax: +49 3641 945702

Email: roy.mueller@uni-jena.de

Abstract

In locomotion, humans have to deal with changes in ground level like pavement or stairs. When they encounter uneven ground with changes in terrain height, they reduce their angle of attack and leg stiffness on a step. This strategy was found for the single step upward movement. However, are these adjustments the result of a general strategy? In our study we focused on leg adjustments while running up and down, implying permanent adaptation to a new track level. To investigate this, we measured ten healthy participants as they ran along a runway with 10 cm increased and 10 cm lowered steps. We found that ground reaction force, leg length, leg stiffness, and angle of attack were adjusted to the direction of the vertical disturbance (up or down) but also to its length. When running upwards, leg stiffness decreased by about 20.4% on the single step and by about 9.3% on the permanently elevated track step. In addition to that – when running downwards – leg stiffness decreased in preparation for the downward step by about 18.8%. We also observed that the angle of attack diminished on elevated contact from 61° to 59°, and increased on lowered contact from 61° to 65°. The adjustment of leg stiffness seemed to be actively achieved, whereas the angle of attack appeared to be passively adjusted, consistent with a running model that includes leg retraction in late swing phase.

Keywords: Biomechanics; Human locomotion; Spring-mass model; Leg stiffness; Angle of attack

1. Introduction

When humans encounter sudden changes in substrate stiffness (Farley, Houdijk, van Strien, & Louie, 1998; Ferris & Farley, 1997; Ferris, Liang, & Farley, 1999; Kerdok, Biewener, McMahon, Weyand, & Herr 2002; Moritz & Farley, 2004), or uneven ground with changes in terrain height (Blickhan et al., 2007; Grimmer, Ernst, Günther, & Blickhan, 2008), they seem to use properties of the spring-mass model (Blickhan, 1989; McMahon & Cheng, 1990) to help passively stabilize their locomotor trajectory.

The spring-mass model consists of a mass-less spring, and the body is represented by a point mass. It is described merely by the parameters “stiffness”, “angle of attack”, and “leg length” (Blickhan, 1989; Geyer, Seyfarth, & Blickhan, 2005; McMahon & Cheng, 1990). In modeled spring-mass running, the simplest strategy is running with a fixed angle of attack and a constant leg stiffness (Seyfarth, Geyer, Günther, & Blickhan, 2002). Here, within a narrow range of the angle of attack, simulations reveal periodic movement patterns as well as the ability to cope with perturbations in ground level (Geyer, Blickhan, & Seyfarth, 2002). Using leg retraction improves the range of stability with constant leg stiffness (Seyfarth, Geyer, & Herr, 2003). Without any control, leg retraction increases the angle of attack proportionally to flight duration. This has been documented for birds and human runners (Daley & Biewener, 2006; Daley, Usherwood, Felix, & Biewener, 2006; Günther & Blickhan, 2002). Accordingly, changes in ground level alter flight time, and thus, the angle of attack changes. An upward step on the ground results in a flatter angle of attack, and a downward step in a steeper angle of attack (Blickhan et al., 2007; Seyfarth et al., 2003). Without leg retraction, there exists a small range of leg stiffness and angle of attack combinations in which the conservative spring-mass model is able to run in a self-stabilized manner (Geyer, Seyfarth, & Blickhan, 2006; Seyfarth et al., 2002). Leg retraction enlarges this range significantly (Seyfarth et al., 2003).

While running on uneven ground with changes in vertical height, humans reduce their angle of attack and leg stiffness with increasing step height (Blickhan et al., 2007; Grimmer et al., 2008). This strategy has been observed for a single step upward, followed by a downward step to the original ground level. The adjustments agree with those required to keep the body in the range of dynamically stable spring-mass motion. It is not known whether these leg adjustments are achieved merely passively or actively in a feed-forward manner. In a feed-forward strategy the perspective for the runner is different for a single elevated contact (where he may avoid rising the center of gravity) as compared to a permanently elevated surface (where effort to lift the center of gravity cannot be avoided). Passive strategies, on the other hand, should be similar in both situations. Accordingly, the response to the different situations may indicate passive and/or active contributions.

In an experimental observation on birds running over an unexpected drop in terrain, it was shown that the delay in ground contact results in a steeper but more variable angle of attack (Daley & Biewener, 2006; Daley et al., 2006). This effect can be attributed to leg retraction. Although leg stiffness shows dramatic variations, systematic adaptations to the drop down situation could not be observed. Experiments on humans are not available, and it is not known whether there is a single general strategy employing passive and/or active mechanisms to overcome surface irregularities in both directions (step up and step down).

In our investigation, we focused on leg adjustments while running up and down steps of different lengths with constant velocities. We addressed three main research questions. (1) Do humans adjust their leg stiffness and angle of attack (and if so, in which phase)? (2) Do the adjustments of leg stiffness and angle of attack show a similar behaviour like the conservative spring-mass model? (3) Are the adjustments the result of a single general strategy?

2. Methods

2.1. Participants

Ten subjects took part in this study. All of them were physically active participants with no health problems that could have affected their performance or behavior in this study. The participants' mean and standard deviation for age, body mass and stature were 25.1 ± 2.7 years, 76.8 ± 10.8 kg, 182.8 ± 9.6 cm, respectively. Informed written consent was obtained from each volunteer. The experiment was approved by the local ethics committee, in accordance to the Declaration of Helsinki.

2.2. Measurements

All participants were instructed to run along a 17 m runway with two consecutive force plates in the middle of the travel path. The ground reaction forces (GRF) were sampled at 2000 Hz by using one ground-level force plate (9281B, Kistler, Winterthur, Switzerland) and one variable-height force plate (9285BA, Kistler) added at a distance of one step. Both force plates could be hit with step lengths from 1.40 to 2.30 m.

Insert Fig. 1 About Here

After running on the unperturbed flat track (0/0cm), the variable-height force plate was set on an elevation of 10 cm, and the participants continued running in the post-force plate zone (upward running). In the upward running setup, the post-force plate zone could be set on two elevations of 0 and 10 cm, so that the participants were forced to step up to a single step (step up, SU; Fig. 1A) or to a permanently elevated track step (track step up, TSU; Fig. 1B) of 10 cm.

In the downward running setup, the first contact force plate remained at 10 cm height, and the pre-force plate zone was set on two elevations of 0 and 10 cm, so that the participants were forced to step down a single step (step down, SD; Fig. 1C), or to a permanently elevated track

step (track step down, TSD) of 10 cm (Fig. 1D). Participants were allowed to choose their running velocity *ad libitum* and performed several (usually 2 to 3) practice trials before every setup. After practicing, the participants were instructed to run along the runway at constant speed. A trial was successful when the participants ran along the whole track, and both left and right touchdowns were centered on the corresponding force platforms.

Trials were recorded with 12 cameras (240 Hz) by a 3D infrared system (MCU 240, Qualisys, Goteborg, Sweden) and synchronized by using the trigger of the Kistler soft- and hardware. At both body sides, reflective joint markers were placed on the distal head of the fifth metatarsal bone, lateral malleolus, epicondylus lateralis, trochanter major, L5 and C7 processus spinosus.

2.3. Data processing

From the collected data, we chose all those trials of each participant that were distributed in a narrow range of their preferred running speed over all trials achieving steady-state running. This resulted in 11 trials on average (minimum eight, maximum 15 trials) per experimental setup and participant. The selection was realized as follows: (1) we calculated the mean of the horizontal velocity of the L5 marker for each force plate. (2) If these two values differed by more than 5% within one trial, then this trial was discarded.

The raw kinematic data were filtered with a third-order low-pass Butterworth filter (Winter, 2005) at 50 Hz cut-off frequency.

The distance between the hip and the ball of the foot marker was defined as leg length l_{leg} of the stance leg (Fig. 2). Leg stiffness k_{leg} was calculated as the ratio between the peak ground reaction force F_{max} and the maximum leg compression $\Delta l_{leg,max} = l_{leg,TD} - \min(l_{leg,TD:TO})$ (where TD is touchdown and TO is take-off) (Grimmer et al., 2008; McMahon & Cheng, 1990).

To compare the results of each participant we used all parameters in dimensionless form (Blickhan, 1989; Geyer et al., 2005). The ground reaction force was normalized to subject mass and gravity constant (body weight, bw). The leg length was normalized to the initial leg length (l_{leg} / l_0).

Insert Fig. 2 About Here

Results were expressed as mean $\pm$ standard deviation over all participants and parameters. We used an analysis of variance (ANOVA, SPSS 15.0; SPSS®, Chicago, IL, USA) to compare normalized global (GRF, leg length, leg stiffness, leg angle) and local parameters (knee and ankle angle) on first and second contact. A p -value $< .05$ based on a post-hoc analysis was considered to be statistically significant.

3. Results

While running on uneven terrain ground reaction force, leg length, leg stiffness, and angle of attack (i.e., leg angle at the beginning of the contact) were adjusted to the direction of the vertical disturbance but also to its length (Figs. 3 and 4; Table 1).

3.1. Upward running

For upward running (Fig. 3), the first contact peak GRF rose by about 0.22 body weights (bw) between the unperturbed running (2.74 ± 0.16 bw) and the single step up (SU; 2.96 ± 0.16 bw ; $p < .05$), and by about 0.24 bw between the unperturbed running and the permanently elevated track step up (TSU; 2.98 ± 0.17 bw ; Fig. 3A; $p < .05$). Furthermore, we observed a significantly longer leg at TD along with an increased leg compression in preparation for TSU (Fig. 3C). Thus, the normalized leg stiffness maintained nearly constant (Table 1).

Table 1

On second contact (Fig. 3B), the peak GRF diminished by about 0.44 bw between unperturbed running (2.66 ± 0.19 bw) and SU (2.22 ± 0.22 bw; $p < .05$), and by about 0.18 bw between unperturbed running and TSU (2.48 ± 0.21 bw; Fig. 3B; $p < .05$). The leg length at TD was shortened significantly in SU whereas leg compression remained almost constant on second contact (Fig. 3D). The normalized leg stiffness decreased significantly on second contact by about 20.4% at SU, and by about 9.3% at TSU (Table 1). The observed shorter leg at TD on second contact was distributed between the knee and the ankle joint (Fig. 5; Table 2).

For the angle of attack α_{TD} we also found adaptations to the different track types (Table 1). The angle of attack remained almost constant on first contact, and diminished significantly on second contact from 61° to 60° (SU), and from 61° to 59° (TSU).

Fig. 3; Table 2

3.2. Downward running

For downward running (Fig. 4), the peak GRF on first contact diminished by about 0.51 bw compared to the single step down (SD; 2.23 ± 0.20 bw; $p < .05$), and by about 0.28 bw compared to the permanently elevated track step down (TSD; 2.46 ± 0.17 bw; $p < .05$; Fig. 4A). The leg length at TD was shortened significantly in SD, whereas leg compression remained almost constant. Only at TSD leg compression increased but not significantly (Fig. 4C). Normalized leg stiffness decreased significantly on first contact by about 13.8% at SD, and by about 18.8% at TSD (Table 1).

On the lowered second contact (Fig. 4B), the peak GRF rose by about 0.40 bw between unperturbed running and SD (3.06 ± 0.23 bw; $p < .05$) and by about 0.45 bw between unperturbed running and TSD (3.11 ± 0.19 bw; $p < .05$; Fig. 4B). Furthermore, we observed a significantly longer leg at TD along with an increased leg compression for SD and TSD on lowered contact (Fig. 4D). Thus, the normalized leg stiffness maintained nearly constant (Table 1). The observed longer leg at TD on second contact was distributed between the knee and the ankle joint (Fig. 6; Table 2).

The angle of attack remained almost constant on first contact and increased significantly on the lowered second contact from 61° to 65° (SD and TSD; Table 1).

Insert Fig. 4 About Here

4. Discussion

4.1. Active control strategy by stiffness adjustment

Runners adjust their leg stiffness to the direction of the vertical disturbance (up or down) but also to its length. This leg stiffness adjustment corresponds to an altered leg force, and an almost unaffected leg compression on the elevated step – and to an altered leg force and leg compression on the lowered step.

Aiming at higher take-off velocity and advanced body height of the following flight phase while running upwards, we identified a small increase in leg force when preparing for first contact (Fig. 3A) because the runners were aware of the perturbation and did not want to stumble (Grimmer et al., 2008; Patla & Rietdyk, 1993). This is in accordance with the results of Grimmer et al. (2008). They measured a small increase in GRF in preparation for the obstacle height. But they did not know if these increased forces were provoked by the increased vertical TO velocity or by the increased vertical landing velocity (effected by the

longer flight phase which was caused by uneven ground before hitting the first force plate) (Grimmer et al., 2008). Due to the fact that higher landing velocities lead to higher ground reaction forces (Blickhan, 1989; Cavanagh & LaFortune, 1980) they could not say which of these effects dominated, and to which extent each effect corresponded to the increase in GRF (Grimmer et al., 2008). In our experiments the TO velocity of the hip on the preparation contact increased (0/0cm: 0.60 ± 0.10 m/s; SU: 0.92 ± 0.11 m/s; TSU: 0.90 ± 0.10 m/s; Table 3; Fig. 1), whereas the TD velocity marginally decreased independently from step length (0/0cm: -0.70 ± 0.15 m/s; SU: -0.67 ± 0.16 m/s; TSU: -0.67 ± 0.17 m/s; Table 3). Relating to the question of Grimmer et al., the increase in leg force on the preparation contact is mainly used to generate a higher take off velocity. Accordingly, step length does not play an important role for the preparation first contact. On the elevated second contact, ground reaction force was diminished by about 0.44 bw between unperturbed running and SU, and by about 0.18 bw between unperturbed running and TSU (Fig. 3B). This effect can be attributed to a lower vertical TD velocity (0/0cm: -0.86 ± 0.16 m/s; SU: -0.51 ± 0.17 m/s; TSU: -0.52 ± 0.16 m/s; Table 3) caused by a reduced body height at TD, and to an altered vertical TO velocity (0/0cm: 0.60 ± 0.13 m/s; SU: 0.35 ± 0.20 m/s; TSU: 0.69 ± 0.14 m/s; Table 3; Fig. 1). Thus, runners did change ground reaction force on the disturbed second contact (between SU and TSU) but not on the preparation first contact. The adaptation to the length of the step was regulated on the first elevated step. Due to the fact that leg compression remained almost constant on second contact, leg stiffness decreased by about 20.4% on the single step (SU) and by about 9.3% on the permanently elevated track step (TSU).

Table 3

Compared to the second contact of the upward running setup (see above) in downward running, ground reaction force on the preparation first contact was diminished by about

0.51 bw between unperturbed running and SD, and by about 0.28 bw between unperturbed running and TSD (Fig. 4A). This effect can be attributed to a decreased vertical TD velocity caused by a reduced body height at TD in SD (0/0cm: -0.70 ± 0.15 m/s; SD: -0.34 ± 0.18 m/s; TSD: -0.66 ± 0.15 m/s; Table 3), and to a decreased vertical TO velocity in SD and TSD (0/0cm: 0.60 ± 0.10 m/s; SD: 0.38 ± 0.13 m/s; TSD: 0.38 ± 0.10 m/s; Table 3). Aiming at smaller take-off velocity and altered body height of the flight phase, we identified an altered leg force on the preparation first contact (Fig. 4A). Due to the fact that leg compression marginally decreased in SD, leg stiffness decreased by about 13.8%. At TSD leg stiffness decreased by about 18.8% corresponding to an increased leg compression. On the lowered second contact, ground reaction force increased by about 0.40 bw between unperturbed running and SD, and by about 0.45 bw between unperturbed running and TSD (Fig. 4B). This effect can be attributed to a higher vertical TD velocity (0/0cm: -0.86 ± 0.16 m/s; SD: -1.09 ± 0.17 m/s; TSD: -1.12 ± 0.11 m/s; Table 3) caused by an increased body height at TD, and to a marginally increased vertical TO velocity (0/0cm: 0.60 ± 0.13 m/s; SD: 0.64 ± 0.13 m/s; TSD: 0.65 ± 0.11 m/s; Table 3; Fig. 1). Furthermore, we observed a significantly longer leg at TD along with an increased leg compression. Thus, the normalized leg stiffness maintained nearly constant at the lowered second contact (Table 1).

Leg stiffness adjustments are well known for hopping and running on surfaces varying with respect to compliance (Alexander, 1997; Farley et al., 1998; Ferris & Farley, 1997; Ferris et al., 1999; Ferris, Louie, & Farley, 1998; Kerdok et al., 2002; Lindstedt, 2003). For stiffened ground Ferris et al. report that leg response is characterized by a higher compliance, i.e., lower stiffness (Ferris & Farley, 1997; Ferris et al., 1998). On uneven ground runners reduce their leg stiffness, too. Here, leg stiffness decreases with the increasing height of the vertical perturbation (Grimmer et al., 2008). In contrast to the results on elastic surfaces, this leg stiffness adjustment corresponds to an altered leg force and an almost unaffected leg compression. Therefore, the strategy on compliant ground is the direct opposite to that on

uneven ground with vertical steps up (Grimmer et al., 2008). In accordance to the results of Grimmer et al. (2008) we found that in running steps up an altered leg force and constant leg compression can be caused by alterations of leg stiffness. However, when running steps down leg stiffness remains almost constant and results in an alteration of leg force and leg compression.

4.2. *Leg adjustments and control*

In modelled spring-mass running, the simplest strategy is running with a fixed angle of attack and constant leg stiffness (Seyfarth et al., 2002). Here, within a narrow range of the angle of attack, simulations reveal periodic movement patterns as well as the ability to cope with perturbations in ground level (Geyer et al., 2002). We found that angle of attack alters (Table 1). An upward step in the ground results in a flatter angle of attack (0/0cm: $61 \pm 2.6^\circ$; SU: $60 \pm 3.2^\circ$; TSU: $59 \pm 3.0^\circ$; Table 1), and a downward step in a steeper angle of attack (SD: $65 \pm 2.4^\circ$; TSD: $65 \pm 2.4^\circ$; Table 1). This would be expected for the case that the runner performs leg retraction (Seyfarth et al., 2003). Leg retraction increases the angle of attack proportionally to flight duration without any control (Daley & Biewener, 2006; Daley et al., 2006; Günther & Blickhan, 2002). Accordingly, the angle of attack changes depending on the change in ground level (Blickhan et al., 2007; Seyfarth et al., 2003). Again, on the preparation first contact, the angle of attack maintains nearly constant (0/0cm: $62 \pm 2.7^\circ$; SU: $62 \pm 3.1^\circ$; TSU: $63 \pm 3.4^\circ$; TSD: $63 \pm 8.8^\circ$; Table 1). The variation in angle of attack appears to be passively adjusted, consistent with a running model (e.g., the spring-mass model) that includes leg retraction in late swing phase. But we also found out that leg length at TD alters and shows a tendency to be shorter in an elevated step and longer in a lowered step (Table 1). Changing the leg length at TD as observed in our experiment makes a steeper (step up) or a flatter (step down) angle of attack possible. Thus, the angle of attack could be actively affected to prevent a stumble or fall.

In an experimental investigation on birds running over an unexpected drop in the terrain similar leg behavior was observed (Daley & Biewener, 2006; Daley et al., 2006). There the delay in ground contact results in a steeper, but more variable, angle of attack. In addition, the leg contacts the ground with a more extended posture, and gastrocnemius force and work output decrease with no change in EMG intensity (Daley, Voloshina, & Biewener, 2009). In our investigation on humans we also observed a longer leg at TD in the lowered contact. An extended leg at TD implies decreased bending in the joints (Fig. 6; Table 2) which in turn results in increased effective mechanical advantage for the musculature (Biewener, 1989; Biewener, Farley, Roberts, & Temaner 2004). In case of unaffected muscle activation and nearly constant muscle force, this results in an increase in leg stiffness (Blickhan et al., 2007). However, in our study leg stiffness remains almost constant in the lowered contact (Table 1). Thus, muscle activation or muscle force must decrease. A more extended leg posture changes the working range of the muscles. Hence, muscle length of extensors decrease which in turn results in decreased extensor muscle force. It is conceivable that both of these effects (increased effective mechanical advantage and reduced extensor muscle force) may lead to almost constant leg stiffness with no change in EMG intensity. In the step up, the leg contacts the ground in a more crouched posture (decreased effective mechanical advantage; Fig. 5; Table 2). In case of unaffected muscle activation and increased muscle force (extensor muscle-length increased), this results in nearly constant leg stiffness. In our investigation, however, leg stiffness decreased on the elevated step (Table 1). As a result, muscle activation could decrease.

Fig. 5, Fig. 6

It has also been reported, that there exists a proper adjustment of the angle of attack to spring stiffness in which the conservative spring-mass model is able to run in a self-stabilized mode

(Geyer et al., 2006, Seyfarth et al., 2002). Leg retraction greatly enlarges the range of leg stiffness and the angle of attack that the model can tolerate (Seyfarth et al., 2003). As mentioned earlier, in our experiments, runners adjust their leg stiffness to the direction of the vertical disturbance (up or down) but also to its length. Similar to Grimmer et al. (2008) the results of leg stiffness and angle of attack in our investigation indicate that runners choose not self-stable combinations but rather combinations that would allow at least five subsequent steps without further adjustment.

We all enhance leg excursion while stalking through high meadows. General movement strategies may exist which allow to cope with increasing uncertainties and demands with a minimum of modification of gait parameters. Runners use their exteroceptive information to adapt their movement strategies to the environment. These adaptations take the magnitude of the envisioned disturbance into account, thus they are not invoked by self-stable mechanisms. However, safety is enhanced by using strategies which keep the system in a self-stable realm. It remains to be shown whether this paradigm helps predict or interpret motor patterns in tasks where stability and low sensory flow are important.

Acknowledgments

We like to thank Michael Ernst and Norbert Pallaske for their support in the experiments and Tobias Siebert for proof-reading the manuscript. This project has been supported by the German Research Foundation (DFG, PAK 146 BI236/15).

References

- Alexander, R. M. (1997). Invited editorial on "Interaction of leg stiffness and surface stiffness during human hopping". *Journal of Applied Physiology*, 82, 13-14.
- Biewener, A. A. (1989). Scaling body support in mammals: Limb posture and muscle mechanics. *Science*, 245, 45-48.
- Biewener, A. A., Farley, C. T., Roberts, T. J., & Temaner, M. (2004). Muscle mechanical advantage of human walking and running: Implications for energy cost. *Journal of Applied Physiology*, 97, 2266-2274.
- Blickhan, R. (1989). The spring-mass model for running and hopping. *Journal of Biomechanics*, 22, 1217-1227.
- Blickhan, R., Seyfarth, A., Geyer, H., Grimmer, S., Wagner, H., & Gunther, M. (2007). Intelligence by mechanics. *Philosophical Transactions. Series A. Mathematical, Physical and Engineering Sciences*, 365, 199-220.
- Daley, M. A., & Biewener, A. A. (2006). Running over rough terrain reveals limb control for intrinsic stability. *Proceedings of the National Academy of Sciences U S A*, 103, 15681-6.
- Daley, M. A., Usherwood, J. R., Felix, G., & Biewener, A. A. (2006). Running over rough terrain: Guinea fowl maintain dynamic stability despite a large unexpected change in substrate height. *Journal of Experimental Biology*, 209, 171-187.
- Daley, M. A., Voloshina, A., & Biewener, A. A. (2009). The role of intrinsic muscle mechanics in the neuromuscular control of stable running in the guinea fowl. *Journal of Physiology*, 587, 2693-2707.
- Farley, C. T., Houdijk, H. H., van Strien, C., & Louie, M. (1998). Mechanism of leg stiffness adjustment for hopping on surfaces of different stiffnesses. *Journal of Applied Physiology*, 85, 1044-1055.
- Ferris, D. P., & Farley, C. T. (1997). Interaction of leg stiffness and surfaces stiffness during human hopping. *Journal of Applied Physiology*, 82, 15-22.
- Ferris, D. P., Liang, K., & Farley, C. T. (1999). Runners adjust leg stiffness for their first step on a new running surface. *Journal of Biomechanics*, 32, 787-794.
- Ferris, D. P., Louie, M., & Farley, C. T. (1998). Running in the real world: Adjusting leg stiffness for different surfaces. *Proceedings. Biological Sciences/The Royal Society*, 265, 989-994.
- Geyer, H., Blickhan, R., & Seyfarth, A. (2002). Natural dynamics of spring-like running: Emergence of selfstability. In P. Bidaud, & F. B. Amar (Eds.), *5th International Conference on Climbing and Walking Robots*. Paris: Professional Engineering Publishing.
- Geyer, H., Seyfarth, A., & Blickhan, R. (2005). Spring-mass running: Simple approximate solution and application to gait stability. *Journal of Theoretical Biology*, 232, 315-328.
- Geyer, H., Seyfarth, A., & Blickhan, R. (2006). Compliant leg behaviour explains basic dynamics of walking and running. *Proceedings. Biological Sciences/The Royal Society*, 273, 2861-2867.
- Grimmer, S., Ernst, M., Günther, M., & Blickhan, R. (2008). Running on uneven ground: Leg adjustment to vertical steps and self-stability. *Journal of Experimental Biology*, 211, 2989-3000.
- Günther, M., & Blickhan, R. (2002). Joint stiffness of the ankle and the knee in running. *Journal of Biomechanics*, 35, 1459-1474.
- Kerdok, A. E., Biewener, A. A., McMahon, T. A., Weyand, P. G., & Herr, H. M. (2002). Energetics and mechanics of human running on surfaces of different stiffnesses. *Journal of Applied Physiology*, 92, 469-478.
- Lindstedt, S. (2003). Springs in legs and running surfaces. *Journal of Experimental Biology*, 206, 8.
- McMahon, T. A., & Cheng, G. C. (1990). The mechanics of running: How does stiffness couple with speed? *Journal of Biomechanics*, 23 Suppl 1, 65-78.
- Patla, A. E., & Rietdyk, S. (1993). Visual control of limb trajectory over obstacles during locomotion: effect of obstacle height and width. *Gait & Posture*, 1, 45-60.
- Seyfarth, A., Geyer, H., Gunther, M., & Blickhan, R. (2002). A movement criterion for running. *Journal of Biomechanics*, 35, 649-655.

- Seyfarth, A., Geyer, H., & Herr, H. (2003). Swing-leg retraction: A simple control model for stable running. *Journal of Experimental Biology*, 206, 2547-2555.
- Winter, D. A. 2005. *Biomechanics and motor control of human movement (third edition)*, New Jersey, John Wiley & Sons.

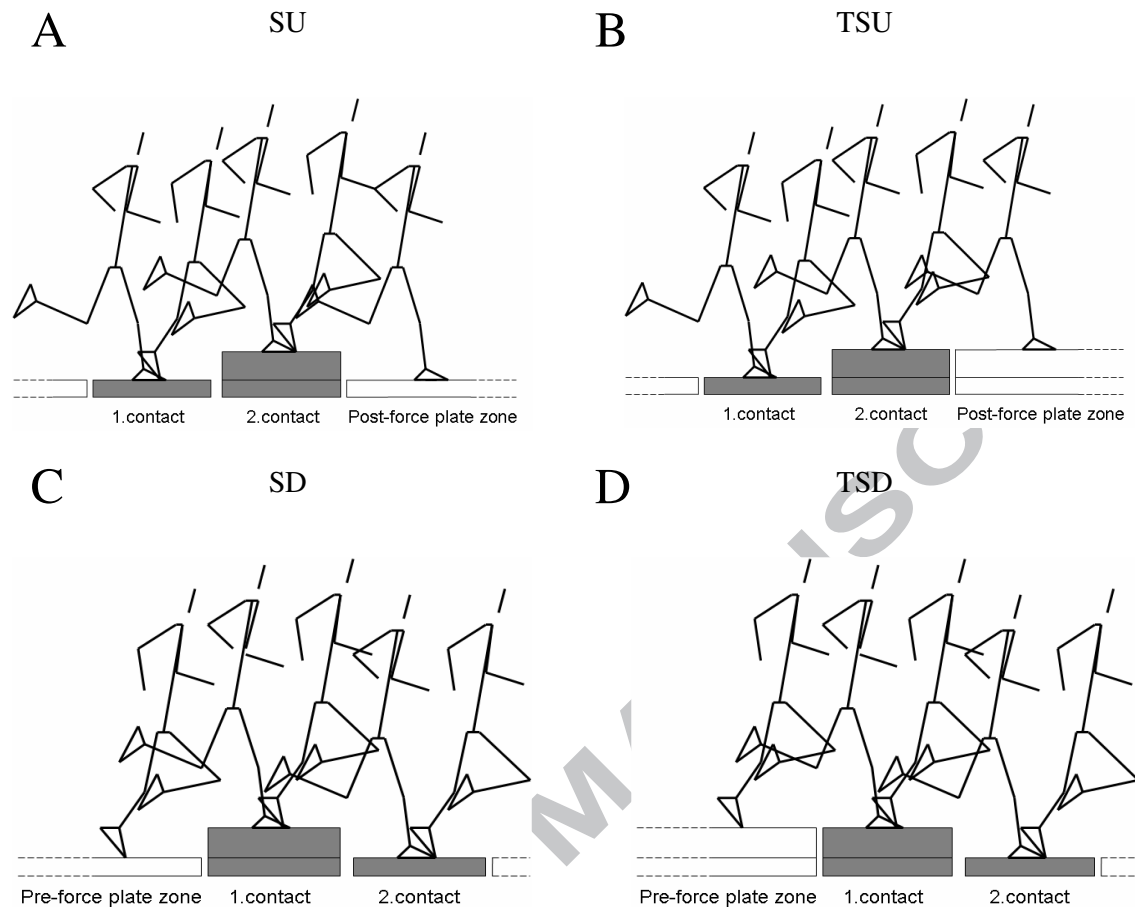


Fig. 1. Side view of the upward (A, B) and downward (C, D) running setup with two consecutive force plates. A: The variable-height plate (2.contact) was set on 10 cm (single step up, SU). B: The second contact plate as well as the post-force plate zone was set on an elevation of 10 cm (permanently elevated track step up, TSU). C: The first contact plate (1.contact) was set on 10 cm (single step down, SD). D: The first contact plate as well as the pre-force plate zone was set on an elevation of 10 cm (permanently elevated track step down, TSD).

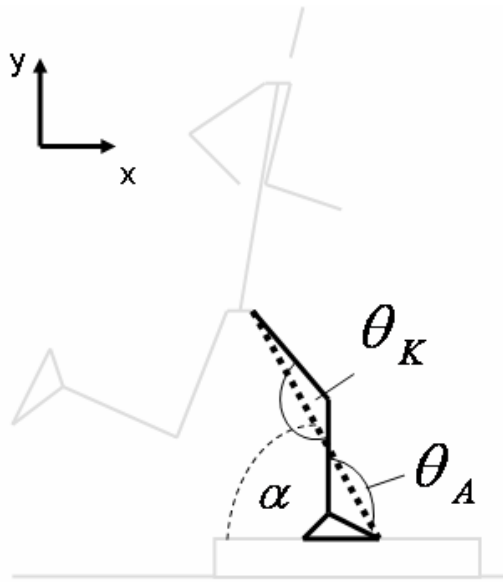


Fig. 2. Directions for joint angles (ankle: θ_A , knee: θ_K). According to the spring-mass model, we defined the leg as the distance between the hip and toe marker (dotted line). The leg angle (α) is measured clockwise with respect to the negative x-axis.

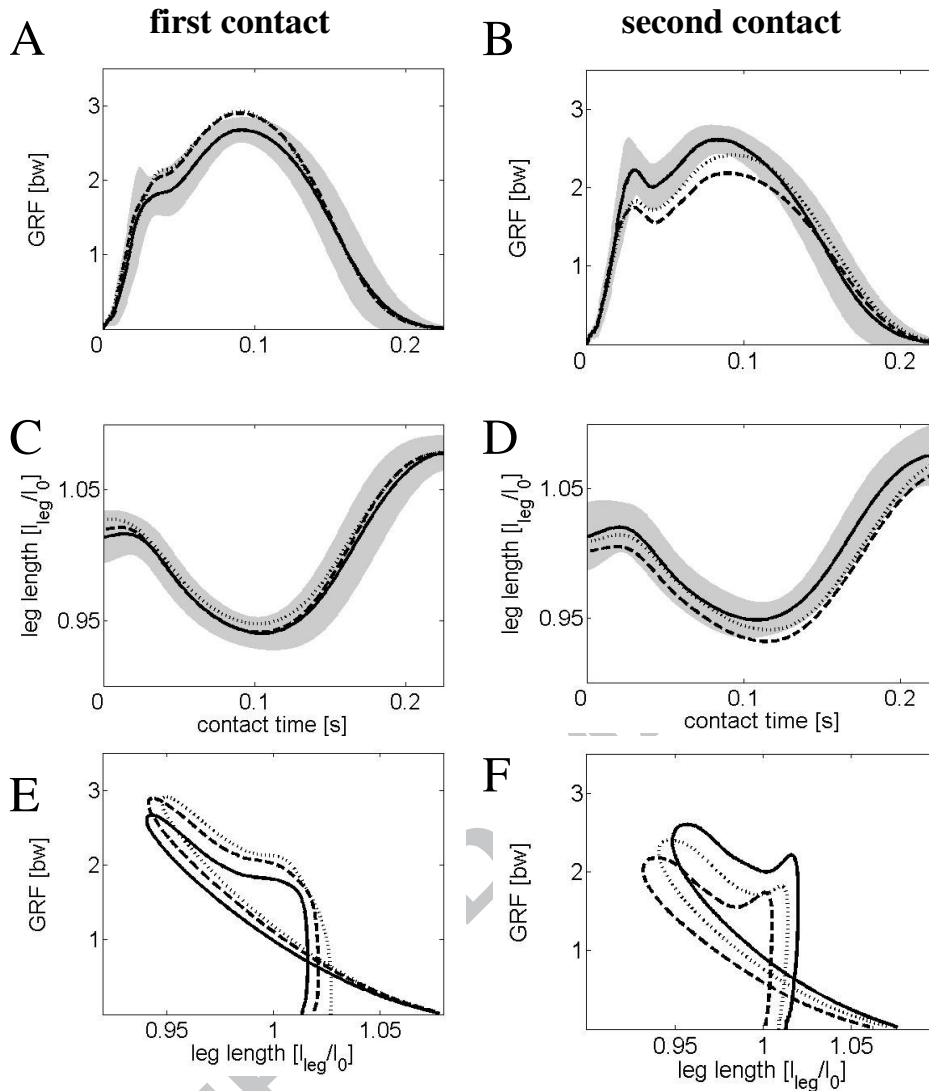


Fig. 3. A, B: GRF during stance phase of the two subsequent contacts in the upward running setup (A: contact 1, B: contact 2). The solid lines represent the mean of the unperturbed running and the grey areas represent the standard deviation of these reference runs ($N = 124$), the dotted lines represent the mean of the single step up (SU), and the dashed lines the mean of the permanently elevated track step up (TSU). A: The peak GRF is slightly increased in preparation for the consecutive steps up (SU, TSU). The dotted line (SU) is covered by the dashed line (TSU) B: The peak GRF diminished in upward running at second contact but differs between the two different step lengths (SU, TSU; $p < 0.05$). The mean of the SU (dashed line) shows the smallest amplitude. E, F: The operation of the human leg was maintained. The leg was still compressed and stretched during stance phase in both contacts. However, the energy balances seem not to be zero (Tab.3).

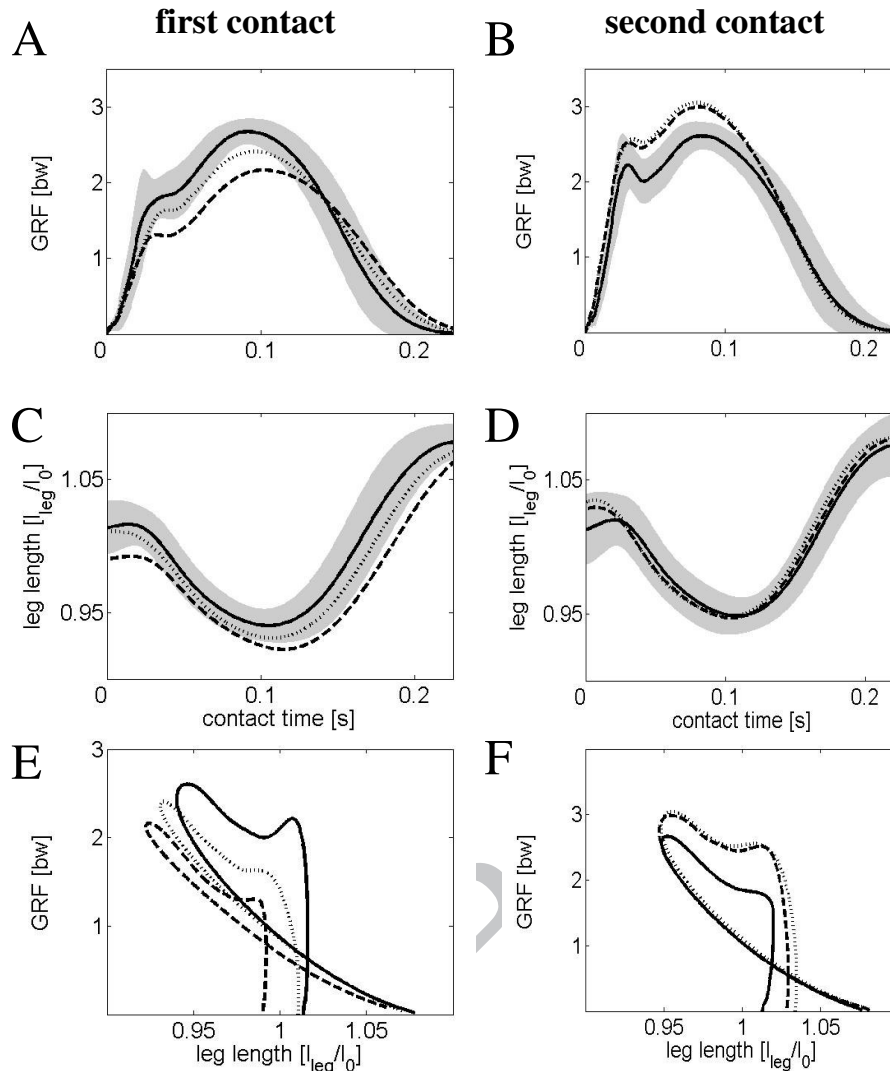


Fig. 4. A, B: GRF during stance phase of the two subsequent contacts in the downward running setup. The solid lines represent the mean of the unperturbed running and the grey areas represent the standard deviation of these reference runs ($N = 124$), the dotted lines represent the mean of the single step down (SD), and the dashed lines the mean of the permanently elevated track step down (TSD). A: The peak GRF diminished in downward running at first contact but differs between the two different step lengths (SD, TSD; $p < 0.05$). The mean of the SD (dashed line) shows the smallest amplitude. B: The peak GRF is slightly increased at second contact (SD, TSD; $p < 0.05$). The dotted line (SD) is covered by the dashed line (TSD). E, F: The operation of the human leg was maintained. The leg was still compressed and stretched during stance phase in both contacts. However, the energy balances seem not to be zero (Tab.3).

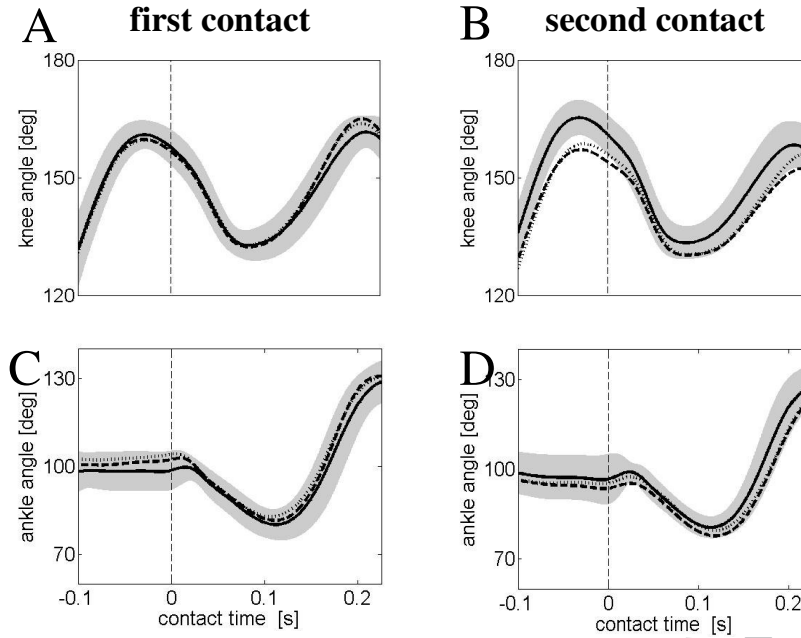


Fig. 5. Knee and ankle joint angle during the two subsequent contacts in the upward running setup. The beginning of the ground contact (TD) is marked by the vertical dotted line. The solid lines represent the mean of the unperturbed running and the grey areas represent the standard deviation of these reference runs ($N = 124$), the dotted lines represent the mean of the single step up (SU), and the dashed lines the mean of the permanently elevated track step up (TSU). A, C: In preparation of the following step up only the ankle does adapt. B, D: In the second contact both knee and ankle do adapt to the disturbance. For detailed values see Tab. 2.

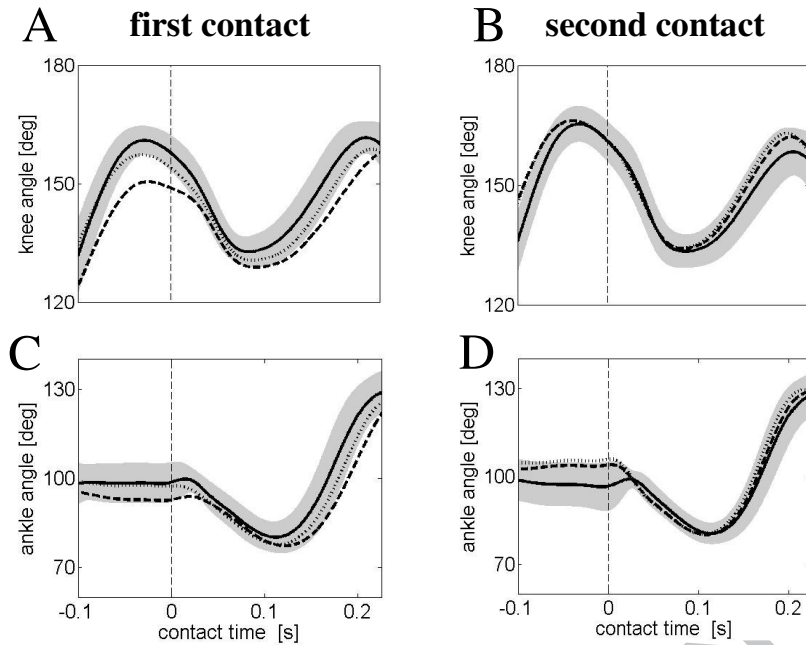


Fig. 6. Knee and ankle joint angle during the two subsequent contacts in the downward running setup. The beginning of the ground contact (TD) is marked by the vertical dotted line. The solid lines represent the mean of the unperturbed running and the grey areas represent the standard deviation of these reference runs ($N = 124$), the dotted lines represent the mean of the single step down (SD), and the dashed lines the mean of the permanently elevated track step down (TSD). A, C: In preparation of the following step down both knee and ankle do adapt. B, D: In the second contact both knee and ankle do adapt to the disturbance. For detailed values see Tab. 2.

Table 1: Parameters of global leg behaviour

	contact	0/0cm	0/10cm (SU)	0/10cm (TSU)	10/0cm (SD)	10/0cm (TSD)
$F_{\max}$ (bw)	1	2.74±0.16	2.96±0.16	2.98±0.17	2.23±0.20	2.46±0.17
	2	2.66±0.19	2.22±0.22	2.48±0.21	3.06±0.23	3.11±0.19
t_{contact} (s)	1	0.201±0.017	0.198±0.015	0.199±0.018	0.223±0.020	0.214±0.020
	2	0.201±0.017	0.208±0.016	0.213±0.020	0.202±0.019	0.199±0.018
$l_{\text{leg(TD)}} (l_{\text{leg}} / l_0)$	1	1.014±0.020	1.019±0.019	1.026±0.022	0.989±0.021	1.007±0.021
	2	1.013±0.026	1.002±0.023	1.008±0.025	1.029±0.037	1.034±0.034
$l_{\text{leg(TO)}} (l_{\text{leg}} / l_0)$	1	1.070±0.012	1.070±0.010	1.073±0.013	1.063±0.014	1.064±0.015
	2	1.072±0.013	1.056±0.016	1.071±0.016	1.076±0.014	1.076±0.014
$\Delta l_{\text{leg,max}}$	1	0.076±0.019	0.081±0.019	0.084±0.016	0.072±0.015	0.083±0.015
	2	0.068±0.025	0.074±0.021	0.072±0.020	0.085±0.030	0.089±0.028
k_{leg}	1	37.7±8.6	38.6±8.9	36.7±7.7	32.5±7.1	30.6±5.9
	2	41.7±15.6	33.2±12.5	37.8±14.4	41.1±15.4	39.6±15.8
α_{TD} (deg)	1	62±2.7	62±3.1	63±3.4	61±3.8	63±8.8
	2	61±2.6	60±3.2	59±3.0	65±2.4	65±2.4
α_{TO} (deg)	1	116±2.9	114±3.0	114±3.2	114±3.3	116±3.5
	2	115±3.4	115±3.6	112±3.5	115±2.4	116±2.5
N		124	124	106	112	114

Mean ± standard deviation over all subjects and parameters separated for the two consecutive contacts. N is the number of successful trials. Bolding values $p < 0.05$ (significantly different from the level condition (0/0cm)).

Table 2: Parameters of local leg behaviour

	contact	0/0cm	0/10cm (SU)	0/10cm (TSU)	10/0cm (SD)	10/0cm (TSD)
$\varphi_{knee,TD}$ (deg)	1	158±4	156±4	157±5	149±4	154±5
	2	161±5	154±6	156±6	161±4	161±4
$\varphi_{knee,TO}$ (deg)	1	163±3	166±2	166±3	159±3	160±5
	2	160±5	153±5	158±4	164±4	165±5
$\varphi_{ankle,TD}$ (deg)	1	98±7	102±8	104±7	93±6	98±8
	2	97±9	94±7	95±5	104±13	106±12
$\varphi_{ankle,TO}$ (deg)	1	124±6	128±4	128±5	124±5	124±5
	2	124±5	119±5	123±4	126±6	126±5
N		124	124	106	112	114

Mean ± standard deviation over all subjects and parameters separated for the two consecutive contacts. N is the number of successful trials. Bolding values $p < 0.05$ (significantly different from the level condition (0/0cm)).

Table 3: Velocity and energy balance

	contact	0/0cm	0/10cm (SU)	0/10cm (TSU)	10/0cm (SD)	10/0cm (TSD)
$v_{y,TD} (ms^{-1})$	1	-0.70±0.15	-0.67±0.16	-0.67±0.17	-0.34±0.18	-0.66±0.15
	2	-0.86±0.16	-0.51±0.17	-0.52±0.16	-1.09±0.17	-1.12±0.11
$v_{y,TO} (ms^{-1})$	1	0.60±0.10	0.92±0.11	0.90±0.10	0.38±0.13	0.38±0.10
	2	0.60±0.13	0.35±0.20	0.69±0.14	0.64±0.13	0.65±0.11
$v_{x,TD} (ms^{-1})$	1	4.71±0.36	4.70±0.44	4.62±0.44	4.45±0.32	4.51±0.33
	2	4.75±0.36	4.83±0.45	4.73±0.47	4.54±0.38	4.63±0.32
$v_{x,TO} (ms^{-1})$	1	5.32±0.39	5.26±0.45	5.17±0.43	5.18±0.42	5.28±0.37
	2	5.21±0.40	5.28±0.48	5.13±0.54	5.15±0.45	5.31±0.38
$\Delta E_{leg} (bw \cdot l_0)$	1	36.5±25.8	48.5±35.0	50.2±43.1	38.9±40.4	8.1±48.0
	2	62.2±45.7	44.5±34.2	49.2±41.3	118.5±55.8	128.8±40.8
N		124	124	106	112	114

Mean ± standard deviation over all subjects and parameters separated for the two consecutive contacts. N is the number of successful trials.