

RESEARCH ARTICLE

Preparing the leg for ground contact in running: the contribution of feed-forward and visual feedback

 Roy Müller^{1,*}, Daniel Florian Benedict Häufle² and Reinhard Blickhan¹
ABSTRACT

While running on uneven ground, humans are able to negotiate visible but also camouflaged changes in ground level. Previous studies have shown that the leg kinematics before touch down change with ground level. The present study experimentally investigated the contributions of visual perception (visual feedback), proprioceptive feedback and feed-forward patterns to the muscle activity responsible for these adaptations. The activity of three bilateral lower limb muscles (*m. gastrocnemius medialis*, *m. tibialis anterior* and *m. vastus medialis*) of nine healthy subjects was recorded during running across visible (drop of 0, –5 and –10 cm) and camouflaged changes in ground level (drop of 0 and –10 cm). The results reveal that at touchdown with longer flight time, *m. tibialis anterior* activation decreases and *m. vastus medialis* activation increases purely by feed-forward driven (flight time-dependent) muscle activation patterns, while *m. gastrocnemius medialis* activation increase is additionally influenced by visual feedback. Thus, feed-forward driven muscle activation patterns are sufficient to explain the experimentally observed adjustments of the leg at touchdown.

KEY WORDS: EMG, Pre-activation, Gastrocnemius, Force feedback, Uneven ground

INTRODUCTION

While running, humans must routinely negotiate varied and sometimes unpredictable changes in ground level, e.g. running across an uneven forest track covered with stones and roots (visible perturbation) or stepping into a puddle of unknown depth (camouflaged perturbation).

In preparation for such perturbations, humans flex their ankle joint angle (dorsiflexion) at touchdown for visible elevations in ground level (Grimmer et al., 2008; Müller and Blickhan, 2010) and extend their ankle joint angle (plantar flexion) for visible drops in ground level (Müller et al., 2012a). Interestingly, they also extend their ankle joint if the drop is invisible because of camouflage (Müller et al., 2012a). In this study, we investigated the muscle activity and neuronal control strategy responsible for these findings with perturbation experiments.

The muscles responsible for plantar flexion and dorsiflexion are, amongst others, *m. gastrocnemius medialis* (*gastrocnemius*) and *m. tibialis anterior* (*tibialis*), respectively. As these muscles are located close to the skin, their activity can be observed with muscle surface electromyography (EMG). The activity of leg muscles continuously changes throughout the running cycle. During unperturbed level

running, *gastrocnemius* activity starts before touchdown and ends before take-off, with peak activation after touchdown. The shape of this peak is similar to the quadriceps peak but delayed. *Tibialis* activity starts at take-off and ends at touchdown, with peak activation before touchdown (Gazendam and Hof, 2007; Müller et al., 2010). On level ground, the movement is periodic and the activity patterns are fairly repetitive (Gazendam and Hof, 2007; Guidetti et al., 1996; Ishikawa et al., 2007; Müller et al., 2010).

In case of a variation of the movement, e.g. due to a variation in ground level, however, the muscle activity differs from the periodic case to adapt to the perturbation. *Gastrocnemius* activity prior to the touchdown (pre-activation) decreases with a visible elevated contact (Müller et al., 2010). This seems to be sufficient to adjust the preparing ankle angle (Müller et al., 2012b) and, consequently, its antagonist, the *tibialis* does not alter activity dependent on step elevation (Müller et al., 2010). In the present study, we investigated running across visible and camouflaged drops in ground level. We report on the altered muscle activity resulting in increased plantar flexion before touchdown for these perturbations. Furthermore, we address here the neuro-mechanical strategy behind these adjustments.

Such an adaptation could be a result of visual perception of the perturbation, principally allowing an adaptation of the pre-activation prior to the perturbed touchdown. Based on experience, a few visual cues might suffice to recall appropriate stored information. The error signal (unevenness of the ground) generated by the perception of the hurdle (visual feedback) allows action to be taken in advance of the perturbed ground contact. This way, the plantar flexion angle at touchdown could be increased.

A different strategy is required if such a visually guided adaptation is not possible, e.g. when the changes in ground level are invisible as a result of camouflage (e.g. stepping into a puddle of unknown depth). In this case, a trained muscle activity pattern can generate an increasing plantar flexion angle in time, e.g. by constantly increasing *gastrocnemius* activity with time, as already observed in the EMG recordings of level running. As the flight time during running on uneven ground depends on ground level height (the higher the next ground contact, the shorter the flight time, and the lower the next ground contact, the longer the flight time), such a trained muscle activity pattern allows an adapted muscle activation and plantar flexion angle at touchdown without the need for any neural feedback. This strategy can thus be seen as a feed-forward muscle activity pattern created, for example, by central pattern generators (Dickinson et al., 2000; Ijspeert, 2008; Prochazka and Yakovenko, 2007). In such rhythmical feed-forward activation, the timing of the pattern has to be adapted to the walking cycle (Prochazka and Yakovenko, 2007; Rybak et al., 2002), e.g. the onset of muscle pre-activation depends on the preceding take-off time. Thus, the preceding take-off is the trigger event for the pattern.

There is experimental evidence for the contribution of both feed-forward and feedback control to running (Dickinson et al., 2000; MacKay-Lyons, 2002; Nielsen, 2003; Prochazka and Yakovenko,

¹Motionscience, Institute of Sport Sciences, Friedrich Schiller University Jena, Seidelstraße 20, 07749 Jena, Germany. ²Department of Sport and Exercise Science, University of Stuttgart, Allmandring 28, 70569 Stuttgart, Germany.

*Author for correspondence (roy.mueller@uni-jena.de)

List of symbols and abbreviations

CD10	running across a camouflaged drop of -10 cm
CL	running on the camouflaged level track
EMG	muscle surface electromyography
Gastrocnemius	m. gastrocnemius medialis
Tibialis	m. tibialis anterior
Vastus	m. vastus medialis
VD5	running across a visible drop of -5 cm
VD10	running across a visible drop of -10 cm
VL	running on the unperturbed level track

2007). The central nervous system incorporates peripheral sensory information from proprioceptive muscle sensor organs (Pearson, 2004; Pearson and Collins, 1993), e.g. muscle spindles and Golgi tendon organs. Such decentralized proprioceptive feedback can also be responsible for generating a certain movement that is the result of neither a planned trajectory nor a predetermined pattern. For example, Geyer et al. (Geyer et al., 2003) show that proprioceptive signals can produce a muscle activation pattern resulting in periodic human hopping. Their hopping model (Geyer et al., 2003) consisted of a two-segment leg with one knee extensor muscle [e.g. m. vastus medialis (vastus)]. The muscle activation patterns were generated by monosynaptic feedback of muscle spindles (length signal) and muscle Golgi tendon organs (force signal) increasing muscle activity with increasing muscle length or force, respectively. These positive force or length feedbacks generated appropriate muscle activation patterns for periodically stable hopping (Geyer et al., 2003). Such decentralized feedback can also generate and stabilize walking and can cause rapid adaptations to (unforeseen) disturbances (Geyer and Herr, 2010). However, if we assume that all feedback information is provided by proprioception and the vestibular system, adaptation of the pre-activation before hitting the ground is not possible. Furthermore, adaptation is not possible within a view milliseconds (~30 ms) (Grey et al., 2007) after ground contact because of the time delay of proprioceptive feedback.

In consequence, visual feedback and a well-designed/trained feed-forward muscle activity pattern both allow an adaptation of muscle pre-activation to varying ground levels, while proprioceptive

feedback can help to counteract perturbations during ground contact. As the plantar flexion before touchdown occurs in running across visual and camouflaged drops in ground level (Müller et al., 2012a), we hypothesize that a feed-forward strategy dominates the muscle activity of the lower leg muscles. Following the results of the previous studies (Müller et al., 2010; Müller et al., 2012b), we expect that gastrocnemius pre-activation therefore increases while tibialis pre-activation remains unaltered for drops in ground level. Furthermore, as visual information can be used to adapt in advance, we expect to see a difference in muscle pre-activation between visible and camouflaged trials. Finally, we expect that after touchdown, decentralized proprioceptive feedback would play a major role in adapting muscle activation.

RESULTS**Running across visible changes**

Gastrocnemius pre-activation (time period extending from 140 ms pre-contact to touchdown) was adjusted to the visual changes in ground level (Fig. 1A,B). Compared with level running (VL), with increasing drop height, gastrocnemius pre-activation increased significantly from -120 ms to actual touchdown for both -5 cm lowered contact (VD5) and -10 cm lowered contact (VD10) (Fig. 1A,B). Between VD5 and VD10, we found no significant difference in gastrocnemius pre-activation. Furthermore, gastrocnemius pre-activation at actual touchdown increased with flight time ($P=0.035$).

After actual touchdown, during ground contact, gastrocnemius activation increased significantly from 20 to 60 ms and decreased from 120 to 160 ms for VD5 and increased from 40 to 60 ms for VD10 compared with VL (Fig. 1A,B). Significant differences between VD5 and VD10 were found between 100 and 120 ms after actual touchdown. Peak activation occurred between 60 and 80 ms after actual touchdown (during ground contact).

Triggered to virtual touchdown of VL, gastrocnemius pre-activation increased significantly for the most part of VD5 and VD10, compared with VL (Fig. 2A,B).

Similar to gastrocnemius, vastus pre-activation increased prior to a visible drop. Compared with level running (VL), vastus pre-activation increased significantly from -20 ms to actual touchdown

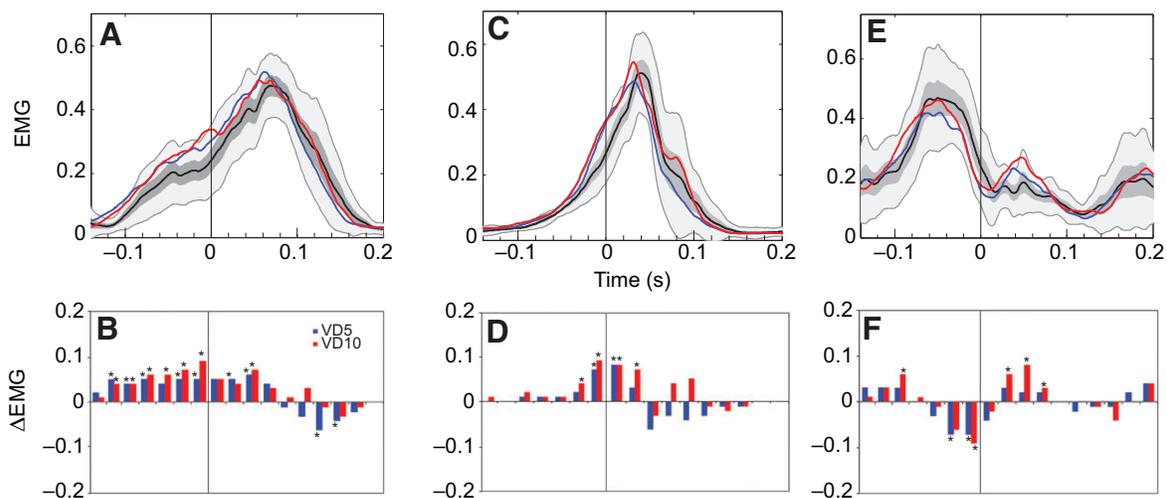


Fig. 1. Electromyography (EMG) triggered to actual touchdown (vertical line) while running across visible changes in ground level. (A,B) M. gastrocnemius medialis, (C,D) m. vastus medialis, (E,F) m. tibialis anterior. (A,C,E) Normalized EMG mean time course of gastrocnemius (A), vastus (C) and tibialis (E). The black line represents the mean of visible level running (VL) and the grey shaded area the s.e.m. of these reference trials (pale shaded area is s.d.). Blue lines, mean during VD5 (visible, -5 cm down); red lines, mean during VD10 (visible, -10 cm down). (B,D,F) EMG residuals of VD5 and VD10 trials with respect to VL. Significant differences from VL are marked by an asterisk.

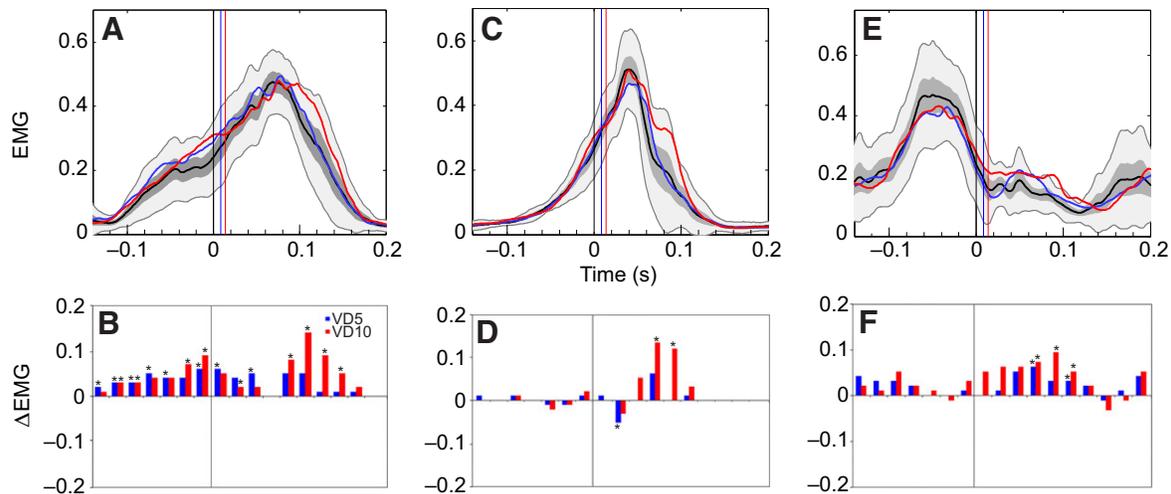


Fig. 2. EMG triggered to virtual level touchdown (black vertical line) while running across visible changes in ground level. (A,B) *M. gastrocnemius* medialis, (C,D) *m. vastus* medialis, (E,F) *m. tibialis* anterior. (A,C,E) Normalized EMG mean time course of gastrocnemius (A), vastus (C) and tibialis (E). The black line represents the mean of visible level running (VL) and the grey shaded area the s.e.m. of these reference trials (pale shaded area is s.d.). Blue lines, mean during VD5 (visible, -5 cm down); red lines, mean during VD10 (visible, -10 cm down). Both the mean of VD5 and the mean of VD10 were triggered to the virtual level touchdown at the height of the level contact. Thus, the actual touchdown of VD5 (vertical blue line) and VD10 (vertical red line) shifts to the right by the remaining flight time calculated by subtracting the flight time of VL from the flight time of VD5 and VD10 for each subject. (B,D,F) EMG residuals of VD5 and VD10 trials with respect to VL. Significant differences from VL are marked by an asterisk.

prior to -5 cm lowered contact and from -40 ms to actual touchdown prior to -10 cm lowered contact (Fig. 1C,D). Vastus pre-activation did not differ significantly between VD5 and VD10. Furthermore, vastus pre-activation at actual touchdown increased but did not depend on flight time ($P=0.102$).

During ground contact in both lowered contacts (VD5 and VD10), vastus activation increased from actual touchdown to peak activation, compared with VL. Peak activation occurred between 20 and 40 ms after actual touchdown (during ground contact).

Triggered to the virtual touchdown of VL, during VD5 and VD10, vastus pre-activation did not differ from VL (Fig. 2C,D).

Tibialis pre-activation increased from -100 to -80 ms and decreased from -60 to 0 ms prior to actual touchdown for VD5 and VD10, as compared with VL. Tibialis pre-activation did not differ between VD5 and VD10. Furthermore, in contrast to gastrocnemius and vastus, tibialis pre-activation at actual touchdown decreased with flight time ($P=0.000$).

During lowered ground contact, the differences were more pronounced in VD10. Tibialis activation increased from 20 to 80 ms after actual touchdown, compared with VL (Fig. 1E,F). Significant differences between VD5 and VD10 were found between 40 and 60 ms after actual touchdown. Peak activation occurred between -60 and -40 ms before actual touchdown, i.e. during flight phase in contrast to gastrocnemius and vastus.

Triggered to the virtual touchdown of VL, during VD5 and VD10, tibialis pre-activation did not differ from VL (Fig. 2E,F).

Running across camouflaged changes

During the camouflaged level contact (CL) and camouflaged -10 cm lowered contact (CD10), gastrocnemius pre-activation did not differ from VL prior to the virtual touchdown at the height of the camouflage (Fig. 3A,B). Furthermore, there was no difference in gastrocnemius pre-activation between CL and CD10 prior to the virtual contact (Fig. 3A,B). After virtual contact in the CD10 trials, gastrocnemius pre-activation at actual touchdown increased with flight time ($P=0.026$).

During ground contact, in the CL trials, gastrocnemius activation decreased significantly from 60 to 100 ms and increased from 100 to 180 ms, compared with VL. During CD10, however, gastrocnemius activation increased from 60 ms to the end of contact as compared with VL (Fig. 3A,B). Peak activation during CD10 occurred between 80 and 100 ms after virtual contact. At the same time, there was a local minimum in CL (Fig. 3A).

Similar to gastrocnemius, vastus pre-activation prior to the virtual touchdown did not differ from VL and there was no difference between CL and CD10 (Fig. 3C,D). After virtual contact, during CD10, vastus pre-activation at actual touchdown increased with flight time ($P=0.016$).

After virtual contact, during CL, vastus activation increased significantly from 40 to 100 ms, whereas during CD10, vastus activation increased significantly from 60 to the end of contact as compared with VL (Fig. 3D). Peak activation occurred between 40 and 60 ms after virtual touchdown.

In contrast to gastrocnemius and vastus, prior to the virtual contact, tibialis pre-activation decreased significantly from -140 to -40 ms and increased significantly from -20 ms to virtual touchdown in CL and CD10 as compared with VL (Fig. 3E,F). Between CL and CD10 we found no significant differences.

After virtual contact, during CD10, tibialis pre-activation at actual touchdown decreased but did not depend on flight time ($P=0.053$). After virtual touchdown, during CL, tibialis activation increased from 0 to 80 ms, whereas during CD10, tibialis activation increased from 60 to 140 ms as compared with VL (Fig. 3F). Peak activation occurred between 40 and 20 ms before virtual touchdown (during flight phase).

DISCUSSION

Previous studies have shown that during running across visible and camouflaged drops in ground level, humans extend their ankle joint before touchdown (Müller et al., 2012a). With this study, we wanted to investigate the neuro-mechanical strategy responsible for the increased plantar flexion angles at touchdown. Our results show that

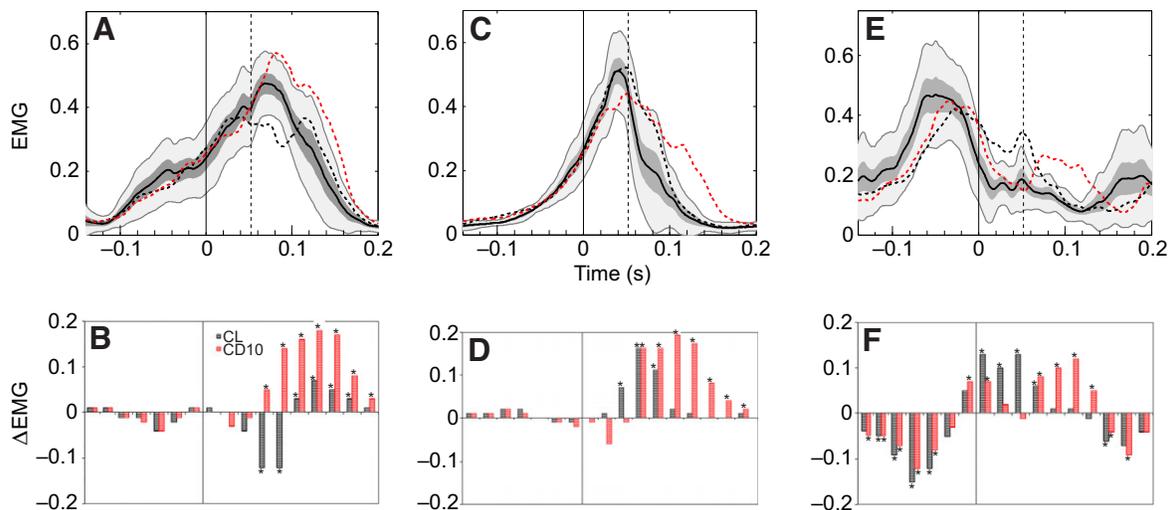


Fig. 3. EMG triggered to virtual level touchdown (black vertical line) while running across camouflaged changes in ground level. (A,B) M. gastrocnemius medialis, (C,D) m. vastus medialis, (E,F) m. tibialis anterior. (A,C,E) Normalized EMG mean time course of gastrocnemius (A), vastus (C) and tibialis (E). The black line represents the mean of visible level running (VL) and the grey shaded area the s.e.m. of these reference trials (pale shaded area is s.d.). Black dashed lines, mean during CL (camouflaged level running); red dashed lines, mean during CD10 (camouflaged, -10 cm drop down). The mean of CD10 was triggered to the touchdown at the height of the camouflage (actual touchdown of CL). Thus, the actual touchdown of CD10 (vertical dashed line) shifts to the right by the remaining flight time calculated by subtracting flight time of CL from flight time of CD10 for each subject. (B,D,F) EMG residuals of VD5 and VD10 trials with respect to VL. Significant differences from VL are marked by an asterisk.

humans increase gastrocnemius and reduce tibialis pre-activation (Fig. 1). Below, we discuss the possible contribution of feed-forward, visual feedback and proprioceptive feedback to the observed changes in muscle activation. In essence, each investigated muscle activity is adjusted with a slightly different control scheme – the basic pattern combined, however, allows a subject to adapt to perturbations.

Muscle pre-activation control

In preparation for ground contact, muscle pre-activation can principally be adapted by feed-forward and visual feedback, but not by proprioceptive feedback. To investigate solely the contribution of feed-forward, we prevented the visual perception by camouflaging the drop in ground level. For these camouflaged trials, we found no significant difference between level contact (CL) and the camouflaged drop (CD10) in gastrocnemius and vastus, as hypothesized. With no visual feedback of an upcoming drop in ground level, there is no need to vary or adapt the pre-activation, and, hence, the same activity pattern is observed. Furthermore, the form of the pre-activation pattern over time is solely responsible for increasing plantar flexion at touchdown (CD10 trials); a longer flight time (Table 1), associated with the drop in ground level, results in flight time-dependent and steadily increasing gastrocnemius activity

(Fig. 3A). In contrast to our hypothesis, we found significant changes in tibialis pre-activation (shifted in time) between the visible level (VL) and camouflaged trials (CL and CD10; Fig. 3F). This indicates that the subjects changed tibialis activity in response to visual feedback when they perceived the camouflage and expected a possible drop – presumably as a protection mechanism to avoid stumbling.

In the presence of visual feedback, we hypothesized an adaptation of the pre-activation pattern for the visual drops in ground level (compare VL with VD10). For this purpose, we triggered all trials on the virtual level touchdown (Fig. 2). Interestingly, only the gastrocnemius pre-activation was adapted (increased) by visual feedback (Fig. 2A,B). Vastus and tibialis pre-activations, however, were still only generated by the same pure feed-forward pattern. In this case, the neuro-mechanical strategy to generate the increased plantar flexion at touchdown is a combination of the visually guided adaptation of the feed-forward increase of gastrocnemius activity and the pure feed-forward driven decrease of tibialis activity due to the longer flight time (Table 1). This is best visualized in Fig. 1, where all trials are triggered on the actual touchdown.

In summary, it can be stated that the adjustments of each muscle vary slightly. However, the feed-forward driven muscle activation patterns are sufficient to adjust the experimentally observed

Table 1. Flight time prior to visible and camouflaged changes in ground level

	VL	VD5	VD10	CL	CD10
Flight time (s)	0.13±0.02	0.15±0.03	0.15±0.02	0.12±0.02	0.17±0.02

Data are means ± s.d. across all subjects. Bold values: $P < 0.05$ (significantly different from running on the unperturbed flat track, VL).

We found that during running across visible changes in ground level, flight time increased significantly prior to the -5 cm (VD5) and -10 cm (VD10) lowered contact. Between VD5 and VD10, flight time did not differ. Compared with VL, during running across camouflaged changes, flight time was significantly decreased prior to the camouflaged level contact (CL) and significantly increased prior to the camouflaged -10 cm lowered contact (CD10).

Please note: in preparation for a visible drop, human runners lower their centre of mass by about 40% of drop height (Ernst et al., 2014). Thus, changes in flight time will be small. In contrast, during running across camouflaged drops of -10 cm, it seems that runners anticipate a drop of about 5–10 cm (Müller et al., 2012a). The absence of the expected contact (CD10) results in increased flight time. In contrast, if the touchdown is earlier than expected (CL), flight time decreases. In both camouflaged situations, the changes in flight time are more pronounced than during running across visible changes in ground level.

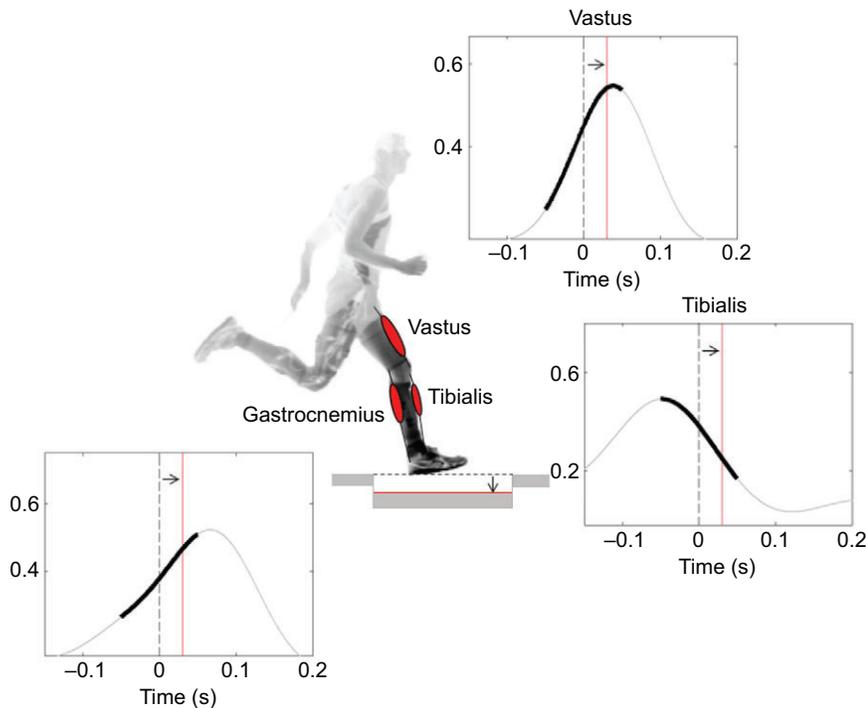


Fig. 4. Delineated EMG of *m. gastrocnemius medialis* (gastrocnemius), *m. vastus lateralis* (vastus) and *m. tibialis anterior* (tibialis) while running across a drop. Muscle activation at touchdown (dashed lines, virtual level touchdown at the height of the camouflage; red lines, lowered actual touchdown) depends on flight time and could be adjusted in a feed-forward manner. The bold part of the curve illustrates the muscle activation segment while facing different ground levels.

adjustments of the ankle joint angle at touchdown (Fig. 4). Whether these feed-forward driven muscle activation patterns are sufficient for larger ground level changes (drops >10 cm) is the subject of further perturbation studies.

The resulting variation of muscle pre-activation found in this study for drops in ground level complements the results of a previous study (Müller et al., 2010). There, muscle activation for running across single bumps showed decreased gastrocnemius pre-activation. For this case, the flight time decreased with increasing step height (in contrast to the present study for a drop in ground level). As it is not possible to camouflage elevations in ground level, the previous study could not exclude the influence of visual feedback. In consequence of the

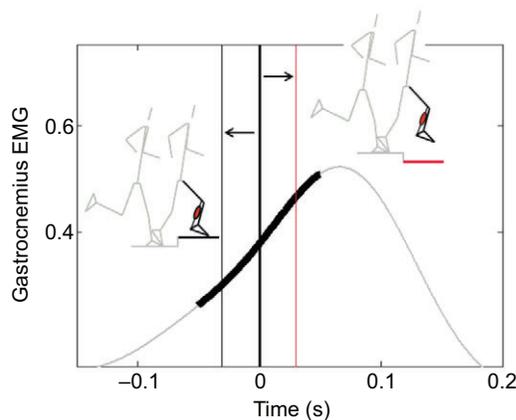


Fig. 5. Normalized gastrocnemius EMG during level running (VL). Muscle activation at touchdown (vertical bold black line, level touchdown; vertical thin black line, elevated touchdown; vertical red line, lowered touchdown) depends on flight time and could be adjusted in a feed-forward manner. The higher the level of support, the shorter the flight time (indicated by the arrow pointing to the left) and the lower the level of support, the longer the flight time (indicated by the arrow pointing to the right). The bold part of the curve illustrates the muscle activation segment while facing different ground levels.

findings of the present study, we expect that the observed decrease in gastrocnemius pre-activation was in fact a combination of a feed-forward time-dependent modulation (Fig. 5) and a visual feedback based adaptation of gastrocnemius activity.

On the basis of the results on running across elevations in ground level, we hypothesized that for drops in ground level, gastrocnemius pre-activation would increase while tibialis pre-activation would remain unaltered. But it would also be conceivable that humans adjust their ankle joint angle by decreasing the pre-activation of one muscle responsible for ankle joint adjustments. Thus, tibialis pre-activation could decrease while gastrocnemius pre-activation remained unaltered. However, our results show that humans increase gastrocnemius and reduce tibialis pre-activation (Fig. 1). To clarify which of the two strategies (gastrocnemius regulation or less pre-activation) is the most effective, further investigation/simulations become necessary.

The functional role of different modulation and adaptation strategies can be interpreted in the context of reduced biomechanical models of hopping and running. While the most reduced models of walking and running – compass gait model and spring mass model – showed that stable walking is possible without the need for any adaptation (Blickhan, 1989; Garcia et al., 1998; Geyer et al., 2006; Goswami et al., 1998; Seyfarth et al., 2002; Srinivasan and Ruina, 2006), some of their offspring models emphasize the benefit of feed-forward timed adaptation of leg characteristics (Birn-Jeffery and Daley, 2012; Blum et al., 2010; Ernst et al., 2012; Karssen et al., 2011) and muscle activity (Haeufle et al., 2010) for the stabilization of locomotion patterns. As our results clearly indicate such a time-dependent feed-forward change in muscle activity in the absence of visual feedback (Fig. 3), we speculate that the functional role of this strategy is to stabilize running with a very simple control strategy.

One simple strategy to adapt the feed-forward pattern to the drop would be to shift the pattern in time by the expected increase in flight time. Interestingly, such a strategy is often assumed in reduced biomechanical models for hopping and running. For example, the

compass gait model, the spring mass model, and most of their derivatives, explicitly set leg angle at touchdown – and in the second case also leg stiffness – to always be the same, independent of the variation in ground level (Blickhan, 1989; Garcia et al., 1998; Geyer et al., 2006; Goswami et al., 1998; Seyfarth et al., 2002; Srinivasan and Ruina, 2006). Later models of similar complexity (also without any explicit muscle dynamics) considered a timed adaptation of leg characteristics and showed the benefit of such feed-forward strategies for the stabilization of walking and running patterns (Birn-Jeffery and Daley, 2012; Blum et al., 2010; Ernst et al., 2012; Karssen et al., 2011). This could be the reason for the modulated feed-forward pattern, which allows adapted pre-activation and thus adapted leg properties at touchdown without any proprioceptive feedback. Simple models, which explicitly consider muscle dynamics, confirmed that either an identical configuration at touchdown, in combination with proprioceptive feedback during ground contact (Geyer et al., 2003; Haeufle et al., 2012), or a feed-forward strategy varying with flight time (Haeufle et al., 2010) allows the stabilization of periodic movements.

All these models predict stable biomechanical movements without any visually guided adaptation of the pre-activation. Our results show that such an adaptation has to be considered in future studies for selected muscles (Fig. 2). Nevertheless, the key feature in muscle pre-activation control seems to be a time-dependent feed-forward strategy. The source of the periodic feed-forward muscle activity could be central pattern generators located in the spinal cord, which have been proven to allow the generation of such trained repetitive patterns in time (Dickinson et al., 2000; Ijspeert, 2008; Prochazka and Yakovenko, 2007). Although proprioceptive feedback cannot be used to prepare for drops in ground level as the perturbation has yet to be perceived, it will influence muscle activity during ground contact.

Muscle activation control during ground contact

Changes in gastrocnemius, vastus and tibialis muscle activation after touchdown become more obvious during running across camouflaged changes than during running across visible changes (Figs 1 and 3). We assume that these changes depend on an exact adjustment of muscle activation at touchdown, as best visualized for gastrocnemius. During running across camouflaged drops of –10 cm, it seems that runners anticipate a drop of about 5–10 cm (Müller et al., 2012a). The absence of the expected contact (CD10) results in increased gastrocnemius activation during ground contact (Fig. 3A). In contrast, if the touchdown is earlier than expected (CL), the gastrocnemius activation decreases during ground contact (Fig. 3A). In contrast to the gastrocnemius, tibialis activation increased after actual touchdown for both camouflaged situations CL and CD10 (Fig. 3E).

A mismatch between the produced and required muscle force at the moment of touchdown has to be adapted by decentralized proprioceptive feedback. Here, different feedback types – force feedback from Golgi tendon sensor organs, length feedback, and velocity feedback from muscle spindles – are conceivable. Simulation studies suggest that a variety of such signals can contribute to – or even generate – stable locomotion movements (Daley et al., 2009; Geyer and Herr, 2010; Geyer et al., 2003; Haeufle et al., 2012; Proctor and Holmes, 2010). As many such signals could contribute to the observed differences in activation, it is not possible to extract their relative contributions from our data. Experimentally, this could only be studied with invasive experiments, for example those of Grey et al. (Grey et al., 2007), who demonstrated the contribution of force-feedback in human walking.

Conclusions

In conclusion, our experiments with human runners negotiating visible or camouflaged steps or holes allow separation of the influence of fixed programmes (feed-forward) and visual feedback while preparing for touchdown. In agreement with predictions from modelling studies, the fixed programme uses the flight time to adapt muscle activity to step height. These adaptations explore system mechanics (Blickhan et al., 2007; Kalveram et al., 2005). In principle, these strategies allow a reduced control effort (Haeufle et al., 2014). Better preparation to touchdown triggered by visual cues or uncertainty (camouflage) is achieved by modifications of these feed-forward strategies. These modifications selectively affect different muscles, indicating a modular role.

MATERIALS AND METHODS

Subjects

Nine male subjects (age, body mass and stature were 24.1 ± 3.3 years, 76.6 ± 10.1 kg and 181.9 ± 7.6 cm, respectively) took part in this study. All of them were physically active participants with no health problems that could affect their performance or behaviour in this study. Informed written consent was obtained from each volunteer. The investigation was approved by the ethics review board of the University of Jena and was in accordance to the Declaration of Helsinki.

Measurements

All subjects were instructed to run along a 17 m runway with two consecutive force plates in its centre (one ground-level force plate at the site of the first contact and one variable-height force plate at the second contact; Kistler, Winterthur, Switzerland). After subjects had run on the unperturbed flat track (VL), the variable-height force plate at the second contact was lowered by –5 cm (VD5) and –10 cm (VD10). Subjects were visually aware of the single step down and had to accomplish 15 runs in a row. After the visible trials, the variable height force plate at the second contact was camouflaged with a non-transparent thin paper and randomly set to an elevation of 0 cm (CL) or –10 cm (CD10). Subjects had to accomplish 21 camouflaged runs (12 CL and nine CD10). On the basis of laboratory conditions and in accordance with the stipulations of the ethics review board of the University of Jena, the setup of the experiment (first: visible trials, second: camouflaged trials) was fixed and not randomized.

From the collected data, we chose all those trials of each subject that were distributed in a narrow range of their preferred running speed achieving steady-state running [where the difference in horizontal velocities measured by markers on spinous processes of the C7 vertebra cervicalis and the L5 vertebrae lumbales during the flight phase prior to the first and second contact was less than 5%; for more experimental details see Müller et al. (Müller et al., 2012a)].

The EMG was triggered by using the Kistler software and hardware, and a bipolar recording was made using Kendall disposable surface electrodes (H93SG Arbo®, Nußdorf/Chiemgau, Germany). All electrodes were placed in the lengthwise direction of the muscle on both legs. The positions of the electrodes were set according to the SENIAM recommendations (Merletti and Hermens, 2000) and placed on the following muscles (Fig. 4): m. gastrocnemius medialis (gastrocnemius), m. tibialis anterior (tibialis) and m. vastus medialis (vastus). All muscles were sampled at 2000 Hz and recorded simultaneously. The electrodes and electrode wires were tied to the shank and thigh with an elastic bandage to prevent dislocation during running.

Data processing

After recording, the EMG signals of the right leg were high-pass filtered with a 20 Hz single pole high-pass filter to remove electrode artefacts, rectified and smoothed with a 30 Hz single pole low-pass filter (Müller et al., 2010; Smith, 1997). The smoothed and rectified EMG was normalized for each subject by the maximum level of activation over all trials (Müller et al., 2010). This procedure corresponds to the one revolution maximum method (Hunter et al., 2002). EMG analysis included a time period extending from 140 ms pre-contact to touchdown (pre-activation), and

another activation phase from touchdown to the end of the ground contact (on average 200 ms) (Müller et al., 2012a). The time course of the EMG was subdivided into segments of 20 ms length, seven during the 140 ms pre-contact period and 10 during the contact. The instant of touchdown and take-off (end of ground contact) was determined from the vertical force data by using a vertical force threshold of 0.02 body weight. Flight time was calculated by subtracting the moment of actual touchdown at (visible or camouflaged) lowered second contact and the moment of take-off one step ahead at first contact (Fig. 4).

To allow a comparison of the trials with visible drops (VD5, VD10) to level running (VL), EMG data for all trials were triggered to actual touchdown (Fig. 1). This way, the overlay of all trials resembles the different state of the muscles before and at ground contact. Additionally, all trials with visible drops were triggered to virtual level touchdown (the instant in time when touchdown would occur at the height of the level contact; dashed horizontal line in Fig. 4), meaning the data were shifted in time to match $t=0.0$ s at the virtual level touchdown (Fig. 2). The virtual level touchdown was calculated by subtracting flight time of VL from flight time of VD5 and VD10 for each subject. This way, the overlay of all trials resembles the different state of the muscles before virtual level touchdown. To compare camouflaged trials in a similar way, EMG data of CD10 were triggered to the virtual level touchdown at the height of the camouflage (Fig. 3).

Statistics

The results are expressed as means \pm s.d. over all subjects separated for ground condition (VL, VD5, VD10, CL and CD10) and muscle (gastrocnemius, tibialis, vastus; SPSS 15.0; SPSS®, Chicago, IL, USA). In order to compare the muscle activation segments, we used repeated measures ANOVA with *post hoc* analysis (Tamhane tests with Bonferroni correction) and ground condition as a factor. We assessed the homogeneity of variances using the Levene test. To determine whether the muscle activation at touchdown varied dependent on flight time, we performed correlations between flight time and pre-activation of muscle. Paired *t*-tests were used to compare flight time and pre-activation at touchdown. The significance level was set at $P < 0.05$.

Acknowledgements

We would like to thank Isabel Kolkka for proof reading an earlier version of the manuscript.

Competing interests

The authors declare no competing or financial interests.

Author contributions

R.M. and R.B. developed the research question and designed the study. R.M. performed the experiments and the data analyses. R.M. and D.F.B.H. interpreted the data and wrote the manuscript.

Funding

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

References

Birn-Jeffery, A. V. and Daley, M. A. (2012). Birds achieve high robustness in uneven terrain through active control of landing conditions. *J. Exp. Biol.* **215**, 2117-2127.

Blickhan, R. (1989). The spring-mass model for running and hopping. *J. Biomech.* **22**, 1217-1227.

Blickhan, R., Seyfarth, A., Geyer, H., Grimmer, S., Wagner, H. and Günther, M. (2007). Intelligence by mechanics. *Philos. Trans. A Math. Phys. Eng. Sci.* **365**, 199-220.

Blum, Y., Lipfert, S. W., Rummel, J. and Seyfarth, A. (2010). Swing leg control in human running. *Bioinspir. Biomim.* **5**, 026006.

Daley, M. A., Righetti, L. and Ljsspeert, A. J. (2009). Modelling the interplay of central pattern generation and sensory feedback in the neuromuscular control of running. *Comp. Biochem. Physiol.* **153A**, S135.

Dickinson, M. H., Farley, C. T., Full, R. J., Koehl, M. A. R., Kram, R. and Lehman, S. (2000). How animals move: an integrative view. *Science* **288**, 100-106.

Ernst, M., Geyer, H. and Blickhan, R. (2012). Extension and customization of self-stability control in compliant legged systems. *Bioinspir. Biomim.* **7**, 046002.

Ernst, M., Götze, M., Müller, R. and Blickhan, R. (2014). Vertical adaptation of the center of mass in human running on uneven ground. *Hum. Mov. Sci.* **38**, 293-304.

Garcia, M., Chatterjee, A., Ruina, A. and Coleman, M. (1998). The simplest walking model: stability, complexity, and scaling. *J. Biomech. Eng.* **120**, 281-288.

Gazendam, M. G. and Hof, A. L. (2007). Averaged EMG profiles in jogging and running at different speeds. *Gait Posture* **25**, 604-614.

Geyer, H. and Herr, H. (2010). A muscle-reflex model that encodes principles of legged mechanics produces human walking dynamics and muscle activities. *IEEE Trans. Neural Syst. Rehabil. Eng.* **18**, 263-273.

Geyer, H., Seyfarth, A. and Blickhan, R. (2003). Positive force feedback in bouncing gaits? *Proc. Biol. Sci.* **270**, 2173-2183.

Geyer, H., Seyfarth, A. and Blickhan, R. (2006). Compliant leg behaviour explains basic dynamics of walking and running. *Proc. Biol. Sci.* **273**, 2861-2867.

Goswami, A., Thuirot, B. and Espiau, B. (1998). A study of the passive gait of a compass-like biped robot: symmetry and chaos. *Int. J. Robot. Res.* **17**, 1282-1301.

Grey, M. J., Nielsen, J. B., Mazzaro, N. and Sinkjaer, T. (2007). Positive force feedback in human walking. *J. Physiol.* **581**, 99-105.

Grimmer, S., Ernst, M., Günther, M. and Blickhan, R. (2008). Running on uneven ground: leg adjustment to vertical steps and self-stability. *J. Exp. Biol.* **211**, 2989-3000.

Guidetti, L., Rivellini, G. and Figura, F. (1996). EMG patterns during running: intra- and inter-individual variability. *J. Electromyogr. Kinesiol.* **6**, 37-48.

Haeufle, D. F. B., Grimmer, S. and Seyfarth, A. (2010). The role of intrinsic muscle properties for stable hopping – stability is achieved by the force-velocity relation. *Bioinspir. Biomim.* **5**, 016004.

Haeufle, D. F. B., Grimmer, S., Kalveram, K. T. and Seyfarth, A. (2012). Integration of intrinsic muscle properties, feed-forward and feedback signals for generating and stabilizing hopping. *J. R. Soc. Interface* **9**, 1458-1469.

Haeufle, D. F. B., Günther, M., Wunner, G. and Schmitt, S. (2014). Quantifying control effort of biological and technical movements: an information-entropy-based approach. *Phys. Rev. E Stat. Nonlin. Soft Matter Phys.* **89**, 012716.

Hunter, A. M., St Clair Gibson, A., Lambert, M. and Noakes, T. D. (2002). Electromyographic (EMG) normalization method for cycle fatigue protocols. *Med. Sci. Sports Exerc.* **34**, 857-861.

Ijspeert, A. J. (2008). Central pattern generators for locomotion control in animals and robots: a review. *Neural Netw.* **21**, 642-653.

Ishikawa, M., Pakaslahti, J. and Komi, P. V. (2007). Medial gastrocnemius muscle behavior during human running and walking. *Gait Posture* **25**, 380-384.

Kalveram, K. T., Schinauer, T., Beirle, S., Richter, S. and Jansen-Osmann, P. (2005). Threading neural feedforward into a mechanical spring: how biology exploits physics in limb control. *Biol. Cybern.* **92**, 229-240.

Karssen, J. G. D., Haberland, M., Wisse, M. and Kim, S. (2011). The optimal swing-leg retraction rate for running. In *Proceedings of the 2011 IEEE International Conference on Robotics and Automation (ICRA)*, pp. 4000-4006. New York, NY: IEEE.

MacKay-Lyons, M. (2002). Central pattern generation of locomotion: a review of the evidence. *Phys. Ther.* **82**, 69-83.

Merletti, R. and Hermens, H. (2000). Introduction to the special issue on the SENIAM European Concerted Action. *J. Electromyogr. Kinesiol.* **10**, 283-286.

Müller, R. and Blickhan, R. (2010). Running on uneven ground: leg adjustments to altered ground level. *Hum. Mov. Sci.* **29**, 578-589.

Müller, R., Grimmer, S. and Blickhan, R. (2010). Running on uneven ground: leg adjustments by muscle pre-activation control. *Hum. Mov. Sci.* **29**, 299-310.

Müller, R., Ernst, M. and Blickhan, R. (2012a). Leg adjustments during running across visible and camouflaged incidental changes in ground level. *J. Exp. Biol.* **215**, 3072-3079.

Müller, R., Siebert, T. and Blickhan, R. (2012b). Muscle preactivation control: simulation of ankle joint adjustments at touchdown during running on uneven ground. *J. Appl. Biomech.* **28**, 718-725.

Nielsen, J. B. (2003). How we walk: central control of muscle activity during human walking. *Neuroscientist* **9**, 195-204.

Pearson, K. G. (2004). Generating the walking gait: role of sensory feedback. *Prog. Brain Res.* **143**, 123-129.

Pearson, K. G. and Collins, D. F. (1993). Reversal of the influence of group Ib afferents from plantaris on activity in medial gastrocnemius muscle during locomotor activity. *J. Neurophysiol.* **70**, 1009-1017.

Prochazka, A. and Yakovenko, S. (2007). Predictive and reactive tuning of the locomotor CPG. *Integr. Comp. Biol.* **47**, 474-481.

Proctor, J. and Holmes, P. (2010). Reflexes and preflexes: on the role of sensory feedback on rhythmic patterns in insect locomotion. *Biol. Cybern.* **102**, 513-531.

Rybak, I. A., Ivashko, D. G., Prilutsky, B. I., Lewis, M. A. and Chapin, J. K. (2002). Modeling neural control of locomotion: integration of reflex circuits with CPG. *Artificial Neural Networks – Iccann 2002* **2415**, 99-104.

Seyfarth, A., Geyer, H., Günther, M. and Blickhan, R. (2002). A movement criterion for running. *J. Biomech.* **35**, 649-655.

Smith, S. W. (1997). *The Scientist and Engineer's Guide to Digital Signal Processing*. San Diego, CA: California Technical Publishing.

Srinivasan, M. and Ruina, A. (2006). Computer optimization of a minimal biped model discovers walking and running. *Nature* **439**, 72-75.