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RESEARCH ARTICLE

Leg adjustments during running across visible and camouflaged incidental changes in ground level

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SUMMARY

During running in a natural environment, humans must routinely negotiate varied and unpredictable changes in ground level. To prevent a fall, changes in ground level, especially those that are invisible, require a quick response of the movement system within a short time. For 11 subjects we investigated two consecutive contacts during running across visible (drop of 0, 5 and 10 cm) and camouflaged (drop of 0 and 10 cm) changes in ground level. For both situations, we found significant variances in their leg parameters and ground reaction forces (GRFs) during the perturbed second contact but also one step ahead, in the unperturbed first contact. At visible first contact, humans linearly adapt their GRF to lower and smooth their centre of mass. During the camouflaged situation, the GRF also decreased, but it seems that the runners anticipate a drop of approximately 5–10 cm. The GRF increased with drop height during the visible perturbed second contact. At the camouflaged second contact, GRFs differed noticeably from the observed reaction when crossing a similar visible drop, whereas the contact time decreased and the initial impact peak increased. This increased impact can be interpreted as a purely mechanical contribution to cope with the event. Furthermore, we observed an increased angle of attack and leg length with drop height for both situations. This is in accordance with results observed in birds running over a track with an unexpected drop, and suggests that adaptations in swing leg retraction form part of the strategy for running across uneven ground.

Key words: biomechanics, human locomotion, spring-mass model.

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INTRODUCTION

When humans run in a natural environment, ground conditions are changing continuously with respect to compliance (e.g. stiff concrete *versus* compliant forest trail), slip (e.g. asphalt partially covered with snow) and level (e.g. uneven pavement, roots). These changes can be visible or camouflaged, e.g. running across a meadow with high grass camouflaging drops and bumps, or running across a field covered with snow and camouflaged ice pits. Nevertheless, it seems that human runners handle such irregularities with ease. Recent studies have shown that humans adapt their leg properties to changing ground conditions and that these adaptations take place within the descriptive realm of a spring-mass model (Ferris et al., 1999; Grimmer et al., 2008; Kerdok et al., 2002; Müller and Blickhan, 2010).

The dynamics of the spring-mass model (Blickhan, 1989; McMahon and Cheng, 1990) consist of a massless spring and a point mass that represents the body. Its dynamics is determined merely by the parameters mass (m), stiffness (k), leg length at touchdown (l_{TD}), angle of attack (α_{TD}; leg orientation at touchdown) and the vector of the touchdown velocity of the mass. In spring-mass running across bumpy ground, the simplest strategy is running with a fixed angle of attack and constant leg stiffness (Seyfarth et al., 2002). For this strategy there exists a small range of leg stiffness values and corresponding angles of attack in which the spring-mass model is able to run in a self-stable manner (Geyer et al., 2005; Seyfarth et al., 2002). In the case of self-stability after a perturbation (e.g. small steps up or down), the mechanics alone drives the system back to a fixed point. Neither model parameters nor the angle of attack must be adjusted. Seyfarth et al. (Seyfarth et al., 2003) also showed that a leg retraction that changes the leg orientation (α) during flight can enhance the tolerance to ground disturbances significantly. Including more than one leg parameter (α, k and l) in the flight phase adaptation process enables further self-stable solutions to be exploited (Blum et al., 2010). Thus, the number of possible leg adjustments that stabilize running after a perturbation increases (in biological as well as in technical systems).

There is experimental evidence that when humans encounter sudden changes in substrate stiffness or damping (Farley et al., 1998; Ferris et al., 1999; Kerdok et al., 2002; Moritz et al., 2004), or uneven ground with changes in terrain height (Grimmer et al., 2008; Müller and Blickhan, 2010), they adapt their leg properties (leg stiffness, orientation and length) to the altered situation. This adaptation process seems to exploit the self-stabilizing properties of the spring-mass model and passively helps to stabilize the locomotion. The identified parameters were found to be in areas in which the system behaves in a self-stable manner. Recent records of muscle activation during running across uneven ground suggest that the observed leg stiffness adjustments (during ground contact) are introduced by an altered pre-activation pattern (during flight before ground contact) of the m. gastrocnemius medialis (Müller et al., 2010). The visual perception of the perturbation allows an adaptation of the motor program prior to the perturbation, overlapping a purely passive response. Such a visually guided pre-adaptation is not possible in experiments where the changes in ground level are invisible because of camouflage and occur by chance. Experiments on humans walking along a walkway with an unexpected loss of ground support

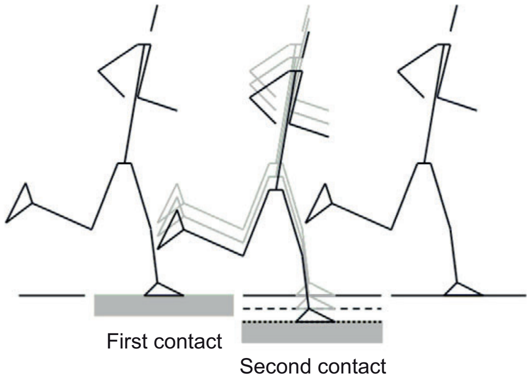

Fig. 1. Side view of the instrumented runway with two consecutive force plates in its centre. The second force plate (second contact) was set at three different elevations: 0 cm [solid line; visible level (VL)], –5 cm [dashed line; visible drop of 5 cm (VD5)] and –10 cm [dotted line; visible drop of 10 cm (VD10)].

have shown that in the unexpected lowered contact the absence of expected heel contact triggered responses in the ipsilateral anti-gravity muscles and contralateral flexor muscles (Shinya et al., 2009; van der Linden et al., 2007), and that after touchdown humans reset the gait rhythm to permit continued walking by delaying the subsequent take-off (Shinya et al., 2009; van Dieën et al., 2007). Compared with walking, during running the duration of the stance phase is shorter and thus adjustments may be necessary prior to contact. Up to now, results of experiments on running over a track with an unexpected drop are available for birds only (Daley and Biewener, 2006; Daley et al., 2006). In these experiments, the delay in ground contact resulted in a steeper but more variable angle of attack. This effect could be attributed to leg retraction. Although leg stiffness varied dramatically, it is not clear how this leg stiffness adjustment contributes to match the varying ground. If humans and birds use similar leg adaptation strategies for unexpected drops, we expect to find a steeper angle of attack, similar to running down a visible step (Müller and Blickhan, 2010). However, it is not known how human runners react if they encounter an unexpected drop and whether they alter their strategies compared with running on uneven ground with visible ground level changes.

In our investigation, we focused on leg adjustments while running on ground with visible and camouflaged changes in ground level. We addressed three main questions: (1) is running across visible changes in ground level different from running across camouflaged changes; (2) how do human runners adjust their leg stiffness, length and angle of attack, and in which phase of running do the adaptations occur; and (3) do humans use a control strategy that can be described with the conservative spring-mass model?

MATERIALS AND METHODS

Subjects

Eleven subjects (24.4±3.4 years old, 73.9±7.0 kg, 179.5±7.3 cm height) took part in this study. All of them were physically active participants with a high performance level in their sport and with no health problems that could have affected their performance or behaviour in this study. Informed written consent was obtained from each volunteer. The experiment was approved by the local ethics committee and was in accordance with the Declaration of Helsinki.

Measurements

All subjects were instructed to run along a 17 m runway with two consecutive force plates in its centre. The ground reaction forces (GRFs) were sampled at 2000 Hz by using one ground-level force plate at the site of the first contact (9281B, Kistler, Winterthur, Switzerland) and one variable-height force plate at the second contact (9287BA, Kistler) within the distance of one step (step lengths from 1.40 to 2.30 m).

After running on the unperturbed flat track (VL, visible level), in a first setup the variable-height force plate (second contact, Fig. 1) was set down to elevations of –5 cm (VD5, visible drop of 5 cm) and –10 cm (VD10, visible drop of 10 cm). Subjects were visually aware of the single step down and were allowed to perform several (usually two to three) practice trials running along the runway with a constant velocity. In each of these expected conditions, the subjects had to accomplish at least 15 runs in a row. After the visible trials, in a second setup, the variable-height force plate (second contact, Fig. 2) was camouflaged with non-transparent paper and randomly set to an elevation of 0 cm (CL, camouflaged level) or –10 cm (CD10, camouflaged drop of 10 cm). Subjects had to accomplish at least 21 camouflaged runs (12× CL and 9× CD10). A trial (visible or camouflaged) was successful when the subjects ran across the whole track, and both left (first contact) and right (second contact) touchdowns were centered on the corresponding force platforms.

All trials were recorded with eight cameras (240 Hz) using a three-dimensional infrared system (MCU 1000, Qualisys, Gothenburg, Sweden) and synchronized using the trigger of the Kistler software and hardware. Reflective joint markers (19 mm) were placed on the ball of the foot, the lateral malleolus, the epicondylus lateralis and the trochanter major on both sides of the body as well as on L5 and C7 proc. spinosus (Perry, 1992).

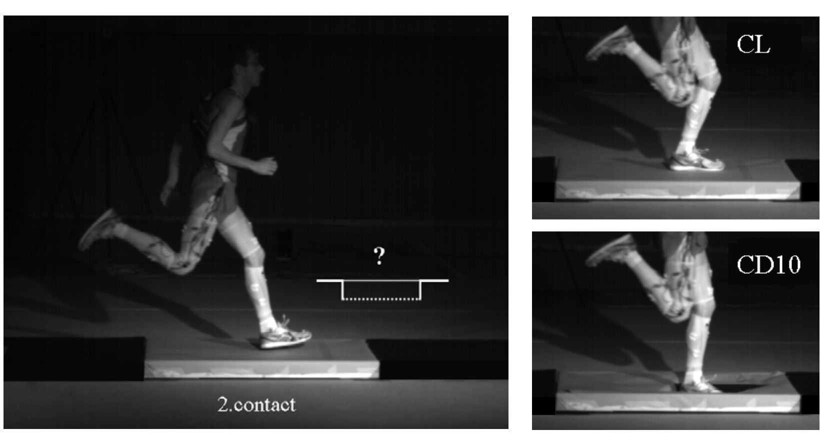

Fig. 2. Side view of the runway with camouflaged second contact. The force plate on the second contact was set at two different elevations: 0 cm [fine solid line; camouflaged level (CL), upper right] and –10 cm [dotted line; camouflaged drop of 10 cm (CD10), lower right].

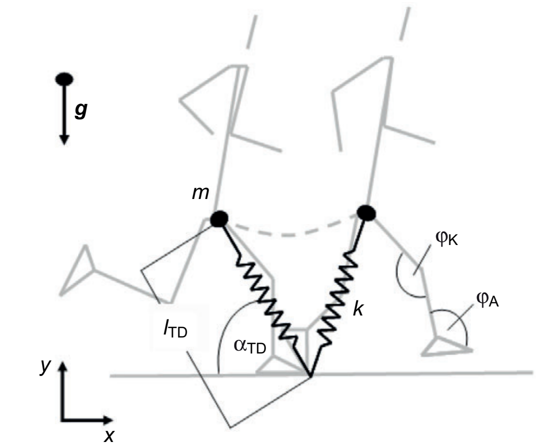

Fig. 3. The spring-mass model consists of a massless spring and a point mass *m* that represents the body. It is described merely by the parameters stiffness *k*, angle of attack α_{TD} (leg orientation at touchdown) and leg length l_{TD}. According to the spring-mass model, we defined the leg as the distance between hip and toe marker. α_{TD} is measured clockwise with respect to the negative *x*-axis. We calculated the inner angles of the knee (φ_K) and ankle (φ_A) joint. ***g***, gravitational acceleration.

Data processing

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 at L5 and C7 during the flight phase prior to the first and second contact was less than 5%). This resulted in 11 trials on average (range=7–15 trials) per experimental setup and subject.

The raw kinematic data were filtered with a third-order low-pass Butterworth filter (Winter, 2005) at a 50 Hz cut-off frequency. The distance between the hip and the ball of the foot marker was defined as leg length (l) of the stance leg (Fig. 3). Leg stiffness (k) was calculated as the ratio between the GRF at midstance (F_{mid}; where the horizontal GRF is zero) and the maximum leg compression, $\Delta l_{max}=l_{TD}-\min(l_{TD:TO})$ (where TD is touchdown and TO is take-off). In contrast to previous studies (Grimmer et al., 2008; Müller and Blickhan, 2010), we used F_{mid} rather than the maximum value of GRF (F_{max}) to calculate leg stiffness. During running across incidental camouflaged changes in ground level, the impact peak (F_{max}) may exceed F_{mid}, which would result in a miscalculation of k. If we assume that the leg can be simplified by a linear spring, then the time of the maximum leg compression, and therefore maximum leg force, is during midstance (because the model holds $F_{mid}=F_{max}$).

To compare the results of each subject, we used all parameters in dimensionless form (Blickhan, 1989; Geyer et al., 2005). The GRF was normalized to the subject mass and gravitation constant [body weight (BW)]. The leg length ($\tilde{l}=l/l_{TD}$) was normalized to the initial leg length at TD (l_{TD}). Both result in dimensionless stiffness, $\tilde{k}$.

The results are expressed as means ± s.d. over all subjects and parameters. We used a one-way ANOVA (SPSS 15.0, IBM, Armonk, NY, USA) to compare normalized global (GRF, leg length, leg stiffness, angle of attack) and local parameters (knee and ankle angle) at the first and second contact. For the ANOVA and the Bonferroni *post hoc* analysis, a *P*-value <0.05 was considered to be statistically significant.

RESULTS

Running across visible drops

During running with visible perturbations, the GRF at the first contact (step prior to the perturbation) diminished (Fig. 4A). Between

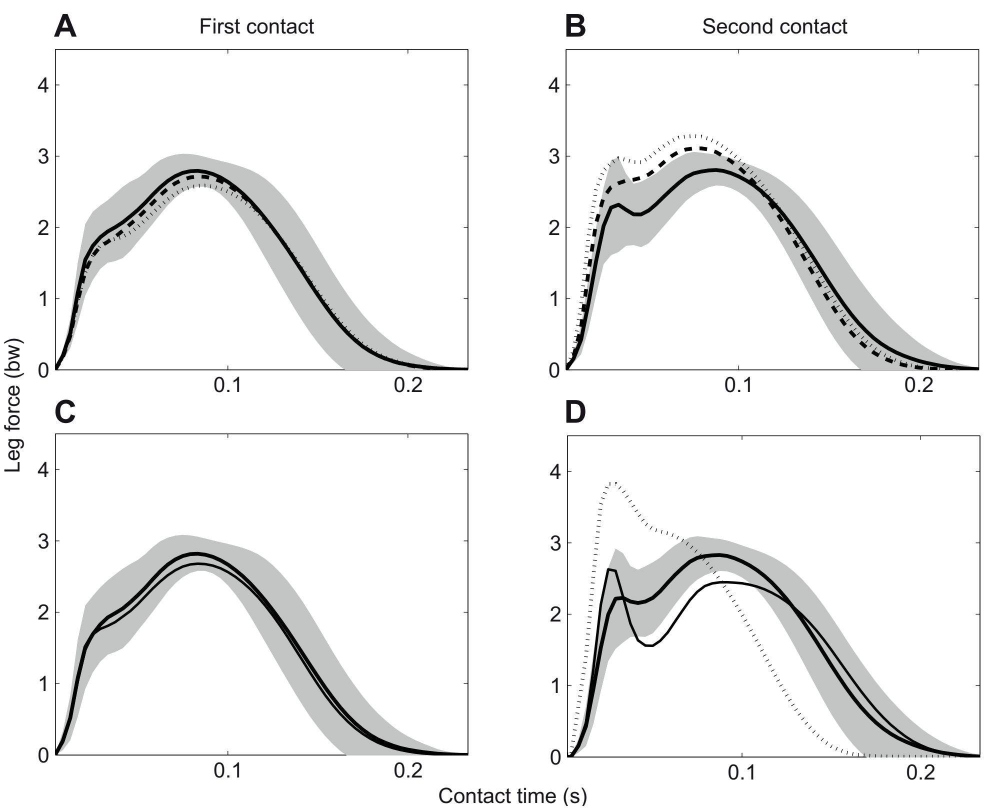

Fig. 4. Leg force during stance phase of two subsequent contacts: (A,B) visible drop and (C,D) camouflaged drop. Solid lines represent the mean of visible level running (VL; *N*=105) and the grey shaded areas represent the standard deviation of this reference run. (A) In preparation for the following step down, the peak ground reaction force (GRF) slightly decreased during the first contact. (B) During the second contact, the peak GRF increased with drop height. (A,B) Dashed lines, mean during VD5 (visible 5 cm down; *N*=115); dotted lines, mean during VD10 (visible 10 cm down; *N*=124). (C) During the first contact, in preparation for the following camouflaged contact, the peak GRF decreased slightly and there were no differences between the incident camouflaged level ground (CL) and the camouflaged 10 cm drop (CD10). (D) During the camouflaged second contact, the peak GRF decreased for CL and increased during CD10. In both situations the initial impact peak increased compared with the control. (C,D) Fine solid lines, mean of CL (*N*=102); dotted lines, mean of CL10 (*N*=71). Note that the values of the GRFs at the impact peak or at midstance are not equivalent to results in Table 1. The latter are obtained as means of the corresponding values for the individual tracings.

Table 1. Parameters of global leg behaviour

	Contact	Reference	Visible		Camouflaged	
		VL	VD5	VD10	CL	CD10
F_{max} (BW)	1	2.92±0.22	**2.82±0.18**	**2.67±0.20**	**2.76±0.20**	**2.74±0.26**
	2	2.92±0.21	**3.22±0.26**	**3.53±0.35**	**3.35±0.74**	**4.45±0.57**
F_{mid} (BW)	1	2.89±0.21	**2.78±0.20**	**2.63±0.24**	**2.73±0.20**	**2.73±0.24**
	2	2.80±0.20	**3.05±0.22**	**3.17±0.26**	**2.60±0.24**	**3.14±0.41**
$t_{contact}$ (s)	1	0.18±0.02	0.19±0.02	0.19±0.02	0.18±0.02	0.18±0.02
	2	0.19±0.02	**0.18±0.02**	**0.18±0.02**	**0.20±0.02**	**0.15±0.02**
$\tilde{l}_{TD}$	1	1.00±0.01	1.00±0.01	1.00±0.01	1.00±0.02	1.00±0.02
	2	1.00±0.01	**1.02±0.02**	**1.03±0.02**	**1.01±0.03**	**1.04±0.03**
$\tilde{l}_{TO}$	1	1.05±0.04	1.05±0.04	1.04±0.04	1.04±0.04	1.04±0.04
	2	1.05±0.03	1.06±0.03	1.06±0.03	1.04±0.04	1.05±0.04
$\Delta\tilde{l}_{max}$	1	0.08±0.03	0.08±0.03	0.09±0.03	0.08±0.03	0.08±0.03
	2	0.08±0.03	0.09±0.03	**0.09±0.03**	**0.11±0.03**	0.08±0.02
$\tilde{k}$	1	39.5±14.7	38.1±12.9	**34.4±11.7**	35.1±10.4	35.5±11.0
	2	39.5±14.4	38.7±12.0	37.3±10.9	**26.5±8.6**	40.0±12.3
α_{TD} (deg)	1	60.0±3.4	60.4±3.6	60.5±3.4	59.9±3.7	60.0±3.4
	2	56.8±3.1	**59.5±2.9**	**59.8±3.6**	**53.3±3.2**	**65.9±3.1**
α_{TO} (deg)	1	114.6±2.3	**115.4±2.4**	**116.8±2.1**	**116.2±2.0**	**115.9±2.2**
	2	113.3±2.3	113.0±2.0	**112.2±1.8**	**112.1±2.7**	113.5±2.5
N		105	115	124	102	71

VL, visible level; VD5, visible drop of 5 cm; VD10, visible drop of 10 cm; CL, camouflaged level; CL10, camouflaged drop of 10 cm.

Data are means ± s.d. across all subjects for investigated global parameters [peak GRF (F_{max}), GRF at midstance (F_{mid}), contact time ($t_{contact}$), leg length at touchdown ($\tilde{l}_{TD}$), leg length at take-off ($\tilde{l}_{TO}$), leg compression ($\Delta\tilde{l}_{max}$), leg stiffness ($\tilde{k}$), leg orientation at touchdown (α_{TD}), and leg orientation at take-off (α_{TO})] separated for the two consecutive contacts.

N, number of successful trials.

Bold values indicate significant difference from the reference, running across visible level ground (P<0.05).

VL (2.92±0.22 BW) and VD5 (2.82±0.18 BW; P<0.05), the peak GRF (F_{max}) diminished during the first contact by approximately 0.10 BW and by approximately 0.25 BW between VL and VD10 (2.67±0.20 BW; P<0.05; Table 1). Furthermore, we observed a nearly unaffected leg compression $\Delta\tilde{l}_{max}$ during first contact (Table 1). The normalized leg stiffness $\tilde{k}$ remained almost constant during VD5 and decreased by approximately 13% during VD10 (P<0.05; Table 1).

During the perturbed second contact, the GRF increased. Here, the changes are more obvious than during the first contact (Fig. 4B). The peak GRF rose by approximately 0.30 BW between VL (2.92±0.21 BW) and VD5 (3.22±0.26 BW; P<0.05) and by approximately 0.61 BW between VL and VD5 (3.53±0.35 BW; P<0.05). Furthermore, we observed a significantly elongated leg at touchdown, whereas leg compression and normalized leg stiffness remained almost constant (Table 1). The observed 2 cm (VD5) and 3 cm (VD10) longer leg at touchdown was achieved by an ankle joint φ_A that was 4 deg (VD5) and 6 deg (VD10) more extended (Fig. 5A, Table 2).

The runners also adapted the angle of attack α_{TD} (Table 1). It remained almost constant at the first contact and increased significantly at the second contact with respect to level ground (VL, 56.8 deg, VD5, 59.5 deg, P<0.05; VD10, 59.8 deg, P<0.05).

Running across a camouflaged incidental drop

During running with camouflaged perturbations, the first contact GRF (step prior to the perturbation) diminished more than during the visible 5 cm lowered contact but less than during the visible 10 cm drops (Fig. 4C). Between the visible (VL) and the camouflaged level contact (CL; 2.76±0.20 BW), the peak GRF diminished by approximately 0.16 BW (P<0.05), and decreased by approximately 0.18 BW between VL and the camouflaged 10 cm lowered contact (CD10; 2.74±0.26 BW; P<0.05; Table 1). Furthermore, we observed a nearly unaffected leg compression Δl_{max} during the first contact (Table 1). The decrease in the GRF together with the unaffected leg compression results in a decreased, but not significantly, normalized leg stiffness $\tilde{k}$ (~9%; Table 1).

During the perturbed second contact, the initial impact peak increased and the changes in GRF were obvious (Fig. 4D). The amplitude of the impact peak rose by approximately 0.43 BW between VL and CL (3.35±0.74 BW; P<0.05) and by approximately 1.53 BW between VL and CD10 (4.45±0.57 BW; P<0.05). Note that because of individual time delays the mean peak amplitude is higher than the peak value of the mean force–time tracings. We observed a 3 cm increase in leg compression $\Delta\tilde{l}_{max}$ during the camouflaged level contact (CL, P<0.05), whereas leg compression remained almost unaffected during the camouflaged lowered contact (CD10, Table 1). The normalized leg stiffness $\tilde{k}$ decreased by approximately 33% during CL (P<0.05) and remained almost unaffected during CD10 (Table 1). Note that k was calculated by F_{mid} and not F_{max} (Ferris et al., 1998; Seyfarth et al., 2002). This is consistent with the spring-mass model (Fig. 3) and takes into account the fact that the quasi-elastic maximum (active peak) is in some situations surpassed by the impact (passive) peak GRF. F_{max} denotes the maximum value independent of the instant of occurrence (Fig. 4D, Table 1). Furthermore, we observed a 4-cm-elongated leg on the camouflaged lowered contact (CD10, P<0.05; Table 1). Although the knee joint φ_K was 7 deg more flexed, this leg elongation was achieved by an ankle joint φ_A that was 6 deg more extended (Fig. 5C,D, Table 2).

The runners also showed adaptations in the angle of attack α_{TD} for the different track types (Table 1). The angle of attack remained almost unaffected at touchdown of the first contact (Table 1). At second contact, the angle of attack decreased from 56.8 deg (VL) to 53.3 deg during camouflaged level running (CL; P<0.05) and increased from 56.8 to 65.9 deg during camouflaged lowered running (CD10; P<0.05).

DISCUSSION

During running on surfaces with visible and camouflaged incidental changes in ground level, human runners adapt their leg and joint

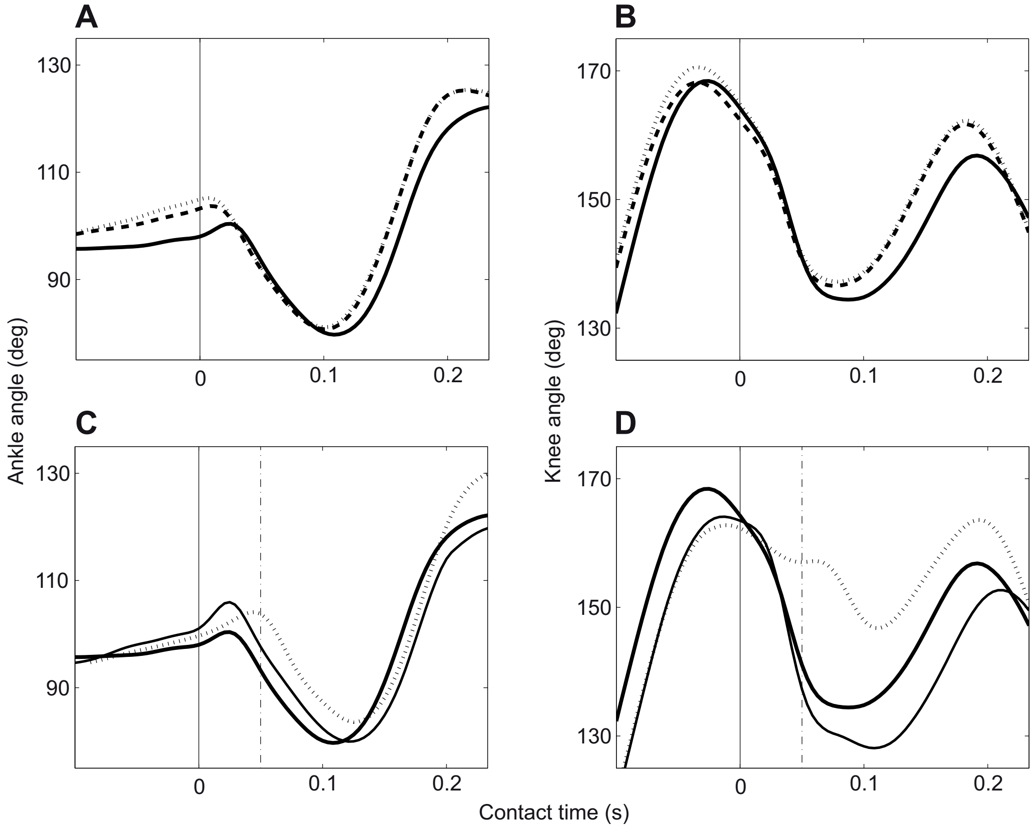

Fig. 5. Ankle and knee joint angle during stance phase of two subsequent contacts: (A,B) visible drop and (C,D) camouflaged drop. The solid line represents the mean of visible level running (VL; N=124). The beginning of the ground contact [touchdown (TD)] is marked by the vertical line. (A,B) dashed lines, mean during VD5 (visible 5 cm down; N=116); dotted lines, mean during VD10 (visible 10 cm down; N=117). Primarily, the ankle joint adapts to the visible disturbance. For detailed values see Table 2. (C,D) Fine solid lines, mean during CL (camouflaged level; N=96); dotted lines, mean during CD10 (camouflaged 10 cm down; N=73). The vertical solid line represents the TD of VL and CL; the vertical dashed line represents the TD of CD10. Both ankle and knee adapt to the camouflaged disturbance. For detailed values see Table 2.

parameters (k, l, α and φ) and the GRF. For both situations (visible and camouflaged), we found significant changes in the perturbed second contact but also in the previous first contact. Furthermore, we observed different control strategies depending on the situation.

Leg adjustments to visible ground changes

When human runners become aware of a perturbation in ground level, they adjust their leg parameters to the visually estimated requirements. We observed these leg adjustments not only during the perturbed contact but also during the previous (first) contact. During the first contact, the leg stiffness decreased by approximately 4% for the 5 cm lowered contact and by approximately 13% for the 10 cm lowered contact (Table 1). This decreasing leg stiffness corresponds to a decreasing leg force and an almost unaffected leg compression accompanied by an increasing drop height of the next step. Furthermore, this is in accordance with results from a similar experiment on humans running down a step lowered permanently by 10 cm, where leg stiffness and GRF diminished by approximately the same amount (Müller and Blickhan, 2010). Extrapolating this to running up steps, an increase in stiffness would be expected. This

Table 2. Parameters of local leg behaviour

		Reference	Visible		Camouflaged	
	Contact	VL	VD5	VD10	CL	CD10
$\varphi_{K,TD}$ (deg)	1	158±5	157±7	157±7	157±6	156±6
	2	164±7	162±7	165±6	164±7	**157±5**
$\varphi_{K,TO}$ (deg)	1	166±6	165±7	**163±7**	**162±8**	**162±8**
	2	160±7	**165±7**	**167±7**	**155±8**	**167±7**
$\varphi_{A,TD}$ (deg)	1	97±10	96±11	95±14	95±11	95±11
	2	98±12	**102±13**	**104±14**	101±11	**104±9**
$\varphi_{A,TO}$ (deg)	1	119±6	118±6	**116±7**	**115±6**	**114±7**
	2	118±7	119±7	120±7	**114±7**	120±7
N		124	116	117	96	73

Data are means ± s.d. across all subjects for joint angles [knee (φ_K) and ankle (φ_A) joint angle at touchdown and take-off] for the two consecutive contacts.
N, number of successful trials.
Bold values indicate significant difference from the reference, running across visible level ground (P<0.05).

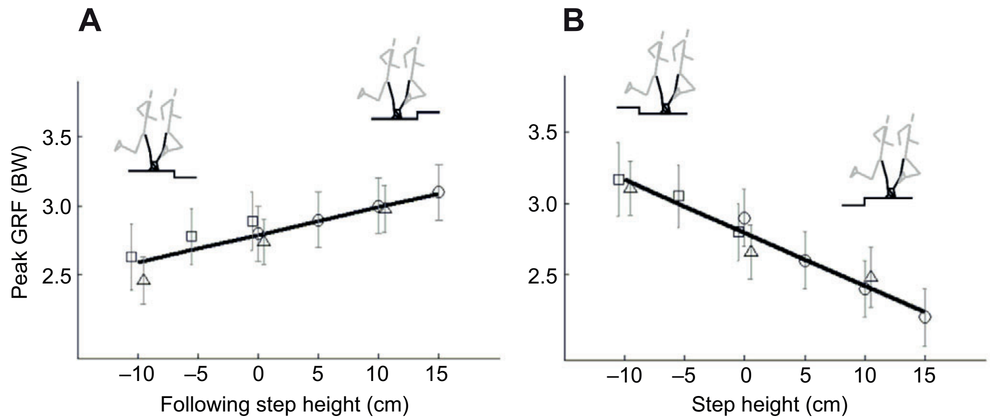

Fig. 6. (A) During running on visible uneven ground, humans show a nearly linear tendency in preparation for a disturbance with respect to the GRF. The peak GRF increased with increasing step height and decreased with increasing drop height of the following step. The regression line (y=0.10x+2.46) represents the data from all three experiments. (B) The tendency we found in the GRF of the previous contact is altered during the perturbed contact. The peak GRF decreased with increasing step height and increased with increasing drop height. The regression line (y=–0.19x+3.35) represents the data from all three experiments. For both A and B, squares represent data from the present study (VL, VD5, VD10), circles represent data from Grimmer et al. (Grimmer et al., 2008) and triangles represent data from Müller and Blickhan (Müller and Blickhan, 2010).

is not the case. In contrast, for a single step up or running across a hump, leg stiffness was unaffected (Grimmer et al., 2008; Müller and Blickhan, 2010). However, the authors showed that the GRF increased with increasing step height of the next step. Thus, during running on visible uneven ground, humans generally show a nearly linear tendency with respect to the GRF in preparation of a disturbance (Fig. 6A). Furthermore, a similar tendency was observed during uphill and downhill walking: uphill walking was characterized by a greater peak propulsive GRF and downhill walking by smaller propulsive peaks (Franz et al., 2011; Kuster et al., 1995; Lay et al., 2006). Both (increased GRF during running and greater propulsive peaks during walking or decreased GRF during running and smaller propulsive peaks during walking) may apply to lift or lower their centre of mass (COM) kinematics (see below).

The tendency we found in the GRF of the first contact is altered during the perturbed second contact (Fig. 6B). Although the GRF increased with drop height during the perturbed contact, the leg stiffness remained almost constant because of slightly increased leg compression. This is in contrast to the contact on a single step up, where runners simultaneously reduce their leg stiffness and GRF with increasing step height (Grimmer et al., 2008). In the same study, Grimmer et al. found an adaptation in the angle of attack and leg length at touchdown. This is in accordance with our findings and with those of Müller and Blickhan (Müller and Blickhan, 2010). Thus, the angle of attack and leg length at touchdown decreased with step height and increased with drop height at touchdown of the perturbed contact. Such adaptations in α_{TD} and l_{TD} could not be found in the previous contact, whether for a step down or up.

We also found a significantly elongated leg at touchdown in the lowered contact, which is achieved by a more extended ankle joint, whereas the knee joint remains constant. When humans run up a single or a permanent step, they reduce their leg length. Here, in contrast to running down, both leg joints (knee and ankle joint) contribute to the adaptation (Grimmer et al., 2008; Müller and Blickhan, 2010). The influence of the ankle joint on an effective shortening of the leg with increasing step height is limited by the leg geometry (heel contact). A further shortening of the leg can only be achieved by bending the knee further. For leg elongation, the limiting role of the two adjusted joints is reversed. An almost extended knee joint cannot contribute significantly to further leg elongation. In addition, human runners avoid excessive knee extension, as this increases joint loads at touchdown and thus the injury potential (Derrick, 2004; Thomas and Derrick, 2003).

Leg adjustments to camouflaged incidental ground changes

When encountering camouflaged incidental changes of the ground level, human runners use adaptations that are principally similar, but different in detail to those used while crossing visible perturbations. They adapt their leg and joint parameters (k, l, α and φ) and the GRF during both the previous contact and the camouflaged and incidental perturbed contact [level (CL) or 10 cm drop (CD10)]. During the first contact, the leg stiffness decreased by approximately 9% (Table 1). This decrease comes along with a reduced leg force and an almost unaffected leg compression. Both leg stiffness and GRF decreased more than during the previous first contact before the visible 5 cm drop (VD5) but less than during the contact before the visible 10 cm drop (VD10). This lowered GRF (integral) and a nearly constant contact time result in a decrease in the COM velocity and a lowered COM height before the camouflaged second contact compared with the reference (VL). Furthermore, differences between CL and CD10 in all investigated leg parameters could not be observed. This indicates that the participants neither knew nor speculated which changes in ground level would actually occur. They used a compromise, which primarily helped them to cope with the surprising drop but also helped them avoid having to adjust poorly for the incident level situation.

At the camouflaged second contact (CL, CD10), the leg parameters and GRFs differed from the reference (VL) as well as from the observed reaction when crossing a similar, visible drop (VD10). The changes in the GRF pattern are obvious. The initial impact peak increased significantly in both situations (compared with VL and VD10), whereas the GRF at midstance decreased during CL (compared with VL) and CD10 (compared with VD10). It appears that most runners successfully adapt to a visibly changing environment by maintaining impact severity below a threshold level and thus optimize their performance and injury potential (Derrick, 2004; Thomas and Derrick, 2003).

Runners encountering camouflaged incident drops are able to cope with the situation but at the cost of a reduced performance (e.g. losses inherent to impacts, increased muscle recruitment) and an increased risk (shock transmission). Such an increased impact peak has also been observed in walkers hitting a support surface at an unexpected height (van der Linden et al., 2009). The impact phase during walking is sometimes characterized by an early 'transient' loading peak. This transient peak occurred more frequently when subjects were unaware of the level of the support surface and was related to shock absorption at foot contact and to a mismatch between the produced and, according to the authors, required muscle force at the moment of impact (van der Linden et al., 2009).

Furthermore, we observed 33% decreased leg stiffness and 6% decreased angle of attack at CL (compared with VL). If we take into account the lowered COM height of the previous flight phase (see above), then running on the camouflaged level (CL) ground can be interpreted as running on a step up, for which Grimmer et al. (Grimmer et al., 2008) reported similar tendencies (for a step of +15 cm: –27% $\tilde{k}_{leg}$ and –9% α_{TD} decrease). In contrast, for running on the incidental 10 cm drop (CD10), leg stiffness increased negligibly and the angle of attack increased significantly by approximately 16% (compared with VL). The same result was observed in $\tilde{k}$ on a visible 10 cm drop (VD10), but the adaptation of the angle of attack α_{TD} was considerably larger. This is in accordance with the results observed in birds running over a track with an unexpected drop (Daley and Biewener, 2006; Daley et al., 2006), and suggests that adaptations in the swing leg retraction are part of the strategies of running across uneven ground. However, it may be largely offset in the case of a visible drop by other adaptations such as the level of the COM.

When walking down a visible step of 10 cm, humans control their forward horizontal and angular momentum by increasing step length (van Dieën et al., 2007). In contrast to such an expected situation, the time between expected and actual ground contact in unexpected stepping down appears to be too short to substantially adjust the movement of the leading leg [according to van Dieën et al. (van Dieën et al., 2007) and Shinya et al. (Shinya et al., 2009)]. This is even more valid during running. In both walking and running (Table 1, CD10), the orientation of the leg in the camouflaged situation was steeper than in the case of visible steps.

Control strategies depend on the situation

Running on uneven ground with expected, visible ground level changes is characterized by a decrease of k, α_{TD} and l_{TD} on elevated contacts and by an increase of α_{TD} and l_{TD} on lowered contacts. But human runners do not rely only on adaptations during the perturbed step. They prepare one step ahead. They adapt their leg force to lift or lower their COM. This strategy smooths COM kinematics (Blickhan et al., 2007). During running on uneven ground with incident camouflaged changes (level or 10 cm drop), the GRF during the previous contact decreased. It seems that the runners anticipate a drop of approximately 5–10 cm. In the case of an earlier contact (decreased flight phase, CL), they used leg parameters observed during running up to an expected, visible elevation. However, when they hit the ground later (increased flight phase, CD10), they used leg parameters observed in running down to an expected, visible elevation.

These strategies diminish risks and costs compared with unadapted strategies; however, they entail higher risks and costs than those possible when the subjects are able to roughly estimate the height of the perturbation and to prepare adequately. The increased impact can be interpreted as a pure mechanical contribution to cope with the event (Günther et al., 2003; Seyfarth et al., 1999). The passive impact increases the impulse (at the cost of the risk of injury). The measured parameters determining the point of operation of the spring-mass system (l_{TD}, α_{TD} and k) support for the camouflaged drop the employment of a k–α strategy in which the leg is retracted during the swing and stiffness increases with falling time (Ernst et al., 2009). Based on numerical simulations, we assume that this should be sufficient to stabilize running (Ernst et al., 2012). The fact that the system resorts to the use of impacts may point either to shortcomings of the pure compliant strategy (e.g. economy, speed) or to limitations of the muscle–skeletal system (e.g. force capacity).

LIST OF SYMBOLS AND ABBREVIATIONS

BW	body weight
CD10	camouflaged drop of 10 cm
CL	camouflaged level
COM	centre of mass
F_{max}	peak ground reaction force
F_{mid}	ground reaction force at midstance
$\boldsymbol{g}$	gravitational acceleration
GRF	ground reaction force
$\tilde{k}$	dimensionless leg stiffness
k	leg stiffness
l	leg length, distance between the hip and the ball of the foot marker
l_{TD}	leg length at touchdown
m	body mass
TD	touchdown, start of contact
TO	take-off, end of contact
VD10	visible drop of 10 cm
VD5	visible drop of 5 cm
VL	visible level
α	leg orientation
α_{TD}	angle of attack
φ	joint angle

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