The Journal of Experimental Biology 203, 229–238 (2000)
Printed in Great Britain © The Company of Biologists Limited 2000
JEB2271

THE INDEPENDENT EFFECTS OF GRAVITY AND INERTIA ON RUNNING MECHANICS

YOUNG-HUI CHANG*, HSUAN-WEN CATHY HUANG, CHRIS M. HAMERSKI AND RODGER KRAM

Locomotion Laboratory, Department of Integrative Biology, University of California, 3060 Valley Life Sciences Building, Berkeley, CA 94720-3140, USA

*e-mail: younghui@uclink4.berkeley.edu

Accepted 15 October; published on WWW 22 December 1999

Summary

It is difficult to distinguish the independent effects of gravity from those of inertia on a running animal. Simply adding mass proportionally changes both the weight (gravitational force) and mass (inertial force) of the animal. We measured ground reaction forces for eight male humans running normally at 3 m s^{-1} and under three experimental treatments: added gravitational and inertial forces, added inertial forces and reduced gravitational forces. Subjects ran at 110, 120 and 130 % of normal weight and mass, at 110, 120 and 130 % of normal mass while maintaining 100 % normal weight, and at 25, 50 and 75 % of normal weight while maintaining 100 % normal mass. The peak active vertical forces generated changed with weight, but did not change with mass. Surprisingly, horizontal impulses changed substantially more with weight than with mass. Gravity exerted a greater influence than inertia on both vertical and horizontal forces generated against the ground during running. Subjects changed vertical and horizontal forces proportionately at corresponding times in the step cycle to maintain the orientation of the resultant vector despite a nearly threefold change in magnitude across treatments. Maintaining the orientation of the resultant vector during periods of high force generation aligns the vector with the leg to minimize muscle forces.

Key words: biomechanics, locomotion, ground reaction forces, gravity, mass, weight, human.

Introduction

The size and speed of a running animal determine the relative importance of gravitational and inertial forces. A small, rapidly moving animal, such as a mouse, can easily overcome gravitational forces to run up a tree. A much larger, relatively slower-moving elephant, in contrast, is constrained by gravity and would face dire consequences if it were to fall. To run over ground, any animal must overcome both gravitational forces to support its body weight and inertial forces to decelerate and accelerate its body mass. Body weight and body mass reflect the gravitational forces and inertial forces acting on the animal, respectively. Since changes in body weight, under natural circumstances, are the result of proportional changes in body mass, it is difficult to dissociate the independent influence of gravity from that of inertia.

The goal of this study was to investigate the independent effects of gravity and inertia on the biomechanics of running. Simply adding a load proportionally increases both gravitational and inertial forces. Thus, the independent effects of each individual force are not readily distinguishable. Simulated-reduced-gravity experiments on humans suggest the possibility of dissociating the independent effects of gravity from inertia on running mechanics (Davis and Cavanagh, 1993; He et al., 1991; Kram et al., 1997; Newman et al., 1994), but no experiments have been performed to compare the relative importance of increased inertia. In this paper, we use strict scientific definitions for both mass and weight. Altered gravitational forces only indicate a change in weight (measured in newtons). In contrast, altered inertial forces only indicate a change in mass (measured in kilograms).

It seems reasonable that acutely changing either the weight or mass of a running animal would alter both the vertical and horizontal forces that are actively generated against the ground. Larger running animals generate greater absolute peak vertical forces than smaller ones. This has been observed intraspecifically in humans of different sizes and interspecifically across a broad size range of running mammals and birds (Cavagna et al., 1977; Frederick and Hagy, 1986; McMahon, 1977). Larger running animals also exert greater horizontal forces to decelerate and accelerate the mass of the body with each step (Cavagna et al., 1977).

Changes in running mechanics caused by differences in either weight or mass will probably affect the energetic cost of running. Previous studies have demonstrated the effects of added weight on the energetic cost of running and hopping in a variety of vertebrate and invertebrate species (e.g. Herreid and Full, 1986; Taylor et al., 1980). Although the metabolic cost of running is proportional to the body weight of an animal (Farley and McMahon, 1992; Kram and Taylor, 1990; Taylor et al., 1980), it is not known how much the inertial forces alone affect energetic costs. Our previous research indicated that generating horizontal propulsive forces against the ground to accelerate the mass of the body with each step constitutes a substantial fraction (approximately 30 %) of the total energetic cost of normal running (Chang and Kram, 1999). An increase in inertia would presumably increase the muscle forces that need to be generated and result in an increase in the total energetic cost of running. Before we can assess the energetic effects of changing the running mechanics with increased inertial forces, we must first assess whether inertial forces have an effect on running mechanics.

We investigated the independent biomechanical effects of altered gravitational and inertial forces on human running. We compared normal running with three different experimental treatments: running with additional gravitational and inertial forces (+GF+IF), running with only additional inertial forces (+IF) and running with only reduced gravitational forces (–GF).

We tested two general hypotheses: (i) that altered gravitational forces affect the vertical (but not horizontal) forces generated by the runner, and (ii) that altered inertial forces affect both the vertical and horizontal forces generated by the runner. On the basis of these hypotheses, we made four specific predictions about our experimental results. First, we expected peak active vertical forces generated during running to increase more with additional gravitational and inertial forces (+GF+IF) than with only additional inertial forces (+IF). Second, we predicted a decrease in peak active vertical forces with reduced gravitational forces (–GF). Third, we predicted an equivalent increase in the horizontal braking and propulsive impulses (i.e. time-integrated force) during running with additional gravitational and inertial forces (+GF+IF) and during running with additional inertial forces alone (+IF). Finally, we predicted that there would be no change in horizontal braking and propulsive impulses generated during running with only reduced gravitational forces (–GF).

Materials and methods

Subjects

Eight male, experienced treadmill runners volunteered to participate in this experiment (age 27±7 years, mass 72.2±4.0 kg; means ± S.D.). They gave informed consent as per university policy.

Equipment

The subjects ran on a force-measuring treadmill that recorded the vertical and horizontal ground reaction forces (Kram et al., 1998). To simulate increased body mass and to increase the inertial forces experienced, we wrapped thin lead strips evenly and snugly over a padded hip belt worn around the subject's waist. These lead strips were attached firmly to the hip belt to minimize movement of the added mass with respect to the subject. To simulate reduced body weight and to reduce the gravitational forces experienced, we applied a

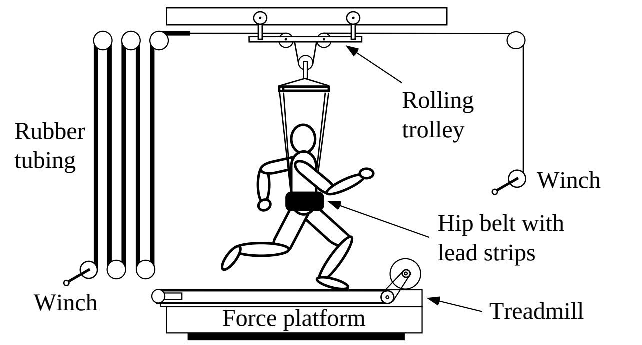

Fig. 1. Diagram of the apparatus used in the gravity and inertia experiments. We applied an upward force to the torso of our subjects near the center of mass *via* a modified rock-climbing harness. A nearly constant force was achieved by stretching rubber tubing using a hand winch over a series of pulleys. The rolling trolley ensured that no horizontal forces were applied. Mass was added by wrapping lead strips around the subject's waist over a padded hip belt. The subjects ran on a force treadmill that recorded the vertical and horizontal ground reaction forces.

nearly constant upward force to the subjects' torso near the center of mass *via* a modified rock-climbing harness. The harness was supported by four straps attached to a light aluminum frame (46.0 cm×49.5 cm) above the subject's head, which kept the straps away from the subject's torso and did not hinder the subject's ability to lean when running.

A cable led from the frame over a series of pulleys mounted on an overhead rolling trolley (Fig. 1). The low-friction trolley ensured that only vertical forces were applied to the subject. During data collection, subjects were instructed to run near the center of the treadmill and to try to maintain their position on the treadmill so as to maintain a constant speed. During a stride, there was no substantial movement of the rolling trolley caused by the minimal movements of the subject relative to the treadmill. The trolley was made from small pieces of 0.25 inch aluminum stock and five lightweight pulleys. The entire assembly had a mass of less than 2 kg. The minimal movements of the subject relative to the treadmill in combination with the small mass of the trolley relative to the runner had a negligible effect on the subject.

The upward-lifting force in the cable was provided by a spring made of rubber tubing. We altered the gravitational forces experienced by the subject by adding springs in series and by changing the length of the spring with a handwinch, thereby simulating different body weights. A force transducer (Kistler, model 9212) indicated that the force fluctuations experienced by the subject were less than ±0.04 $\boldsymbol{g}$ for all conditions (where $\boldsymbol{g}$ is the Earth's gravitational acceleration).

Our method of simulating reduced gravity by suspending the subject only 'reduces' gravity for the trunk, but not for the legs while they are swinging with respect to the body. The method that best simulates reduced gravity involves subjects running inside an airplane flying in a parabolic flight pattern (e.g. Cavagna et al., 1998). Parabolic flight, however, has many disadvantages. For example, the time available for data collection for one trial of a simulated reduced gravity condition is only 20–30 s, and steady, accurately measurable speeds are not reliably achieved. In addition, motion sickness in subjects is frequently encountered. Other methods (such as utilizing drop towers or elevators) would also be impractical because of the brief periods available for data collection. The advantage of our method (upright vertical cable suspension) was that we were able to perform a treadmill study for extended periods. Furthermore, our force-measuring treadmill enabled us to collect ground reaction forces produced at accurate steady speeds for numerous strides under multiple conditions. Many of the methods for simulating reduced gravity have previously been summarized and the advantages and disadvantages of each method outlined (Davis and Cavanagh, 1993).

Although our simulation method does not simulate reduced gravity on the swinging limbs, there is substantial evidence that it provides results comparable with those of the other methods. Our peak force data for subjects running at $3\,\mathrm{m\,s^{-1}}$ follow the expected range and pattern compared with subjects running at $2.3\,\mathrm{m\,s^{-1}}$ with the underwater immersion method (Newman, 1996; Newman et al., 1994). Furthermore, our contact time data also are within the expected range of what is observed with data collected on subjects running at $2\,\mathrm{m\,s^{-1}}$ in the KC-135 aircraft during parabolic flight (Newman, 1996). There are obvious trade-offs for any method of simulating reduced gravity; however, given our hypotheses and the data we needed to collect, our method of vertical suspension was by far the most practical, while providing us with data comparable with those of other simulation methods.

Protocol

To familiarize the subjects with the apparatus, they practiced running in the reduced-gravity simulator and with the lead weights. Subjects practiced running at two levels of each of our three experimental treatments. The entire familiarization process lasted approximately 30 min and took place within 7 days prior to data collection.

During data collection, subjects ran normally at $3\,\mathrm{m\,s^{-1}}$ and in three experimental treatments (see Table 1 for a summary of the conditions for each treatment). In one treatment, we increased both the gravitational and inertial forces (+GF+IF). We attached lead strips equal to 10, 20 and 30 % of body mass to increase both weight and mass. In a second treatment, we increased inertial forces (+IF) by adding 10, 20 and 30 % of body mass, while at the same time applying a constant upward force *via* a harness to compensate for the added weight. In this way, we were able to add inertia to subjects while maintaining their normal body weight. In a third treatment, we reduced gravitational forces (–GF) by applying a constant upward force to simulate running at 25, 50 and 75 % body weight, while the subjects maintained the same mass. In total, each subject ran under nine different experimental conditions (three conditions for each treatment). We also studied normal running before and after the experimental trials to establish a control for comparison. We collected the data after the subjects had been running at a steady speed for 1 min. We used a randomized block design for the order of experimental treatments and conditions.

Table 1. *Summary of experimental treatments and conditions*

Treatment	Condition (% Body mass/% body weight)		
+GF+IF	110/110	120/120	130/130
+IF	110/100	120/100	130/100
–GF	100/25	100/50	100/75

The order of trials followed a randomized block design.

+GF indicates additional gravitational forces, +IF indicates additional inertial forces and –GF indicates reduced gravitational forces.

Data processing

We collected the vertical and horizontal components of the ground reaction force for 5 s at a rate of 1 kHz per channel. We filtered the ground reaction force data using a fourth-order recursive, zero-phase-shift Butterworth low-pass filter with a cut-off frequency of 25 Hz. We had previously determined that 99 % of the integrated power content of the vertical ground reaction force signal for normal running has frequencies less than 10 Hz, while 98 % of the horizontal ground reaction force signal has frequencies less than 17 Hz (Kram et al., 1998). A custom-written software program (LabView4) adjusted the filtered ground reaction force data so that the mean vertical and horizontal components of the ground reaction force during the aerial phases were equal to zero. The software determined per step averages of peak active vertical force, vertical impulse, peak braking force, peak propulsive force, braking impulse, propulsive impulse and time of contact in addition to average stride time and stride length for each condition.

An automated algorithm was used to calculate the time of ground contact. The instant of ground contact was determined by a positive change in the vertical ground reaction force greater than $1\,\mathrm{N\,ms^{-1}}$ (or $1000\,\mathrm{N\,s^{-1}}$), occurring while the force was below a threshold of 100 N. The end of ground contact was calculated in a similar manner.

Peak active vertical force was determined by taking the maximum vertical force produced after the initial passive impact peak produced by heel-strike (usually after approximately 20 % of the contact phase). Peak horizontal forces were taken as the minimum (greatest negative value) and maximum (greatest positive value) horizontal forces during the braking and propulsive phases, respectively.

Statistical analyses

In all instances, we used an analysis of variance (ANOVA) with repeated-measures design (N=8) to determine statistical significance. Furthermore, we performed a Tukey's HSD *post-hoc* test to analyze the differences between conditions. Statistical significance was defined as P<0.05.

Results

Vertical ground reaction force

The peak active vertical forces generated against the ground changed with weight, but did not change with mass. Typical ground reaction force data for the control and for each of the experimental treatments are given in Fig. 2. For the control treatment (i.e. normal running), subjects on average generated a peak active vertical force of 2.45 times body weight (1737 N). When the subjects ran with additional gravitational and inertial forces (+GF+IF), their average peak active vertical force increased only modestly (Figs 2, 3B; Table 2). At 130 % body weight (+GF+IF), the average peak active vertical force was 112 % of the control value, corresponding to 2.75 times control body weight (1951 N). In contrast, when only additional inertial forces were applied (+IF), subjects generated essentially the same average peak active vertical force as the control trials (*P*=0.21, Figs 2, 3B). In simulated reduced gravity (–GF), subjects generated smaller peak active vertical forces that were nearly proportional to the reduction in weight (Figs 2, 3A). At 25 % body weight (–GF), the average peak active vertical force was 38 % of the control value, corresponding to 0.93 times the control body weight (662 N). The vertical impulses generated generally followed a similar trend to that of the peak active vertical forces. These data are summarized in Table 2.

Horizontal ground reaction force

The horizontal impulses generated against the ground changed substantially more with weight than with mass. For the control treatment, subjects had an average braking impulse of −13.6 N s and an average propulsive impulse of 13.4 N s. With additional gravitational and inertial forces (+GF+IF), the magnitudes of both braking and propulsive impulses increased nearly proportionally (Figs 2, 3D). At 130 % body weight (+GF+IF), the average magnitudes of braking and propulsive impulses applied to the ground were 128 % of control values (−17.3 N s and 17.2 N s, respectively). The magnitudes of braking and propulsive impulses for running with only additional inertial forces (+IF) also increased from the control value, but not in direct proportion (Figs 2, 3D). At 130 % body mass (+IF), the magnitudes of braking and propulsive impulses were only 110 % of control values (–14.9 and 14.7 N s, respectively). The magnitudes of horizontal braking and propulsive impulses decreased when gravitational forces were reduced (–GF; Figs 2, 3C). At 25 % body weight (–GF), the magnitudes of braking and propulsive impulses were 47 %

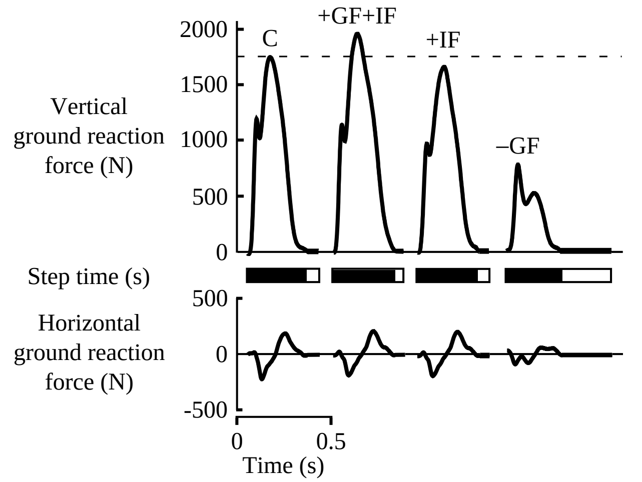

Fig. 2. Vertical and horizontal ground reaction forces for a typical subject (72.1 kg) running normally (control, C), with 30 % additional gravitational and inertial forces (+GF+IF), with 30 % additional inertial forces (+IF) and with a 75 % reduction in gravitational forces (–GF). Bars indicate stance phase duration (filled) and aerial phase duration (open).

Table 2. *The peak forces and impulses generated by the runners in different conditions*

Treatment	% Body mass/ % body weight	Peak vertical force (N)	Vertical impulse (N s)	Peak braking force (N)	Peak propulsive force (N)	Magnitude of horizontal impulse (N s)
Control	100/100	1737±35	264±5	221±5	169±4	13.5±0.4
+GF+IF	110/110	1796±65	288±8*	228±8	179±7*	15.1±0.7*
	120/120	1869±76	310±8*,‡	229±8	187±9*,‡	16.0±0.7*,‡
	130/130	1951±97*,‡	333±9*,‡,§	235±9*	198±6*,‡,§	17.3±0.8*,‡,§
+IF	110/100	1653±61	266±7	214±9	175±7	14.4±0.6*
	120/100	1679±72	273±7*	213±9	180±8*	15.0±0.7*
	130/100	1653±61	271±7	203±9*	177±7	14.8±0.8*
–GF	100/75	1427±44*	208±5*	183±6*	152±6*	11.5±0.6*
	100/50	1068±39*,‡	154±5*,‡	135±6*,‡	122±5*,‡	9.4±0.6*,‡
	100/25	662±37*,‡,§	90±5*,‡,§	110±9*,‡,§	84±7*,‡,§	6.4±0.6*,‡,§

Data represent the mean ± S.E.M., *N*=8.

With a criterion of *P*<0.05, asterisks denote a statistically significant difference compared with the control, and ‡ and § denote a statistically significant difference compared with the first and second conditions for each treatment, respectively.

+GF indicates additional gravitational forces, +IF indicates additional inertial forces and –GF indicates reduced gravitational forces.

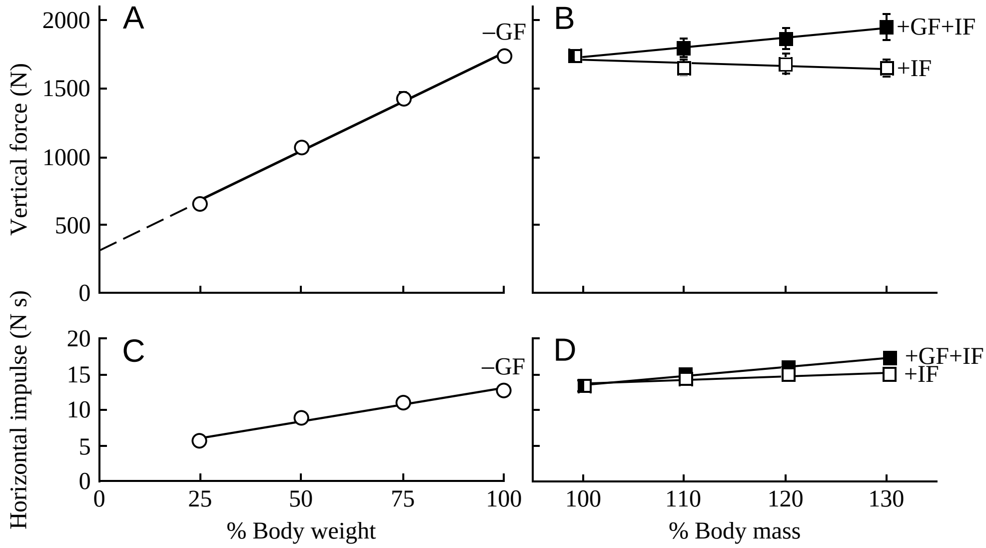

Fig. 3. The peak active vertical force (A,B) and the magnitude of horizontal impulse (C,D) generated by the runners for normal running and for three different conditions: added gravitational force and inertial force (+GF+IF, filled squares), added inertial force (+IF, open squares) and reduced gravitational force (–GF, open circles). All data points represent the mean ± S.E.M. (N=8). The lines are linear least-squares regressions. Note in A that the extrapolation of the peak active vertical forces (broken line) has a non-zero intercept.

of control values (–6.6 N s and 6.1 N s, respectively). Peak braking forces and propulsive forces generally followed the same trends as those for the horizontal impulses. A summary of these data is given in Table 2.

Kinematics

Only relatively small changes in running kinematics were observed across the three experimental treatments. The time of contact increased slightly with added weight (+GF+IF). At 130 % body weight (+GF+IF), the average time of contact was 338 ms, representing a 10 % increase from the control (Table 3). Time of contact increased similarly with added mass (+IF). At 130 % body mass (+IF), the average time of contact was 340 ms. Time of contact decreased slightly with reduced body weight (–GF). At 25 % body weight, the average time of contact was 278 ms, corresponding to a 9 % decrease from the control. Some statistically significant differences in the time of contact across experimental conditions were seen, but these differences were never more than 34 ms (Table 3). Contact length (i.e. the forward distance covered by the center of mass during ground contact) is calculated as the velocity multiplied by the time of contact and is a good indicator of the angle swept by the leg while the foot is on the ground. Since contact length is a function of the time of contact, it also only changed slightly with the experimental treatments.

The average stride time did not change substantially with added weight (+GF+IF) nor with added mass (+IF) (Table 3). With added weight (+GF+IF), stride time showed a slight decreasing trend, but was only 22 ms lower than control at 130 % body weight (+GF+IF). With only added mass (+IF), stride time showed a small increasing trend. We observed a 22 ms increase over the control at 130 % body mass (+IF). With

Table 3. *The time of ground contact, stride time and stride length for each condition*

Treatment	% Body mass/ % body weight	Time of ground contact (s)	Stride time (s)	Stride length (m)
Control	100/100	0.306±0.005	0.746±0.010	2.24±0.03
+GF+IF	110/110	0.322±0.089	0.741±0.015	2.22±0.04
	120/120	0.331±0.008*	0.731±0.013	2.19±0.04
	130/130	0.338±0.007*,‡	0.724±0.012*	2.17±0.04*
+IF	110/100	0.319±0.009	0.749±0.014	2.25±0.04
	120/100	0.328±0.006*	0.772±0.015*,‡	2.32±0.04*,‡
	130/100	0.340±0.007*,‡	0.768±0.017*	2.30±0.05*
−GF	100/75	0.301±0.011	0.794±0.016	2.38±0.05
	100/50	0.296±0.009	0.855±0.018*	2.56±0.06*
	100/25	0.278±0.011*	0.985±0.035*,‡,§	2.95±0.11*,‡,§

Data represent the mean ± S.E.M., N=8.

With a criterion of P<0.05, asterisks denote a statistically significant difference compared with the control, and ‡ and § denote a statistically significant difference compared with the first and second conditions for each treatment, respectively.

+GF indicates additional gravitational forces, +IF indicates additional inertial forces and –GF indicates reduced gravitational forces.

decreased body weight (–GF), there was a significant increase in stride time. At 25 % body weight (–GF), the stride time had increased by 239 ms over the control value, although contact time actually decreased by 28 ms.

Since stride length was calculated as a function of a constant running speed ($3.0\,\mathrm{m\,s^{-1}}$) and stride time, stride length varied accordingly. At 130 % body weight (+GF+IF), stride length had decreased slightly by 7 cm from the control value. At 25 % body weight (–GF), stride length increased by 71 cm from the control value. With added mass, there were slight increases in stride length (6 cm at 130 % body mass, +IF) but no obvious trend.

Discussion

In this section, we discuss how gravity and inertia independently influence how humans run, especially the relative importance of body weight on running mechanics and the relative unimportance of body mass. Although some of our results were counterintuitive with respect to our original predictions, some clear rules began to emerge. We propose how the resultant force vector can explain our counterintuitive results. Finally, we suggest a testable explanation for why gravity, rather than inertia, has a greater influence on running mechanics.

Before considering how altered loading affects the ground reaction force patterns, it is important to outline the salient features of the normal pattern for human running. A typical plot of the vertical and horizontal components of ground reaction force *versus* time for one step of the control condition is shown in Fig. 2. At the beginning of the stance phase (i.e. heel-strike), a transient spike of passive vertical force, known as the impact peak, occurs as a result of the passive collision of the foot and lower leg mass with the ground (Denoth, 1986). When the person's center of mass is at its lowest position, a maximum vertical force is actively generated on the ground by the muscles and is referred to as the active vertical force peak. This active vertical force peak typically reaches approximately 2.5 times body weight at the speed used in our study (Table 2; Munro et al., 1987). As the leg then extends, the center of mass rises and the vertical ground reaction force falls to zero at toe-off. Naturally, there is no ground reaction force during the aerial phase (when both feet are off the ground). When running on a level surface, the average vertical ground reaction force over a complete stride cycle is equal to body weight. In this study, we were interested in the effects of gravity and inertia on the ability of humans to produce force actively against the ground. Therefore, our discussion will only refer to the active vertical forces produced by the subjects in each condition.

The anterior–posterior horizontal ground reaction force typically has a sinusoidal pattern (Fig. 2). At the onset of the stance phase, the ground reaction force is negative and decelerates the forward movement of the center of mass. At midstance, when the vertical ground reaction force is at its maximum, the horizontal force is nearly zero. During the second half of stance, the ground reaction force is positive and accelerates the forward movement of the center of mass as the person extends their leg. As the instant of toe-off approaches, the horizontal ground reaction force again returns to zero. It is important to note that, for a person running at a steady speed, the time-integrated braking force, or impulse, must equal the propulsive impulse. The patterns of ground reaction forces for human running have previously been reported in substantially more detail (Cavanagh and Lafortune, 1980; Munro et al., 1987; Nilsson and Thorstensson, 1989). Our control data fall within these established norms.

Gravity

Our first hypothesis was that altered gravitational forces would affect only the vertical forces generated by a running person. This seemed reasonable since gravitational acceleration only acts in the vertical direction. Over an integral number of strides, all running animals must on average generate a vertical force on the ground that is equal to body weight. An acute change in body weight can be accommodated by changing the magnitude of the active vertical force generated, the time over which the force is applied, the rate at which the force is applied or some combination of all three variables. Any of these strategies could result in an appropriate change in the vertical impulse (time-integrated force) that maintains support of body weight.

As predicted, increased gravitational and inertial forces (+GF+IF) resulted in a much greater increase in the peak active vertical force generated than with increased inertial forces alone (+IF; Fig. 3B). Thus, any difference in peak active vertical forces generated against the ground between these two treatments can be attributed entirely to the effect of gravity alone. Furthermore, decreased gravitational force alone (–GF) also resulted in nearly proportional decreases in the peak active vertical force magnitude (Fig. 3A). These data support our first hypothesis that gravity is the primary determinant of the vertical forces generated during running.

Surprisingly, gravity also affected the horizontal impulses generated against the ground to brake and accelerate the runner with each step. With a 30 % increase in gravitational and inertial force (+GF+IF), there was a 28 % increase in the horizontal impulses generated against the ground. In contrast, with a 30 % increase in inertial force (+IF) alone, there was only an approximately 10 % increase in horizontal impulses. By deduction, our data indicate that the difference in the horizontal impulses between the two treatments (approximately 18 %) is due solely to gravity. Furthermore, with a 75 % reduction in only gravitational force (–GF), there was a 53 % decrease in horizontal impulse. A related phenomenon was actually seen by W. O. Fenn as early as 1930. Fenn (1930) observed a coupling between vertical and horizontal forces with changes in forward running speed. Contrary to our original hypothesis and intuition, these data indicate that gravity affects not only the generation of active vertical forces but also indirectly affects the generation of horizontal forces. Gravity (rather than inertia) appears to exert the major influence over both vertical and horizontal force generation during running.

Gravity had a relatively small effect on the time of ground contact compared with inertia. The greatest increases in contact time for both added weight (+GF+IF) conditions and added mass (+IF) were comparable (10 % and 11 %, respectively). With reduced weight (−GF), however, the contact time decreased by 9 %, but over a much greater change in weight relative to the +GF+IF treatment. The changes in stride time and stride length were predominantly the result of changes to the aerial phase of the stride, which was particularly evident in the reduced body weight data (−GF). Since no forces are generated against the ground during the aerial phase, the rest of our discussion will only consider the contact phase of the stride.

Inertia

Our second hypothesis was that inertia affects the generation of both active vertical and horizontal forces generated against the ground during running. The generation of a horizontal braking force followed by a horizontal accelerating force is a universal characteristic of all running animals. Although humans can maintain a constant average forward running speed, the fluctuation in forward velocity within each step can be substantial (the average change in forward velocity for our control runs was $\pm 0.2\,m\,s^{-1}$). Since inertial forces appear to be the only forces acting on a runner in the horizontal direction, we predicted that altered inertia would have the greatest effect on the generation of horizontal forces.

Although we expected the horizontal impulses generated on the ground to be influenced by mass and not by weight, inertia had a smaller effect on the generation of horizontal forces compared with gravity. The horizontal impulses generated against the ground changed slightly with altered mass alone (Fig. 3D; Table 2). This effect, however, was small compared with the much greater effect of gravitational forces. Even when mass alone was increased by 30 %, the additional inertia alone had no significant effect on the generation of peak active vertical forces on the ground (P=0.25).

Our data on running with reduced gravitational forces, however, do suggest that inertia may have some small effect on the generation of active vertical forces. The relationship between peak active vertical force and gravitational force is not directly proportional, and a linear extrapolation to zero gravity revealed a non-zero intercept (Fig. 3A). Thus, given some initial downward velocity in a hypothetical zero-gravity running situation, some force would need to be exerted against the ground to reverse the direction of the body's mass and to raise the center of mass. Although this is not truly 'running' *per se*, since there would be no way to land again once off the ground, it illustrates that some of the vertical force generated on the ground by the legs acts to oppose only inertial forces.

Resultant force vector

Our data suggest that it is important to consider both the vertical and horizontal forces taken together rather than as independent entities. Our results contradicted our intuitive reasoning for the role of horizontal forces generated by running animals. If horizontal forces are not generated in proportion to overall mass, then why is there such a universal pattern of braking and accelerating characteristic of all running animals? Although it is sometimes easier to consider force data as independent components in a Cartesian coordinate system, there is no justification for expecting biological systems inherently to operate in such a system. Analyzing the resultant force vector, rather than its components, may explain why gravity (rather than inertia) has such a great effect on horizontal forces.

Despite a nearly threefold change in the magnitude of the

Table 4. *The peak resultant force and the angles of resultant ground reaction force vectors at times of peak resultant force (Φ_r), peak braking force (Φ_b) and peak propulsive force (Φ_p) for each condition*

Treatment	% Body mass/ % body weight	Peak resultant force (N)	Peak resultant angle (degrees)	Peak braking force angle (degrees)	Peak propulsive force angle (degrees)
Control	100/100	1738±36	87.3±0.1	80.1±0.3	102.4±0.4
+GF+IF	110/110	1799±65	87.0±0.2	80.4±0.4	102.6±0.6
	120/120	1871±7*	87.1±0.2	80.7±0.4*	102.9±0.6
	130/130	1954±97*,‡	87.2±0.2	80.7±0.3*	103.2±0.6
+IF	110/100	1656±61	86.9±0.1	80.3±0.3	102.7±0.7
	120/100	1681±72	87.2±0.2	80.2±0.4	102.6±0.7
	130/100	1656±61	87.0±0.1	80.6±0.3	102.2±0.8
−GF	100/75	1428±45*	87.3±0.2	80.2±0.5	102.2±0.5
	100/50	1071±38*,‡	87.3±0.4	79.5±1.2	102.1±0.6
	100/25	709±36*,‡,§	87.8±1.0	75.2±1.7*,‡,§	104.3±0.4*,‡,§

Data represent the mean ± S.E.M., N=8.

With a criterion of P<0.05, asterisks denote a statistically significant difference compared with the control, and ‡ and § denote a statistically significant difference compared with the first and second conditions for each treatment, respectively.

+GF indicates additional gravitational forces, +IF indicates additional inertial forces and –GF indicates reduced gravitational forces.

resultant force vector generated across three different experimental treatments and 10 conditions, the orientation of the resultant force vectors at corresponding instants remained nearly constant during times of high force generation (Table 4). We calculated and compared the angle (Φ) of the resultant force (resultant vector of vertical force and horizontal force components) generated against the ground at three instants corresponding to the times of peak horizontal braking force (Φ_b), the peak resultant force (Φ_r) and the peak horizontal propulsive force (Φ_p) (Fig. 4). The values are given in Table 4. Changes in the magnitude of the vertical component of force are accompanied by proportional changes in the horizontal component of force to maintain the orientation of the resultant force vector.

We suggest that the resultant force vector at these corresponding times of the step cycle remained nearly constant across the different trials to maintain the alignment with the leg. During legged locomotion, this alignment may be a universal mechanism for running animals to minimize net muscle moments about each joint and, therefore, muscle forces. Many running mammals align the resultant force vector with the long axis of the leg (Biewener, 1989, 1990). A similar mechanism has also been observed in arthropod locomotion (Full et al., 1991). Furthermore, a mathematical model of a running biped indicated that alignment of the resultant force vector with the leg would minimize joint moments (Alexander, 1991). Given the empirical and theoretical support, it is likely that our subjects were also aligning the resultant force vector with the leg to minimize muscle forces in both our control and experimental treatments in response to acute changes in weight and mass.

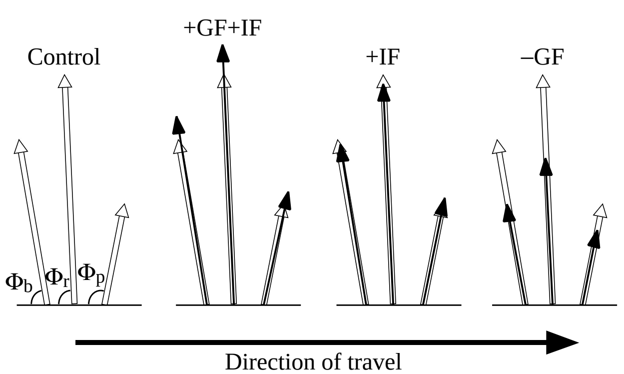

Fig. 4. Average resultant ground reaction force vectors (N=5) at times of peak braking force (Φ_b), peak resultant force (Φ_r) and peak propulsive force (Φ_p) for one condition from each treatment. The control treatment is shown as open arrows, and other treatments are shown as filled arrows superimposed on the control arrow for comparison. Arrow lengths and angles represent mean values for eight subjects. From left to right, the respective conditions are control, 130 % body weight (+GF+IF), 130 % body mass (+IF) and 50 % body weight (–GF). The resultant force vectors for each step are displayed at a constant spacing only for illustrative purposes and do not indicate absolute distance or time scale. Although the force magnitudes varied for each treatment, the orientation of the vectors remained nearly constant.

Aligning the resultant force vector with the leg during running may have important metabolic as well as mechanical consequences. The amount of muscle force generated during running has been closely associated with the energetic cost of running (Kram and Taylor, 1990). Aligning the resultant vector with the long axis of the leg would minimize net muscle moments about each joint and would also reduce the muscle forces necessary to produce these moments. Lower muscle forces would require a smaller volume of muscle to be activated, which would presumably result in a reduced metabolic cost of running. A similar situation is observed in larger mammals that run with their legs in a more upright posture. As a result, the leg muscles of larger, more upright mammals have a greater effective mechanical advantage (Biewener, 1990). With such straighter limb postures, each joint of the leg is closer to the line of action of the resultant force vector, and the net muscle moments are correspondingly smaller. Measurements of the metabolic cost of humans running with flexed knees (‘Groucho running’) show that changes in the angle of the knee at midstance (of approximately 14 %) dramatically increase metabolic cost (by approximately 40 %; McMahon et al., 1987).

In our study, maintenance of the orientation of the resultant force was seen in all but one situation. Subjects running at the lowest body weight condition showed a minor deviation from the ‘rule’ that the orientation of the resultant force vector should remain unchanged. At the 25 % body weight condition, the angle of the resultant force vector at the time of peak braking force Φ_b was 5 ° lower than for control runs, and the angle of the resultant force vector at the time of peak propulsive force was 2 ° higher. Perhaps forces generated against the ground when running at 25 % body weight were low enough such that the mechanism of aligning the resultant force with the leg was no longer a major determinant of running mechanics. There were some small but statistically significant increases in the angle of resultant force at time of peak braking Φ_b for the 120 and 130 % body weight (+GF+IF) conditions; however, these increases represented an average change of only 0.6 °. In most situations, this unifying principle of resultant force vector alignment with the leg for running may be a valuable predictive tool for understanding the locomotion biomechanics of legged animals in different habitats and under different conditions.

Studying the biomechanics of human running provides a tractable experimental model that can predict the responses of other legged animals to different force environments. Martinez et al. (1998) were able to predict kinematic trends in the underwater locomotion of intertidal crabs on the basis of studies of reduced-gravity terrestrial locomotion in humans (He et al., 1991; Kram et al., 1997; Margaria and Cavagna, 1964; Newman et al., 1994). Similarly, a better understanding of how gravity and inertia independently influence running mechanics may provide insight into the general principles that govern legged locomotion in different habitats and across phylogenetic aquatic–terrestrial transitions (e.g. secondary aquaticism) as well as across ontogenetic aquatic–terrestrial transitions (e.g. amphibians).

Threshold to leg force generation

There are common thresholds to musculoskeletal strength that are observed in many mammalian species despite a wide variation in size (Biewener, 1990). Our data suggest that there may be some upper threshold to the magnitude of vertical force that can be actively generated during running under different conditions. The increase in peak active vertical force observed with increased gravitational and inertial forces (+GF+IF) was much smaller per newton of body weight than the decrease in peak active vertical force observed with reduced gravity (−GF, Fig. 3). This suggests that the generation of vertical forces may be reaching some asymptote as body weight is increased. A power fit of peak active vertical force F *versus* body weight W (%) data (combining the +GF+IF and −GF data) provides a good fit (F=85.02$W^{0.65}$, r^2=0.995) and supports the suggestion of a plateau in peak active vertical force with increased gravitational forces.

Our data show that peak vertical force magnitudes did not change enough to accommodate the entire increase in impulse required for the increased body weight condition. To support a greater body weight without proportionally increasing the peak active vertical force, either an increase in the time of ground contact or a change in the rate of force generation provided the means to increase vertical impulse. Therefore, an increase in one or both of these variables was necessary. We noted an approximately 10 % increase in time of contact. By deduction, any remaining increase in impulse had to be accommodated by a change in shape of the force/time curve. The shape of a force *versus* time plot is difficult to quantify without extensive mathematical treatment. A Fourier analysis of ground reaction forces can be used to quantify the shape (Alexander and Jayes, 1980). The preference of changing one impulse variable over another for increasing impulse generation may deserve future attention.

Similar physiological thresholds to force production have previously been observed in running animals. Among quadrupeds, horses change gait from a trot to a gallop when they reach a physiological threshold of musculoskeletal force production (Farley and Taylor, 1991). Switching from a trot to a gallop allows horses to keep each foot on the ground for a greater proportion of the stride. This allows a galloping horse to support its body weight with more feet on the ground at the same time, reducing peak active vertical forces by 14 % compared with trotting at the same speed (Farley and Taylor, 1991). Humans running along a curved path need to generate additional lateral (centripetal) forces on the ground. Since humans cannot gallop like horses to reduce musculoskeletal forces, a similar threshold of leg force production has been suggested to cause the decrease in maximum sprint speed observed on curved tracks (Greene, 1985, 1987). In both examples of quadrupedal and bipedal locomotion, increasing the average force production of each leg while avoiding any undesirable levels of peak musculoskeletal force required that the animals either change gait or slow down, respectively.

In conclusion, in human running, gravity, and not inertia, exerts the major influence on both vertical and horizontal forces generated against the ground. The peak active vertical forces are modulated so that they match the changes in body weight, but do not increase beyond some physiological threshold. The horizontal forces are modulated so that they change in proportion to the vertical force. Proportional changes in both vertical and horizontal forces allow the alignment of the resultant force vector with the leg to be maintained across a wide variety of running conditions. We suggest that the alignment of the resultant force vector with the leg during times of high force generation may be a universal mechanism for minimizing net muscle moments, muscle forces and metabolic costs during running. Our data also suggest, however, that there may be situations in which the relative importance of this mechanism is reduced (e.g. at low gravity levels when there is no need to generate high forces). In addition, increasing the time of contact or changing the rate of force generation may be secondary mechanisms for accommodating high impulse production requirements when a threshold to peak force generation is reached.

We wish to thank the members of the University of California, Berkeley Locomotion Laboratory, and two anonymous reviewers for their helpful comments and suggestions. This project was funded in part by NIH R29-AR44688, Howard Hughes Medical Institute Biology Fellows Program, the California Space Institute and the University of California, Berkeley Undergraduate Research Apprenticeship Program.

References

Alexander, R. McN. (1991). Energy-saving mechanisms in walking and running. *J. Exp. Biol.* **160**, 55–69.

Alexander, R. McN. and Jayes, A. S. (1980). Fourier analysis of forces exerted in walking and running. *J. Biomech.* **13**, 383–390.

Biewener, A. A. (1989). Scaling body support in mammals: limb posture and muscle mechanics. *Science* **245**, 45–48.

Biewener, A. A. (1990). Biomechanics of mammalian terrestrial locomotion. *Science* **250**, 1097–1103.

Cavagna, G. A., Heglund, N. C. and Taylor, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243–R261.

Cavagna, G. A., Willems, P. A. and Heglund, N. C. (1998). Walking on Mars. *Nature* **393**, 636.

Cavanagh, P. R. and Lafortune, M. A. (1980). Ground reaction forces in distance running. *J. Biomech.* **13**, 397–406.

Chang, Y.-H. and Kram, R. (1999). Metabolic cost of generating horizontal forces in running. *J. Appl. Physiol.* **86**, 1657–1662.

Davis, B. L. and Cavanagh, P. R. (1993). Simulating reduced gravity: a review of biomechanical issues pertaining to human locomotion. *Aviat. Space Env. Med.* **64**, 557–566.

Denoth, J. (1986). Load on the locomotor system and modeling. In *Biomechanics of Running Shoes* (ed. B. Nigg), pp. 63–116. Champaign, IL: Human Kinetics.

Farley, C. T. and McMahon, T. A. (1992). Energetics of walking and running: insights from simulated reduced-gravity experiments. *J. Appl. Physiol.* **73**, 2709–2712.

Farley, C. T. and Taylor, C. R. (1991). A mechanical trigger for the trot–gallop transition in horses. *Science* **253**, 306–308.

Fenn, W. O. (1930). Work against gravity and work due to velocity changes in running. *Am. J. Physiol.* **93**, 433–462.

Frederick, E. C. and Hagy, J. L. (1986). Factors affecting peak vertical ground reaction forces in running. *Int. J. Sport Biomech.* **2**, 41–49.

Full, R. J., Blickhan, R. and Ting, L. H. (1991). Leg design in hexapedal runners. *J. Exp. Biol.* **158**, 369–390.

Greene, P. R. (1985). Running on flat turns: experiments, theory and applications. *Trans. ASME* **107**, 96–103.

Greene, P. R. (1987). Sprinting with banked turns. *J. Biomech.* **20**, 667–680.

He, J. P., Kram, R. and McMahon, T. A. (1991). Mechanics of running under simulated low gravity. *J. Appl. Physiol.* **71**, 863–870.

Herreid, C. L. and Full, R. J. (1986). Energetics of hermit crabs during locomotion: the cost of carrying a shell. *J. Exp. Biol.* **120**, 297–308.

Kram, R., Domingo, A. and Ferris, D. P. (1997). Effect of reduced gravity on the preferred walk–run transition speed. *J. Exp. Biol.* **200**, 821–826.

Kram, R., Griffin, T. M., Donelan, J. M. and Chang, Y. H. (1998). A force-treadmill for measuring vertical and horizontal ground reaction forces. *J. Appl. Physiol.* **85**, 764–769.

Kram, R. and Taylor, C. R. (1990). Energetics of running: a new perspective. *Nature* **346**, 265–267.

Margaria, R. and Cavagna, G. A. (1964). Human locomotion in subgravity. *Aerospace Med.* **35**, 1140–1146.

Martinez, M. M., Full, R. J. and Koehl, M. A. R. (1998). Underwater punting by an intertidal crab: a novel gait revealed by the kinematics of pedestrian locomotion in air *versus* water. *J. Exp. Biol.* **201**, 2609–2623.

McMahon, T. A. (1977). Scaling quadrupedal galloping: frequencies, stresses and joint angles. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 143–151. London: Academic Press.

McMahon, T. A., Valiant, G. and Frederick, E. C. (1987). Groucho running. *J. Appl. Physiol.* **62**, 2326–2337.

Munro, C. F., Miller, D. I. and Fuglevand, A. J. (1987). Ground reaction forces in running: a reexamination. *J. Biomech.* **20**, 147–155.

Newman, D. J. (1996). Modeling reduced gravity human locomotion. *Int. J. Appl. Sci. Comp.* **3**, 91–101.

Newman, D. J., Alexander, H. L. and Webbon, B. W. (1994). Energetics and mechanics for partial gravity locomotion. *Aviat. Space Env. Med.* **65**, 815–823.

Nilsson, J. and Thorstensson, A. (1989). Ground reaction forces at different speeds of human walking and running. *Acta Physiol. Scand.* **136**, 217–227.

Taylor, C. R., Heglund, N. C., McMahon, T. A. and Looney, T. R. (1980). Energetic cost of generating muscular force during running: a comparison of small and large animals. *J. Exp. Biol.* **86**, 9–18.