

EXPLORING DYNAMIC SIMILARITY IN HUMAN RUNNING USING SIMULATED REDUCED GRAVITY

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Summary

The Froude number (a ratio of inertial to gravitational forces) predicts the occurrence of dynamic similarity in legged animals over a wide range of sizes and velocities for both walking and running gaits at Earth gravity. This is puzzling because the Froude number ignores elastic forces that are crucial for understanding running gaits. We used simulated reduced gravity as a tool for exploring dynamic similarity in human running. We simulated reduced gravity by applying a nearly constant upward force to the torsos of our subjects while they ran on a treadmill. We found that at equal Froude numbers, achieved through different combinations of velocity and levels of gravity, our subjects did not run in a dynamically similar manner. Thus, the inertial and gravitational forces that comprise the Froude number were not sufficient to characterize running in reduced gravity. Further, two dimensionless numbers that incorporate elastic forces, the Groucho number and the vertical Strouhal number, also failed to

predict dynamic similarity in reduced-gravity running. To better understand the separate effects of velocity and gravity, we also studied running mechanics at fixed absolute velocities under different levels of gravity. The effects of velocity and gravity on the requirements of dynamic similarity differed in both magnitude and direction, indicating that there are no two velocity and gravity combinations at which humans will prefer to run in a dynamically similar manner. A comparison of walking and running results demonstrated that reduced gravity had different effects on the mechanics of each gait. This suggests that a single unifying hypothesis for the effects of size, velocity and gravity on both walking and running gaits will not be successful.

Key words: biomechanics, biped, Froude number, locomotion, running, reduced gravity, dynamic similarity.

Introduction

Dynamic similarity is potentially the most general theory for the locomotion of legged animals (Alexander and Jayes, 1983). The theory proposes that different-sized animals, moving at different velocities, may still move in a similar fashion. For example, consider the locomotion of a mouse and a horse. While they move very differently at the same absolute velocity (e.g. a mouse would have to gallop to keep up with a walking horse), their movements may be similar at the same relative velocity (e.g. at their preferred trotting velocities).

Alexander and Jayes (1983) defined six requirements for locomoting animals to be considered dynamically similar: (i) geometric similarity (corresponding linear dimensions of different-sized animals can be made equal by multiplying each dimension by the same constant), (ii) equal phase relationships (relative timing of limb movements), (iii) equal duty factors (the fraction of the stride time that a foot is in contact with the ground), (iv) equal relative stride lengths (the distance between two consecutive ground contacts of the same foot normalized for leg length), (v) equal relative ground reaction forces, and (vi) equal relative mechanical power outputs. They hypothesized that different-sized animals would meet these six

criteria when they travel at velocities that translate to equal values of the Froude number.

The Froude number Fr is a dimensionless ratio of inertial force to gravitational force. For legged locomotion, the inertial force typically used is the centripetal force acting on the animal as it arcs over a stance leg. Because body mass is in both the numerator and denominator, this Froude number reduces to:

$$Fr = \frac{u^2}{gL_{\text{leg}}}, \quad (1)$$

where u is forward velocity, g is gravitational acceleration and L_{leg} is the animal's leg length (usually measured as height to hip). Alexander and Jayes (1983) tested their hypothesis by comparing the locomotion mechanics of small and very large animal species (from rodents to rhinoceroses) walking, running, trotting and galloping over a wide velocity range. They found that, despite very large differences in sizes and velocities, animals move with remarkably similar mechanics at equal values of the Froude number. The success of their dynamic similarity hypothesis has led investigators in fields ranging from anthropology to zoology to use the Froude

number for analyzing both walking and running gaits (examples are, for walking, Alexander, 1984; Alexander and Jayes, 1980; Cavagna et al., 1983; McGeer, 1990, 1992; Minetti et al., 1994; Moretto et al., 1996; Wagenaar and Beek, 1992; Zani and Claussen, 1994; Zijlstra et al., 1996; for running, Alexander, 1991; Alexander and Maloij, 1984; Bennett, 1987; Blickhan and Full, 1993; Cavanagh and Kram, 1989; Farley et al., 1993; Full and Tu, 1990; Gatesy and Biewener, 1991; Muir et al., 1996; Newman, 1996).

We found it puzzling that a single dimensionless parameter describes the relationship between size, velocity and mechanics for both walking and running animals because fundamentally distinct mechanisms underlie each gait. A walk is a series of vaults over relatively stiff legs. This inverted pendulum-like mechanism conserves mechanical energy by exchanging kinetic and potential energy within each step (Cavagna et al., 1977). In contrast, running is a bouncing gait in which the legs act like compliant springs (Cavagna et al., 1977). Energy is conserved in this spring-mass system by the storage and return of elastic energy within each step by tendons, ligaments and muscles.

Inertial and gravitational forces dominate the motion of a simple pendulum. Since walking involves an inverted pendulum mechanism, the Froude number could reasonably be expected to describe the effects of size, velocity and gravity on walking mechanics. However, by investigating the effect of simulated reduced gravity on human walking kinematics, we have previously demonstrated that humans do not walk in a dynamically similar fashion at equal Froude numbers achieved with different combinations of velocity and gravity (Donelan and Kram, 1997). In fact, decreasing gravity had only a modest effect on the kinematics of walking.

Unlike an inverted pendulum system, gravitational and inertial forces are not sufficient to describe the motion of a spring-mass system. A third force, the elastic force, also plays an important role. Accordingly, Alexander (1989) noted that, on theoretical grounds, having equal Froude numbers is necessary for dynamically similar running but it is not sufficient.

To be dynamically similar, running animals must be elastically similar. Structures, including those of animals, are considered elastically similar if they deform under gravity in a geometrically similar manner (McMahon, 1973). For example, elastic similarity requires larger animals to have relatively thicker bones than smaller animals in order to have comparable deformations. McMahon (1975) demonstrated that the concept of elastic similarity not only describes relationships between size and structure, but also accurately predicts how measures of locomotion such as stride frequency and gait transition velocities scale with body size. While recognizing the morphological inconsistencies between elastic and geometric similarity, Alexander (1989) revised the original dynamic similarity requirements to include aspects of elastic similarity. To be dynamically similar, the joints of running animals must move through equal angles. Similar changes in joint angles equate to geometrically similar changes in leg length. Elastic

similarity requires geometrically similar length changes. In this sense, elastic similarity is a requirement for dynamic similarity (Alexander, 1989).

Following Alexander's (1989) synthesis of dynamic and elastic similarity theory, Farley et al. (1993) added an elastic similarity requirement to the original set of dynamic similarity criteria. They proposed that, to be elastically similar, running animals must undergo equal relative peak virtual leg compressions. Relative peak virtual leg compression is the virtual leg length change (called 'peak leg spring compression'; Farley et al., 1993) normalized for the animal's resting leg length. Farley et al. (1993) showed that, at approximately the same Froude number (1.5), a variety of trotting animals met both the elastic similarity requirement and the original dynamic similarity criteria. This may account for the potential discrepancy between the empirical observation that different-sized animals run in a similar manner at equal Froude numbers (Alexander and Jayes, 1983) and the theory that states that the Froude number is not sufficient to predict dynamic similarity (Alexander, 1989). It is not clear how general the findings of Farley et al. (1993) are because their Froude number comparisons were only at one velocity for each species and only at Earth gravity.

The occurrence of dynamic similarity at equal Froude numbers has been attributed to the importance of gravitational forces in determining locomotion mechanics (Alexander and Jayes, 1983). In the present study, we used simulated reduced gravity as a tool for exploring dynamic similarity in human running. We had three goals for our experiments. First, we wanted to test whether humans run in a dynamically similar manner at equal values of the Froude number achieved with different combinations of velocity and simulated reduced gravity. Second, we wanted to collect a comprehensive data set for a wide range of velocity and gravity combinations to explore their separate and combined effects on running mechanics. This also allowed us to investigate whether dimensionless variables other than the Froude number better define dynamic similarity in reduced-gravity running. Finally, we wanted to compare the effects of reduced gravity on the mechanics of walking and running to determine whether a single unifying hypothesis might adequately describe dynamic similarity for both gaits across size, velocity and gravity.

While there has been a moderate amount of applied research on human locomotion in reduced gravity (for a review, see Davis and Cavanagh, 1993), few studies have investigated general principles underlying running mechanics. Experiments that have addressed basic mechanisms (Davis et al., 1996; He et al., 1991; Newman et al., 1994) were restricted to a narrow range of velocities or levels of gravity. As a result, the interactive effects of size, velocity and gravity on running mechanics are not well understood. Our study expands on previous studies by comparing running mechanics at equal Froude number combinations and by encompassing a more complete range of velocities and levels of gravity.

Materials and methods

Experimental design

Our experimental design had two parts: equal Froude number comparisons and equal fixed absolute velocity comparisons. For both parts, subjects ran in Earth gravity (1.00g) and in conditions simulating 0.75, 0.50 and 0.25g (where g represents Earth gravity, 9.81 m s^{-2}). For the equal Froude number comparisons, the subjects ran at velocities corresponding to four Froude numbers (0.5, 1.0, 2.0 and 3.0) at each level of simulated gravity. The velocities for each individual subject depended on their leg length (see equation 1). At each of the four levels of gravity, subjects also ran at four fixed absolute velocities (2, 3, 4 and 5 m s^{-1}). In total, each subject ran at 32 different combinations of velocity and gravity. Our experimental design was such that each subject served as his or her own control. This ensured that all comparisons were made between perfectly geometrically similar individuals, which is a requirement for dynamic similarity (Alexander and Jayes, 1983).

Subjects

Ten human subjects volunteered to participate in this experiment (five male, five female, leg length $0.98 \pm 0.02 \text{ m}$; body mass $68.9 \pm 7.1 \text{ kg}$; means \pm s.D.). We measured leg length as the height from the ground to the greater trochanter of the femur while the subjects stood with their shoes on. In keeping with the policies of our university, subjects gave their informed consent to participate after reading a description of the purpose, risks and basic procedures of the experiment.

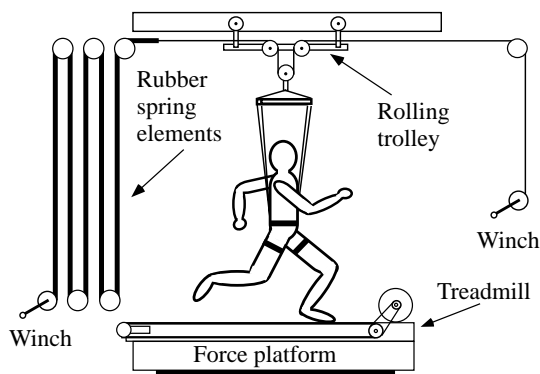


Fig. 1. Our reduced gravity simulator applied a nearly constant upward force to the subject's torso *via* a modified rock-climbing harness. The harness was attached to a rolling trolley and pulley system that moved horizontally with the subject. This ensured that the apparatus applied purely vertical forces. The force was provided by long rubber spring elements stretched over several pulleys. Additional parallel spring elements were added only when the force of the original spring elements was inadequate, thus maximizing spring stretch and minimizing the force fluctuations. Force fluctuations, measured with a force transducer (model 9212; Kistler Instrument Corporation, USA), were less than $\pm 0.03g$ at all levels of simulated reduced gravity.

Reduced gravity simulator

We simulated reduced gravity using a device that applied a nearly constant upward force to the torso (Fig. 1). Similar reduced-gravity devices have been used previously to study the effects of simulated reduced gravity on human locomotion (Donelan and Kram, 1997; Farley and McMahon, 1992; Griffin et al., 1999; He et al., 1991; Kram et al., 1997). We address the possible limitations of our simulation technique in the Appendix.

Force treadmill

Subjects ran on a motorized, custom-built treadmill mounted on a commercially available force platform (model ZBP-7124-6-4000, Advance Mechanical Technology Inc., AMTI, Watertown, MA, USA) (Kram et al., 1998). This force treadmill measures the ground reaction forces for numerous consecutive steps at a constant running velocity. It is lightweight and mechanically rigid, resulting in a high natural frequency of the overall device (greater than 170 Hz in the vertical direction). We filtered the ground reaction force signals at 25 Hz using a fourth-order, recursive, zero-phase-shift Butterworth low-pass digital filter.

Kinetic analysis

We analyzed the filtered ground reaction force signals to determine heel-strike and toe-off events as well as peak vertical ground reaction forces. We used the heel-strike and toe-off events to calculate ground contact time (t_c), stride time and duty factor (contact time divided by stride time). We calculated stride length from the product of stride time and the treadmill belt velocity. We calculated relative stride length as stride length divided by standing leg length. Relative peak vertical ground reaction force is the mid-stance peak in the vertical ground reaction force (F_{peak}) signal divided by the subject's body weight in that particular level of simulated gravity. Relative peak virtual leg compression is the peak virtual leg length change (ΔL_{leg}) during stance normalized for standing leg length (McMahon and Cheng, 1990). Virtual leg length is the distance between the foot's point of contact with the ground and the center of mass during the stance phase. We calculated the peak virtual leg compression from the peak vertical displacement of the center of mass (Δy), the subject's leg length (L_{leg}), and half the angle swept by the leg during stance (θ):

$$\Delta L_{\text{leg}} = \Delta y + L_{\text{leg}}(1 - \cos\theta). \quad (2)$$

We calculated the peak vertical displacement of the center of mass (Δy) by integrating the vertical acceleration signal, with respect to time, twice (for further explanation, see Cavagna, 1975). We calculated θ as:

$$\theta = \sin^{-1} \left(\frac{ut_c}{2L_{\text{leg}}} \right). \quad (3)$$

This traditional formula (McMahon and Cheng, 1990) for calculating θ ignores the forward movement of the point of force application during ground contact. Thus, our calculations slightly overestimate the angle swept by the leg during stance

and, as a result, overestimate virtual leg compression and underestimate leg stiffness. However, Lee and Farley (1998) have shown that the point of force application translation is independent of running velocity. This results in a nearly constant ratio between values calculated using traditional formulae and those that account for point of force application translation. Thus, the patterns of reported values do not depend strongly upon the calculation method.

Preliminary procedures

In a preliminary study, we habituated 10 subjects to treadmill running and familiarized them with running in our reduced gravity simulator (Donelan et al., 1997). All subjects ran on the treadmill for just over 10 min at 3.0 m s^{-1} in Earth gravity. The subjects demonstrated almost immediate kinematic habituation to treadmill running. There were no significant differences in duty factor ($P=0.89$) or relative stride length ($P=0.78$) between the first 10 strides of the second minute and the first 10 strides of the eleventh minute.

Next, we familiarized the subjects to running in the reduced gravity simulator. The subjects ran at 3.0 m s^{-1} for just over 5 min in conditions simulating 0.75, 0.50 and 0.25g. As with treadmill habituation in 1.00g, the subjects demonstrated almost immediate familiarization to running in simulated reduced gravity. Even at the lowest level of gravity, there were no significant differences in either duty factor ($P=0.18$) or relative stride length ($P=0.16$) between the first 10 strides of the second minute and the first 10 strides of the sixth minute.

During the present experimental trials, we collected data only after subjects had run for 1 min at each velocity and level of simulated gravity. On the basis of our analysis of the preliminary procedures, we are confident that we measured representative mechanics.

Statistical analyses

For each condition, we calculated the mean values of each variable for five strides (10 steps) per subject. We used repeated-measures analysis of variance (ANOVA) to determine statistical differences. Our criterion for significance was $P < 0.05$.

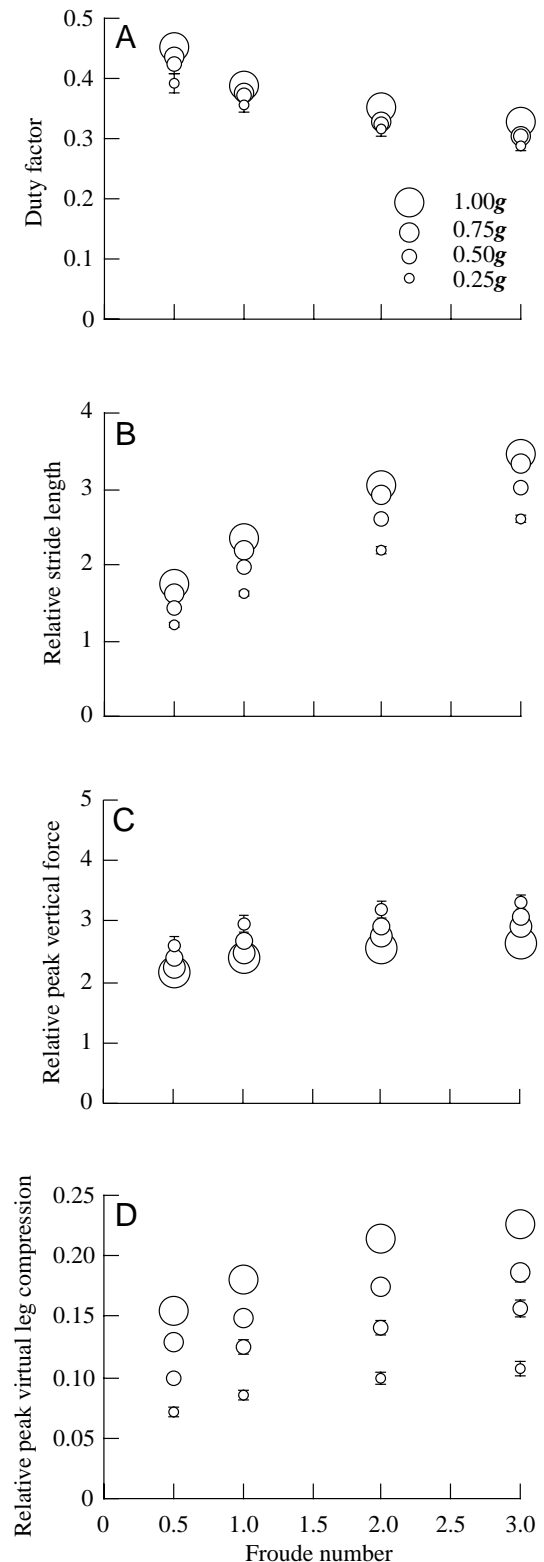
Results

Equal Froude number conditions

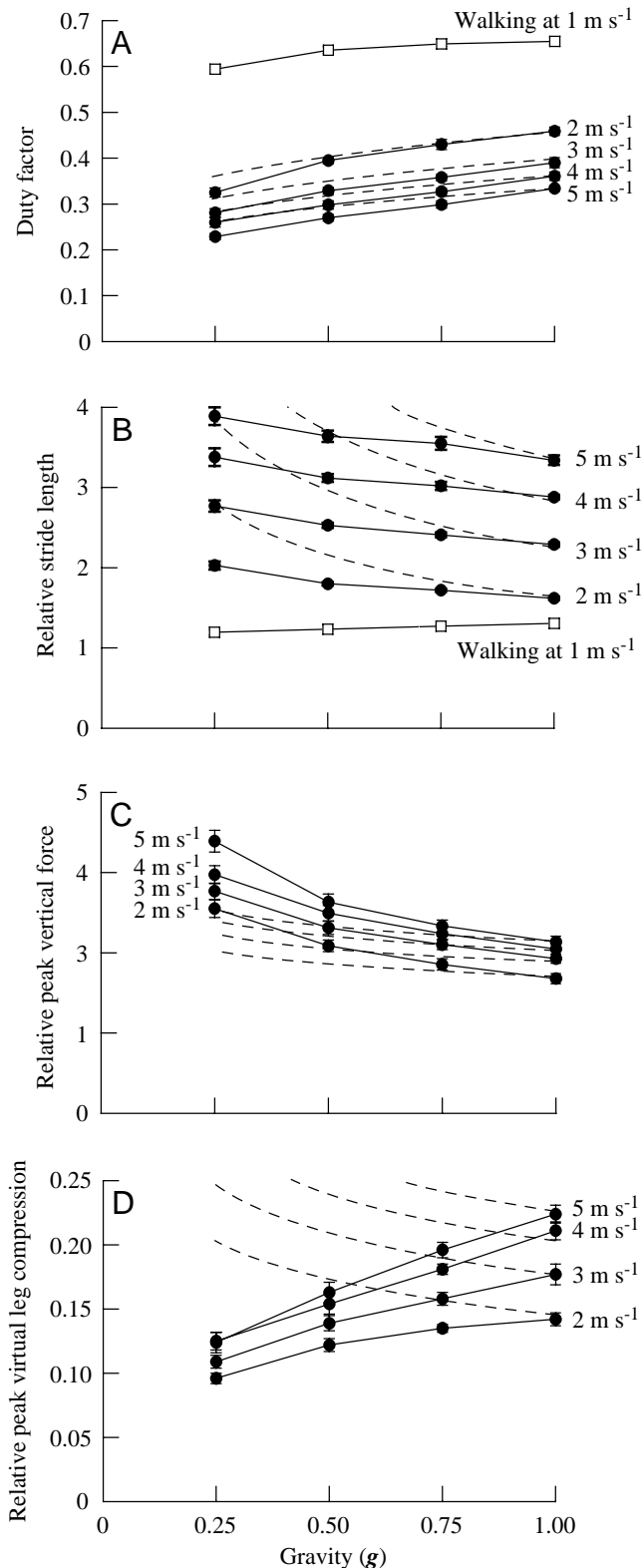
One prediction of the dynamic similarity hypothesis is that running animals use equal duty factors at equal Froude

Fig. 2. The effects of reduced gravity on the mechanics of running at equal Froude numbers, achieved with different combinations of velocity and gravity. In reduced gravity, the subjects ran with (A) different duty factors, (B) different relative stride lengths, (C) different relative peak vertical forces and (D) different relative peak vertical leg compressions. The size of each symbol indicates the magnitude of simulated gravity. If perfect dynamic similarity occurred, the circular symbols would be concentric. Values are means ± 1 S.E.M., $N=10$. Some error bars are not visible because they are smaller than the symbols.

numbers. However, as Fig. 2A demonstrates, this was not the case for our subjects when equal Froude numbers were achieved through different combinations of velocity and gravity. At the same Froude number, as we decreased gravity from 1.00g to 0.25g, duty factor systematically decreased by



an average of 11% ($P < 0.0005$). This discrepancy is further illustrated by the duty factor data for fixed absolute velocities plotted in Fig. 3A. The dynamic similarity hypothesis predicts that reducing gravity, while maintaining a constant absolute velocity, would cause a more subtle decrease in duty factor



(dashed lines) than we measured (solid lines). At 0.25g, the average difference between measured and predicted duty factors was 11%. Thus, our subjects did not strictly meet this first requirement for dynamic similarity.

A second prediction of the dynamic similarity hypothesis is that animals run with equal relative stride lengths at the same Froude number. We found, however, that at equal Froude numbers our subjects chose to run with different relative stride lengths (Fig. 2B) ($P < 0.0001$). At equal Froude numbers, as we decreased gravity from 1.00g to 0.25g, relative stride length systematically decreased by an average of 29%. This departure from the predicted pattern is also demonstrated by the relative stride length data for fixed absolute velocities (Fig. 3B). For example, the Froude-based dynamic similarity hypothesis predicts an increase in relative stride length to 5.8 leg lengths for running at 5.0 m/s in 0.25g. In fact, our subjects increased their relative stride length to only 3.9 leg lengths. On average, the difference between measured and predicted relative stride length at 0.25g was 43%. Our subjects did not fulfill this second requirement for dynamic similarity.

In addition to the kinematic predictions, the hypothesis of Alexander and Jayes (1983) predicts that, at equal Froude numbers, animals exert equal relative forces on the ground at corresponding times in a stride. They normalized the ground reaction forces by dividing the force by the animal's weight. This prediction requires that both the magnitudes and patterns of ground reaction force records be similar. We only assessed the magnitude component of this requirement because the patterns of ground reaction forces during bipedal running at different velocities and levels of reduced gravity are generally similar (He et al., 1991). We found that our subjects ran with different relative peak vertical forces at equal values of the Froude number ($P < 0.0001$) (Fig. 2C). At equal Froude numbers, as we decreased gravity from 1.00g to 0.25g, relative peak vertical force systematically increased by an average of

Fig. 3. The effects of reduced gravity on the mechanics of running at fixed absolute velocities. In reduced gravity, the subjects ran with (A) different duty factors, (B) different relative stride lengths, (C) different relative peak vertical forces and (D) different relative peak virtual leg compressions. Dashed lines represent the predicted mechanics based on the dynamic similarity hypothesis of Alexander and Jayes (1983). To calculate these predictions, we first determined the relationship between Froude number and each of the requirements for dynamic similarity using the portion of our data collected exclusively at Earth gravity. As is typically found (Alexander and Jayes, 1983), these relationships were described well by power-law equations of the form $y = aFr^b$, where Fr is the Froude number. Duty factor = $0.394Fr^{-0.174}$ ($r^2 = 0.99$); relative stride length = $2.312Fr^{0.390}$ ($r^2 = 0.99$); relative peak vertical force = $2.379Fr^{0.123}$ ($r^2 = 0.97$); relative peak virtual leg compression = $0.180Fr^{0.238}$ ($r^2 = 0.98$). Dashed lines are the solutions to these equations for each fixed absolute velocity at different levels of reduced gravity. For comparison, we have included data for walking at 1 m/s from Donelan and Kram (1997). Values are means \pm 1 s.e.m., $N = 10$. All changes were statistically significant ($P < 0.0001$). Some error bars are not visible because they are smaller than the symbols.

23%. This discrepancy is further illustrated by the relative peak vertical force data for fixed absolute velocities plotted in Fig. 3C. The dynamic similarity hypothesis predicts that reducing gravity, while maintaining a constant absolute velocity, would cause a more subtle increase in relative peak vertical force than we measured. There was, on average, a 21% difference between the predictions of the dynamic similarity hypothesis and our relative peak vertical force results at 0.25g. Thus, our subjects did not meet this third requirement for dynamic similarity.

A fourth prediction of the dynamic similarity hypothesis is that animals run with equal relative peak virtual leg compressions at the same Froude number. We found, however, that people ran with very different relative peak virtual leg compressions at equal values of the Froude number ($P < 0.0001$) (Fig. 2D). At the same Froude number, as we decreased gravity from 1.00g to 0.25g, relative peak virtual leg compression systematically decreased by an average of 53%. This departure from the predicted pattern is also demonstrated by the relative peak virtual leg compression data for fixed absolute velocities (Fig. 3D). The Froude-based dynamic similarity hypothesis predicts that, at a given absolute velocity, reducing gravity would substantially increase relative peak virtual leg compression. In fact, people ran with decreased relative peak virtual leg compressions at lower levels of simulated reduced gravity. On average, the difference between measured and predicted relative peak virtual leg compression at 0.25g was 129%. Our subjects did not fulfill this fourth requirement for dynamic similarity.

Fixed absolute velocity conditions

Duty factors were smaller in lower levels of simulated reduced gravity (Fig. 3A) ($P < 0.0001$). At the four velocities tested, between 1.00g and 0.25g, the decrease in duty factor averaged 29%. At each level of gravity, our subjects ran with smaller duty factors at faster velocities ($P < 0.0001$). The average decrease in duty factor between 2.0 m s^{-1} and 5.0 m s^{-1} was 30%. In general, the effect of decreasing gravity on duty factor paralleled the effect of increasing velocity.

Relative stride lengths were longer in lower levels of simulated reduced gravity (Fig. 3B) ($P < 0.0001$). The increase in relative stride length between 1.00g and 0.25g averaged 20% at the four velocities tested. At each level of gravity, our subjects ran with longer relative stride lengths at faster velocities ($P < 0.0001$). The average increase in relative stride length between 2.0 m s^{-1} and 5.0 m s^{-1} was 102%. While reduced gravity and increased velocity both resulted in longer stride lengths, the effect of reduced gravity on relative stride length was small compared with the effect of increased velocity.

Relative peak vertical ground reaction forces were greater in lower levels of simulated reduced gravity (Fig. 3C) ($P < 0.0001$). Recall that relative peak vertical force is equal to the peak vertical force divided by body weight (mg). At the four velocities tested, between 1.00g and 0.25g, the increase in relative peak vertical ground reaction forces averaged 50%. At

each level of gravity, our subjects ran with greater relative peak vertical ground reaction forces at faster velocities ($P < 0.0001$). The average increase in relative peak vertical force between 2.0 m s^{-1} and 5.0 m s^{-1} was 28%.

Relative peak virtual leg compressions were smaller in lower levels of simulated reduced gravity (Fig. 3D) ($P < 0.0001$). At the four velocities tested, the decrease in relative peak virtual leg compression between 1.00g and 0.25g averaged 39%. At each level of gravity, our subjects ran with larger relative peak virtual leg compressions at faster velocities ($P < 0.0001$). The average increase in relative peak virtual leg compression between 2.0 m s^{-1} and 5.0 m s^{-1} was 42%. In contrast to the other criteria for dynamic similarity, decreased gravity and increased velocity had opposite effects on relative peak virtual leg compression.

Discussion

Equal Froude number comparisons

Humans do not run in a dynamically similar fashion at equal Froude numbers achieved through different combinations of velocity and simulated reduced gravity (Fig. 2). While the departure of even a single requirement from the predictions of dynamic similarity is sufficient for the rejection of strict dynamic similarity, our conclusion is based on the systematic departure of four requirements. These requirements are duty factor, relative stride length, relative peak vertical force and relative peak virtual leg compression. The phase relationship requirement of the dynamic similarity hypothesis was technically met. However, it did not provide a discriminating test of the dynamic similarity hypothesis because, during normal bipedal locomotion, the left leg is always half a stride cycle out of phase with the right leg.

The prediction of the dynamic similarity hypothesis that we have left untested requires that animals run with equal relative mechanical power outputs at the same Froude number. We have not tested this requirement because the methodology and meaning of mechanical power measurements in running are not clear (van Ingen Schenau and Cavanagh, 1990; Williams, 1985). An alternative is to consider the metabolic cost of transport (Alexander and Jayes, 1983). Farley and McMahon (1992) have demonstrated that the metabolic cost of transport (per unit body weight) in running is nearly constant across different velocities and levels of gravity. While this criterion is technically met, the cost of transport is not a discriminating test of the dynamic similarity hypothesis because it is not altered with changes in velocity or levels of gravity.

One possible reason for the failure of the Froude number to predict dynamic similarity in reduced-gravity running is that it is only the ratio of inertial to gravitational forces. These forces are not sufficient to describe bouncing gaits (Alexander, 1989). The Froude number ignores the important contribution of elastic forces to running mechanics (for a review, see Farley and Ferris, 1998). This omission of elastic forces is illustrated by the departure of the relative peak virtual leg compression data, the elastic similarity requirement, from the predictions of

the dynamic similarity hypothesis (Fig. 3D). We concur that, for two running animals to be dynamically similar, it is necessary that they have equal Froude numbers (Alexander, 1989). However, our results indicate that equal values of the Froude number are not sufficient for their movements to be dynamically similar. Even if a new dynamic similarity hypothesis could incorporate inertial, gravitational and elastic forces, it too might fail to predict dynamic similarity in reduced-gravity running. This is because animals have the ability to control their movement using their nervous system and are not constrained to the same responses as passive mechanical systems.

Is dynamic similarity in reduced gravity possible?

Dynamic similarity is usually used to compare animals that differ in size. It might at first seem futile to explore dynamic similarity by changing gravity and not size because a structure cannot be elastically similar to itself in different levels of gravity. That is, the same structure will not deform under its own weight in a geometrically similar fashion at different gravity levels. However, animals are not simply passive structures; they can adjust the effective elastic properties of their musculoskeletal system (Farley and Gonzalez, 1996; Farley et al., 1998; Ferris et al., 1998). As a result, it cannot be determined *a priori* whether an animal may behave in an elastically similar manner to itself in different levels of gravity.

Indeed, we found that humans do adjust their effective elastic properties in response to changes in gravity level. The relevant elastic property for a running animal that behaves like a spring-mass system is the leg spring stiffness (k_{leg}) (Blickhan, 1989; McMahon and Cheng, 1990). Leg spring stiffness largely determines the dynamic interaction between the stance leg and the ground and, thus, plays an important role in the overall running mechanics. Leg spring stiffness is defined as the ratio of the peak vertical ground reaction force to the peak virtual leg compression, both of which occur at mid-stance when the leg is vertical (Farley and Ferris, 1998):

$$k_{\text{leg}} = \frac{F_{\text{peak}}}{\Delta L_{\text{leg}}} \quad (4)$$

Averaged across the four absolute velocities tested, we found that leg spring stiffness decreased by 37% between 1.00g and 0.25g ($P < 0.0001$) (Fig. 4). The data of He et al. (1991) showed a similar trend but, because of their small sample size ($N=4$), it was not statistically significant.

Is dynamic similarity in reduced gravity preferred?

Although leg stiffness changes with gravity, our results indicate that there are no two velocity and gravity combinations at which humans will prefer to move in a dynamically similar manner. This is because the effects of velocity and gravity on the requirements of dynamic similarity differed in both magnitude and direction as shown by the slopes of the lines in Fig. 5. The single intersection of

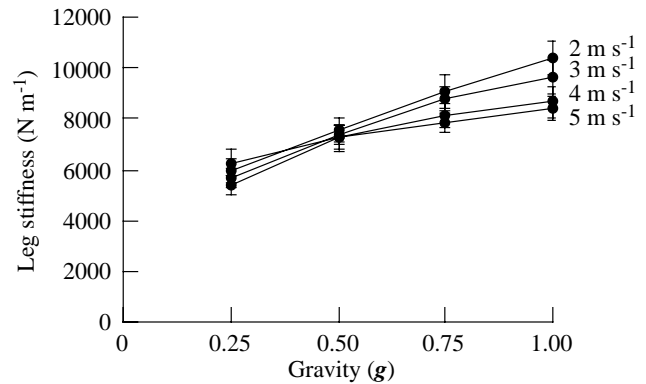


Fig. 4. The effect of reduced gravity on leg stiffness for four fixed absolute velocities. Values are means ± 1 s.e.m., $N=10$.

the lines at 1.00g indicates that the subjects' preferred responses to reduced gravity were such that it would never be the case that all the dynamic similarity requirements would be met simultaneously. Although our subjects did not prefer to run in a dynamically similar way in different levels of gravity, it might be possible for them to alter their running

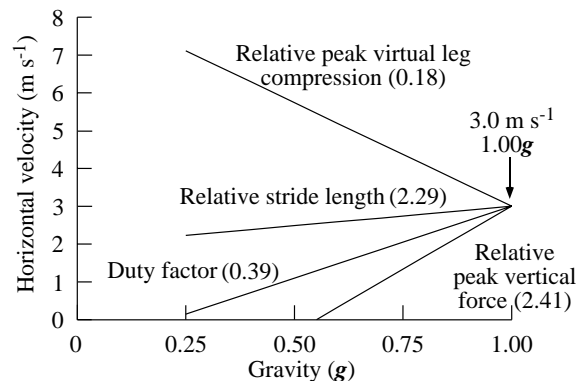


Fig. 5. The effects of velocity and gravity on the requirements of dynamic similarity. There were no two combinations of velocity and gravity where our subjects preferred to run in a dynamically similar manner. At 3.0 m s⁻¹ and 1.00g, on average, our subjects ran with a duty factor of 0.39, a relative stride length of 2.29, a relative peak vertical force of 2.41 and a relative peak virtual leg compression of 0.18. Each line on this graph represents combinations of velocity and gravity that keep each requirement constant and equal to these values. In other words, the lines are isograms for each requirement. At any given gravity level, different velocities would be needed to keep each requirement equal to the 1.00g, 3.0 m s⁻¹ value. To obtain the equations for these lines, we used a multiple linear regression of velocity and gravity on our measured values for each requirement: duty factor = 0.377 - 0.039u + 0.015g ($r^2=0.81$, $P=0.005$); relative stride length = 1.024 + 0.604u - 0.063g ($r^2=0.93$, $P=0.160$); relative peak vertical force = 3.092 + 0.238u - 0.162g ($r^2=0.68$, $P=0.013$); relative peak virtual leg compression = 0.028 + 0.018u + 0.010g ($r^2=0.74$, $P=0.003$), where u is horizontal velocity and g is gravitational acceleration. We set each equation equal to the measured 1.00g, 3.0 m s⁻¹ values and solved for the corresponding velocity at different levels of gravity.

mechanics and run in a way that meets the dynamic similarity criteria.

Alternative dimensionless numbers for dynamic similarity

Dimensionless numbers that use only horizontal velocity and gravity as variables (such as our use of the Froude number) are not sufficient for predicting dynamic similarity in reduced gravity running (Fig. 5). However, other dimensionless ratios may provide the basis for useful alternative dynamic similarity hypotheses for running. Recognizing the role of elastic forces, investigators have proposed the Strouhal number St and the Groucho number Gr as such alternatives (Alexander, 1989; Blickhan and Full, 1993; McMahon et al., 1987; Minetti et al., 1994). The Strouhal number can be thought of as a relative frequency of vibration (Alexander, 1989), and for running it can be represented by:

$$St = (v/L_{leg})/\omega_0, \quad (5)$$

where v is the vertical landing velocity and ω_0 is the natural frequency of the spring-mass system (McMahon et al., 1987). Another formulation of the Strouhal number uses horizontal rather than vertical velocity and stride frequency rather than natural frequency (Minetti et al., 1994). This formulation, as of yet, has not met with much success. The Groucho number (McMahon et al., 1987) can be thought of as a dimensionless vertical landing velocity:

$$Gr = \frac{v\omega_0}{g}. \quad (6)$$

The Groucho number is the ratio of a vertical Froude number and a vertical Strouhal number (Alexander, 1989).

We found that neither the Groucho number nor the vertical Strouhal number predicted dynamic similarity in reduced-gravity running (Fig. 6). For example, when our subjects ran at different speeds and levels of simulated gravity that equated to the same Groucho number, they had different relative stride lengths (Fig. 6B) and relative leg compressions (Fig. 6D), but approximately equal duty factors (Fig. 6A) and relative peak vertical forces (Fig. 6C). Therefore, the Groucho number described the combined effects of speed and gravity on duty factor and relative peak vertical force remarkably well, but failed to describe the combined effects on relative stride length and relative leg compression. The vertical Strouhal number did not accurately describe any of the relationships (Fig. 6E–H). Just as for the Froude number, for two running animals to be dynamically similar, it might still be necessary that they have equal Groucho or Strouhal numbers. However, our results indicate that an equal value of either dimensionless number alone is not sufficient for dynamic similarity.

Dynamic similarity and the walk–run transition

It is intriguing that, in simulated reduced gravity, the Froude number predicts walk–run transition velocities (Kram et al., 1997) but not the biomechanics of either walking (Donelan and Kram, 1997) or running (present study). In normal and reduced

gravity, humans prefer to switch from a walk to a run at a Froude number of approximately 0.5 (Kram et al., 1997). Our subjects did not run in a dynamically similar manner at this critical Froude number (Fig. 2) nor would we expect them to walk in a dynamically similar manner (Donelan and Kram, 1997). It appears that the relationship between inertial and gravitational forces is a key trigger for the walk–run transition, but it is not the lone determinant of walking and running biomechanics. This is not without precedent. For example, the Froude number is used in hydraulics to predict the abrupt transition between two very different flow regimes characteristic of a ‘hydraulic jump’ or a ‘bore’ (Stoker, 1957). On either side of the fluid transition, the Froude number describes a balance between inertial and gravitational forces that may affect the flow in more subtle ways, but additional dimensionless ratios of forces need to be considered to describe completely the mechanics of the fluid flow. Similarly, the transition between walking and running in reduced gravity occurs at a critical Froude number, but at slower or faster velocities the Froude number is not sufficient for describing dynamic similarity.

Can a single dynamic similarity hypothesis for walking and running be successful?

Although Alexander and Jayes (1983) applied their dynamic similarity hypothesis to both walking and running gaits, we suggest that a single dynamic similarity hypothesis for the effects of size, velocity and gravity on both gaits will not be successful. This is because simulated reduced gravity has different effects on walking and running mechanics (Fig. 3). A particularly illustrative example is shown in Fig. 3B. As we decreased gravity from 1.00g to 0.25g, subjects ran with longer relative stride lengths (+20%) but walked with slightly shorter relative stride lengths (–8%). Thus, the effect of gravity on relative stride length during walking and running was different in both direction and magnitude. While subjects used lower duty factors at lower levels of gravity in both gaits, during running the duty factor decreased three times as much as during walking (–29% versus –9%, Fig. 3A). The different effects of gravity are not surprising because, from a mechanical viewpoint, running (spring-mass system) and walking (inverted pendulum) are fundamentally different. The effect of gravity on spring-mass mechanics is different from the effect of gravity on inverted pendulum mechanics (Meriam, 1975). Our empirical kinematic discrepancies and the fundamental mechanical differences demonstrate that a single unifying hypothesis will not adequately describe dynamic similarity across size, velocity and gravity for both walking and running.

Concluding remarks

The Froude number has proved to be a very useful tool for predicting the mechanics of legged animal locomotion over a wide range of body sizes and velocities at Earth gravity (Alexander, 1989; Alexander and Jayes, 1983). However, the Froude number fails to predict dynamic similarity in reduced-gravity running. Thus, as a dynamic similarity hypothesis for

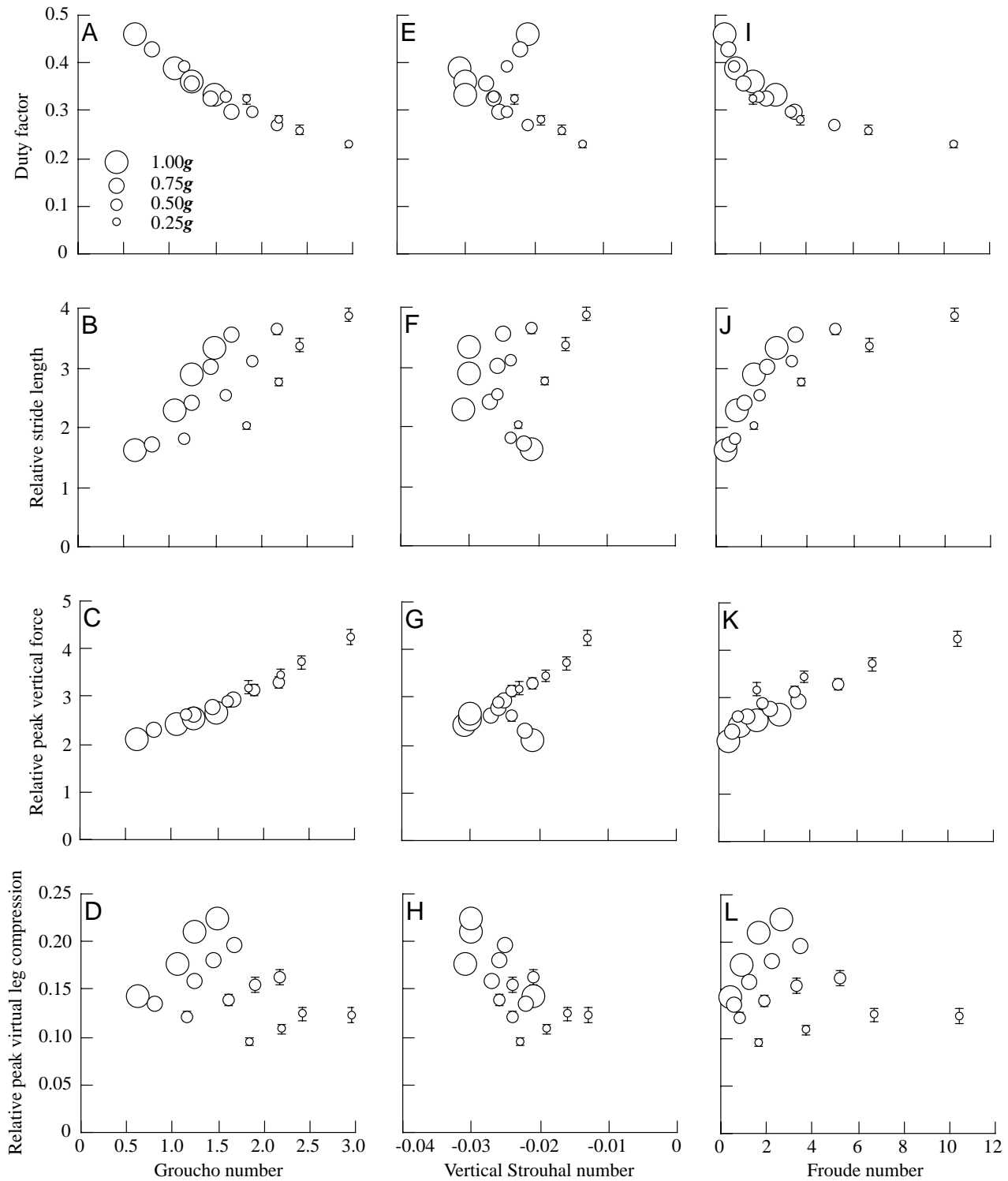


Fig. 6. The requirements of dynamic similarity plotted as a function of the Groucho, vertical Strouhal and Froude numbers. In these plots, if a dimensionless number describes the combined effects of velocity and gravity, the data for a given requirement would fall along a single line. For a single dimensionless number to describe dynamic similarity, this must occur for all the requirements. Thus, the Groucho (A–D) and vertical Strouhal (E–H) numbers do not predict dynamic similarity in reduced-gravity running. The requirements of dynamic similarity, plotted as a function of the Froude number (I–L), are shown for comparison. The plotted data are from the fixed absolute velocity portion of our study ($2\text{--}5\text{ m s}^{-1}$) and, as a result, the Froude numbers span a greater range than the data depicted in Fig. 2. The size of symbol indicates the magnitude of simulated gravity. Values are means ± 1 s.e.m., $N=10$. Some error bars are not visible because they are smaller than the symbols.

running, it is either incorrect or incomplete. As a consequence, the Froude number alone should not be used to interpret the underlying mechanisms behind running biomechanics. It appears that the inertial and gravitational forces that comprise the Froude number are not sufficient to characterize bouncing gaits because elastic forces also play an important role (Alexander, 1989). Spring-mass models incorporate inertial, gravitational and elastic forces, and they have been shown to accurately predict running, trotting and hopping mechanics in a variety of conditions (Blickhan, 1989; Farley and Ferris, 1998; McMahon and Cheng, 1990). A dynamic similarity hypothesis should reflect the physical principles underlying the movement. Thus, future work

should further explore dynamic similarity in bouncing gaits using models of spring-mass systems. A successful dynamic similarity hypothesis should not only describe dynamic similarity across size, velocity and gravity, but also explain why the Froude number works so well at Earth gravity.

Appendix

Limitations of our reduced gravity simulation technique

The primary criticism of our simulation technique is that it applies vertical force only at the torso and, as a result, the limbs still experience Earth gravity at all levels of simulated reduced gravity. Nonetheless, evidence suggests that our device closely approximates running in true reduced gravity. When humans run, they behave like simple spring-mass systems (Blickhan, 1989; McMahon and Cheng, 1990). These models consider the body as a point mass, located at the center of mass, and the legs as massless linear springs. Despite disregarding swing limb dynamics, spring-mass models accurately predict the mechanics of running in a variety of situations (for a review, see Farley and Ferris, 1998) including simulated reduced gravity (He et al., 1991; Newman, 1996).

Further, our simulator results correspond closely to those obtained during parabolic flight experiments, a truly accurate simulation of reduced gravity. In such experiments, subjects walk or run inside an aircraft that is following a parabolic trajectory (Davis and Cavanagh, 1993). For brief portions of the trajectory, all body segments experience true reduced gravity without the use of springs, counterweights or water submersion. Using parabolic flight, Newman (1996) investigated the effect of reduced gravity on the mechanics of two subjects running at 2 m s^{-1} . Despite the differences in simulation techniques, our results for duty factor, relative stride length and relative peak vertical force are remarkably similar in both pattern and magnitude to those of Newman (1996) (Fig. 7). It is difficult to compare these results quantitatively because the two experiments were performed at different levels of reduced gravity. However, it appears that, for the purposes of this study, our simulation method was valid.

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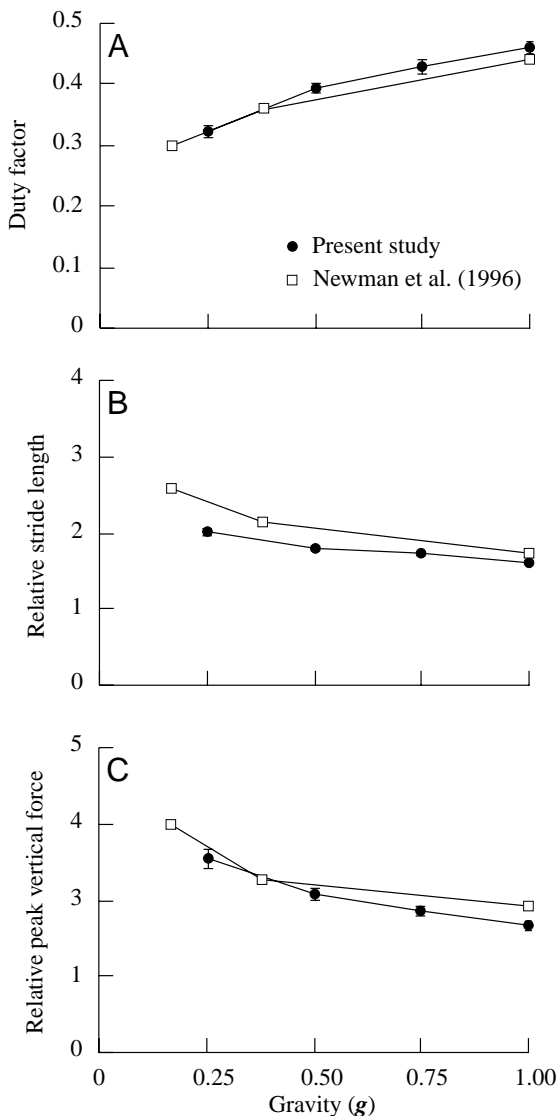


Fig. 7. Comparison of results obtained using our reduced gravity simulation technique (filled circles) with those obtained using parabolic flight (open squares) (Newman, 1996) for (A) duty factor, (B) relative stride length and (C) relative peak vertical force. The data for both studies were collected at 2 m s^{-1} . Present data are means ± 1 s.e.m., $N=10$. Error bars for the parabolic flight results are not shown since $N=2$. Some error bars are not visible because they are smaller than the symbols.

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