Hopping frequency in humans: a test of how springs set stride frequency in bouncing gaits

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FARLEY, CLAIRE T., REINHARD BLICKHAN, JACQUELINE SAITO, AND C. RICHARD TAYLOR. *Hopping frequency in humans: a test of how springs set stride frequency in bouncing gaits.* J. Appl. Physiol. 71(6): 2127-2132, 1991.—The storage and recovery of elastic energy in muscle-tendon springs is important in running, hopping, trotting, and galloping. We hypothesized that animals select the stride frequency at which they behave most like simple spring-mass systems. If higher or lower frequencies are used, they will not behave like simple spring-mass systems, and the storage and recovery of elastic energy will be reduced. We tested the hypothesis by having humans hop forward on a treadmill over a range of speeds and hop in place over a range of frequencies. The body was modeled as a simple spring-mass system, and the properties of the spring were measured by use of a force platform. Our subjects used nearly the same frequency (the "preferred frequency," 2.2 hops/s) when they hopped forward on a treadmill and when they hopped in place. At this frequency, the body behaved like a simple spring-mass system. Contrary to our predictions, it also behaved like a simple spring-mass system when the subjects hopped at higher frequencies, up to the maximum they could achieve. However, at the higher frequencies, the time available to apply force to the ground (the ground contact time) was shorter, perhaps resulting in a higher cost of generating muscular force. At frequencies below the preferred frequency, as predicted by the hypothesis, the body did not behave in a springlike manner, and it appeared likely that the storage and recovery of elastic energy was reduced. The combination of springlike behavior and a long ground contact time at the preferred frequency should minimize the cost of generating muscular force.

locomotion; elastic energy; running

IT IS OBVIOUS that a person hopping on a pogo stick uses springs to store and recover energy. Although less obvious, a person running at high speeds uses springs in much the same way. In their classic paper, Cavagna et al. (10) found that running humans literally bounce along the ground, storing and recovering energy like a bouncing ball. In subsequent studies, it was found that this spring mechanism is common to running, hopping, trotting, and galloping in birds and mammals (8, 13).

Where are the springs? The tendons and cross-bridges of the muscles both act as good springs. The most obvious spring is the large Achilles tendon. In running humans, this tendon alone can conserve 35% of the total mechanical energy required during each stride (16). This is only one of a series of muscle-tendon springs involved in running. The "total spring" extends up the legs and throughout the body, involving many of the skeletal muscles and tendons (1). The attached cross-bridges of the active muscles as well as the tendons can be stretched and recoil, and the relative contributions of these two springs in series depend on their geometry (3, 9, 15). In muscles with long compliant tendons, the tendons can store much more elastic energy than the muscles. For example, the Achilles tendons in humans, wallabies, and dogs can store ~10 times more elastic energy than the ankle extensor muscles (3).

There is an important difference between the passive pogo-stick spring and the muscle-tendon springs in animals. The pogo spring operates for free, whereas the muscles have to be activated and consume metabolic energy for the running springs to work (2). The muscles are activated before hitting the ground (12, 19), thus reducing the amount that they are stretched during landing. Most of the stretch can be taken up by the tendons, resulting in elastic energy storage in these spring elements (3). The purpose of this study is to investigate the tuning of these muscle-tendon springs for elastic energy storage.

We consider the whole body as a simple spring-mass system and measure the properties of the spring. This simplification is reasonable. Recent models of running that treat humans and animals in this way accurately predict how the mechanics of running, trotting, hopping, and galloping change with speed and animal size (4, 5, 20). Furthermore, a recent study has shown that runners, trotters, and hoppers, including humans, rebound from the ground as if they were simple spring-mass systems (7).

The properties of the spring have to be adjusted with increasing speed (21). Stiffer springs are needed to allow shorter rebound times at higher speeds. According to the models, there is a unique stride frequency and rebound time for each speed if reasonable assumptions are made for several other variables (5, 20). These models correctly predict the stride frequency used by running humans. Metabolic cost is minimized at this frequency, increasing at higher and lower frequencies (11). This suggests a finely tuned system in which storage and recovery of elastic energy are maximized at the preferred frequency.

We test the hypothesis that the muscle-tendon spring system behaves most like a spring-mass system at the preferred hopping frequency. We use human hopping to test this hypothesis because it is an extremely simple spring-mass system in which frequency can be varied. Furthermore, we find basic similarities between hopping in place and forward hopping, allowing a further simplification of the measurements by having subjects vary frequency while hopping in place. We begin by measuring

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the range of spring adjustment as speed is varied. Then we vary frequency during hopping in place and compare the behavior of the muscle-tendon spring system with that of an ideal spring-mass system.

MATERIALS AND METHODS

Subjects. Four subjects (2 males and 2 females) participated in the study. They were between the ages of 20 and 22 yr and in good health. Their average mass was 63.5 kg, and the range was from 60 to 68 kg.

Protocols. We measured the adjustments in the spring system as the subjects hopped on two legs on a treadmill over a speed range from 0 to 3 m/s. The measurements were made after the subjects had hopped at a given speed for 2 min.

According to our hypothesis, the use of stored elastic energy should decrease at frequencies above and below the preferred frequency at any speed. To test this prediction, the subjects hopped in place, using a range of frequencies higher and lower than their preferred; and we measured the properties of the spring. The hopping frequencies were set by a metronome and ranged from 1.2 to 3.6 hops/s.

To examine the effect of muscle recruitment on the tuning of muscle-tendon springs, the subjects hopped at each frequency in two ways. In one case, they were allowed to hop in any way that they wanted ("normal" hopping); and in the other case, they hopped as high as possible at each frequency ("maximum height" hopping). The subjects were told that each hop had to be a continuous motion and they could not just wait motionless on the ground between hops. Maximum height hopping was studied because it was thought to resemble high-speed forward hopping in terms of muscle recruitment. A recent study has shown that faster muscle fibers are recruited when a person hops higher at any frequency (22). We predicted that the spring system would be adjusted to match the properties of the active muscle fibers and thus optimize the use of elastic energy at the preferred frequency for each kind of hopping.

Measurements. For forward hopping on the treadmill, vertical ground reaction force was measured by use of a treadmill-mounted force platform. A strain-gauge force platform (model OR6-5-1, Advanced Mechanical Technology, Newton, MA) was mounted under the tread (17). The cross-talk from a horizontal force to the vertical is <1%. The natural frequency of vertical vibration of the force platform mounted in the treadmill is 160 Hz. The signal-to-noise ratio for the measurement of the ground reaction force of a human runner (weight = 700 N) is ~100:1.

The subjects hopped in place on a ground-mounted Kistler force platform (model 9261A). This force platform is linear (±0.5%) over a force range of 0–2.0 kN and has a natural frequency >200 Hz when loaded with a 70-kg person. The force signal was sampled at 500 Hz.

Mechanical properties of the spring. To evaluate whether the body behaved like a simple spring-mass system, we compared the vertical ground reaction force with the vertical displacement of the center of mass. The vertical displacement was calculated by integrating the vertical ground reaction force twice in software. Cavagna (6) has described the calculations in detail.

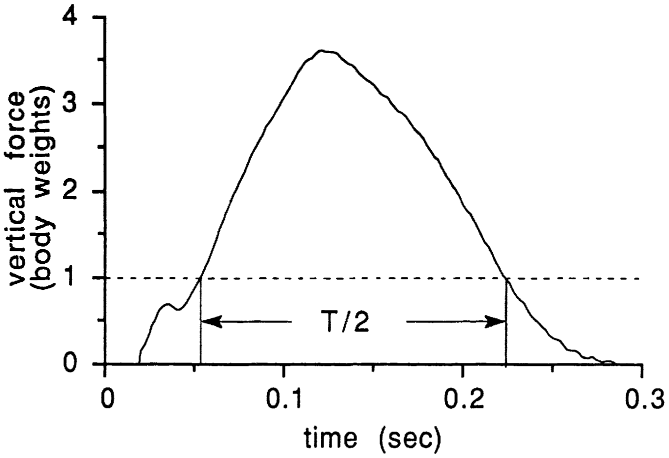

FIG. 1. Vertical spring stiffness of whole body was calculated by measuring one-half of a resonant period ($T/2$) and using *Eqs. 1* and *2*. $T/2$ is time when vertical ground reaction force is greater than one body weight.

We compared the relationship between force and displacement of the body's vertical spring with that of a simple mechanical spring. When a mechanical spring is stretched, the force in it rises and it stores elastic energy. The energy is released as the spring recoils and the force in it falls. The area under the stretching force-displacement curve is the elastic energy stored in the spring, and the area under the recoil curve is the energy returned. If the spring is ideal, the two areas are the same, and the paths of the stretch and recoil force-displacement curves are identical.

Although it was possible to compare the relationship between force and displacement of the muscle-tendon spring system with that of a simple mechanical spring, it was not possible to calculate how much elastic energy was stored and returned by the muscle-tendon spring system from the areas under the force-displacement curves. An important difference between the muscle-tendon spring system and a mechanical spring system is that the muscles can add mechanical energy to the system. In a series of identical hops, the areas under the landing and takeoff force-displacement curves must be the same so that no mechanical energy is lost or gained. If some elastic energy is dissipated during a hop, the muscles must add enough energy to make up for the loss. Because the muscles can add energy to the system, we could not compare the areas under the landing and takeoff force-displacement curves to evaluate elastic energy storage and recovery.

The effective vertical stiffness (k) of the muscle-tendon system was calculated from the vertical force exerted on the ground during the ground contact phase (Fig. 1). If a simple spring-mass system were dropped onto the ground, the force that it would exert on the ground would pass through its weight, $M \cdot g$ (M is mass and g is gravitational acceleration), during landing and takeoff. The time between these two points ($T/2$) would be one-half of a resonant period of vibration (ω). We measured $T/2$ for our subjects with the use of the force platform. The reso-

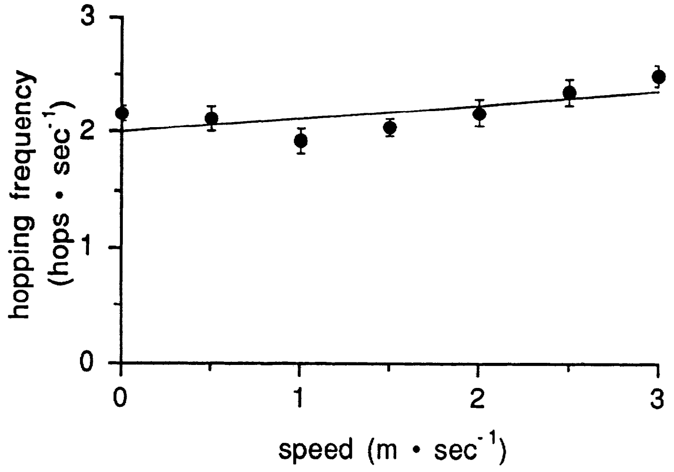

FIG. 2. Nearly the same frequency was used for forward hopping as for hopping in place (zero forward speed). Each data point represents mean for all subjects at each speed; error bars, SE. Line, least-squares regression (hopping frequency = 2.00 + 0.12 • speed, $r^2 = 0.461$).

nant frequency and k of the spring-mass system were calculated from $T/2$ (5, 7, 20, 21)

$$\omega = 2\pi/T \tag{1}$$

$$k = M \cdot \omega^2 \tag{2}$$

The effective vertical stiffness was only calculated at frequencies at which the system behaved like a simple spring-mass system (≥2.2 hops/s).

RESULTS

Hopping frequency, time of contact, and speed. The subjects used an almost constant hopping frequency as they increased speed (Fig. 2). On average, hopping frequency did not increase between 0.5 and 2.0 m/s and then began to increase at higher speeds. Surprisingly, the subjects used nearly the same hopping frequency when the treadmill was turned off and they simply hopped in place. This frequency varied by 9% between individuals, and the variation was not related to body mass. The average frequency for hopping in place was 2.17 ± 0.07 (SE) hops/s, and this was defined as the preferred frequency.

Behavior of the muscle-tendon spring system during forward hopping. The body bounced along the ground much like a simple spring-mass system over the entire range of hopping speeds (Fig. 3). Figure 3 plots the vertical ground reaction force as a function of the vertical displacement of the center of mass for a person hopping forward. The force was zero while the person was in the air. After the person landed, the force increased as the center of mass moved downward and the muscle-tendon spring system was stretched. The highest force was reached when the center of mass was at its lowest point. The force-displacement curve followed almost the same path as the center of mass moved upward and the person became aerial.

As forward hopping speed increased, the properties of the vertical spring were adjusted to allow the person to rebound from the ground more quickly. Force increased more rapidly with displacement, and the vertical stiffness of the body almost doubled with only a small change in the hopping frequency (Fig. 4).

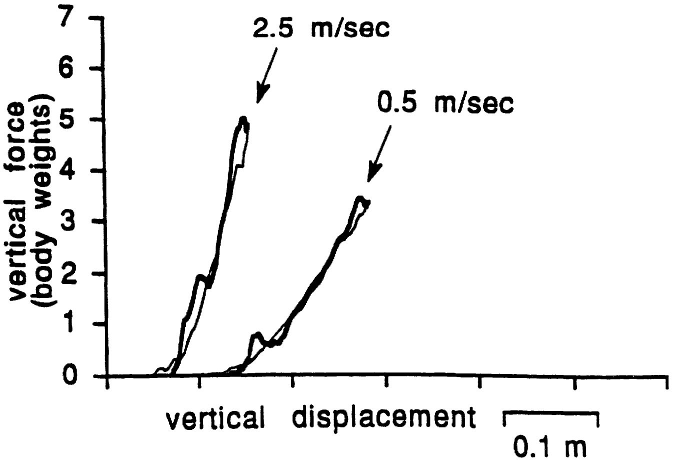

FIG. 3. Body behaved like a simple spring-mass system at all forward hopping speeds. Vertical force (normalized to bodyweight) is plotted as a function of vertical displacement of center of mass for ground contact phase. Convention used here is that displacement increases as center of mass moves downward. These are typical records (from *subject 2,* mass 64 kg). Thicker lines represent landing (spring is being stretched); thinner lines represent takeoff (spring recoils).

Behavior of the muscle-tendon spring system during hopping in place at high frequencies. The subjects preferred to hop in place at 2.2 hops/s. Our hypothesis suggests that the body behaves most like a simple spring-mass system at this frequency. However, the body behaved as much like a simple spring-mass system when subjects hopped at higher frequencies, up to and including the maximum possible frequency, 3.6 hops/s (Fig. 5).

As hopping frequency increased above the preferred frequency, the vertical stiffness more than doubled during both normal and maximum height hopping (Fig. 6). In the same frequency range, the ground contact time decreased by 30% from 0.302 ± 0.008 s at the preferred frequency to 0.204 ± 0.004 s at the highest frequency (Fig. 7). Similarly, during maximum height hopping, the ground contact time decreased from 0.203 ± 0.005 to 0.173 ± 0.004 s between the preferred and the highest frequencies.

At each frequency, the subjects spent less time on the

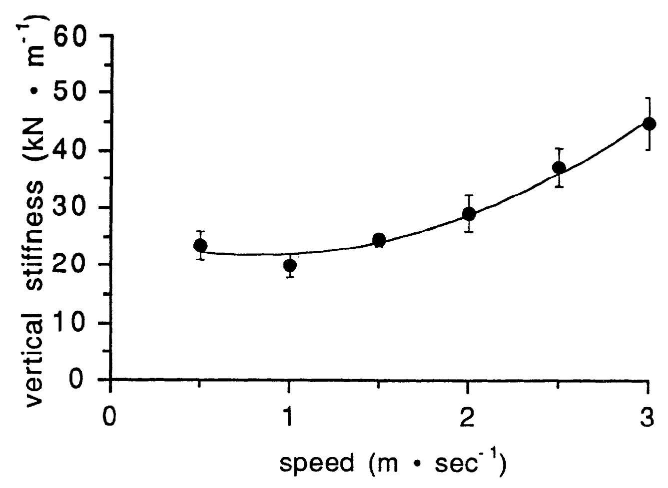

FIG. 4. Vertical spring stiffness (k) increased with increasing speed, allowing subjects to rebound from ground more rapidly at higher speeds. Each point is mean for all subjects; error bars, SE. Line, least-squares regression ($k = 25.3 - 8.24 \cdot \text{speed} + 5.02 \cdot \text{speed}^2$, $r^2 = 0.982$).

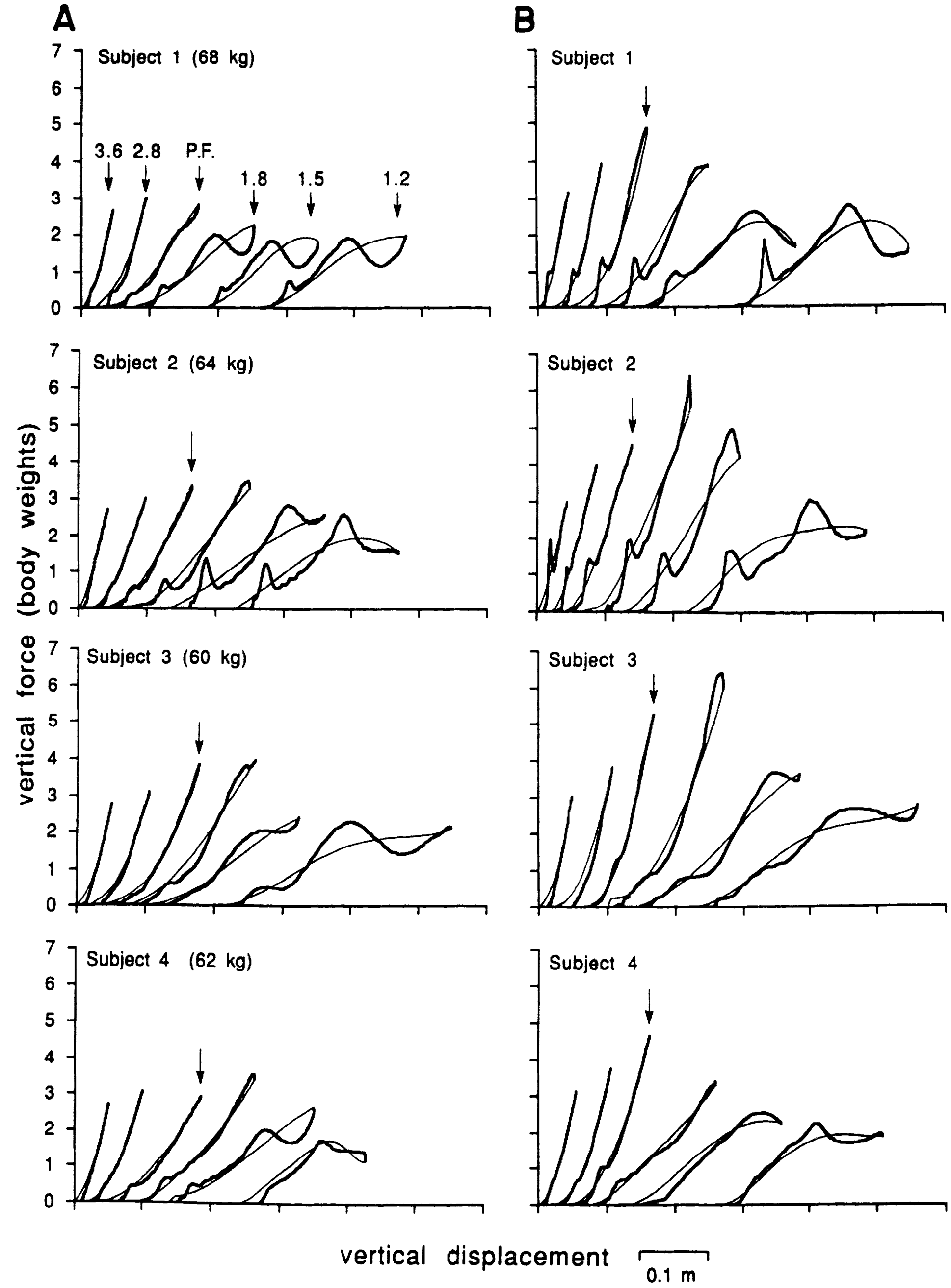

FIG. 5. During hopping in place, body behaved like a simple spring-mass system at preferred frequency and at higher frequencies. However, this was not true at lower frequencies, when force was not dependent on displacement in a way that is typical of a simple spring. Vertical force is plotted as a function of displacement of center of mass for ground contact phase. Convention used here is that displacement increases as center of mass moves downward. Force-displacement curves are labeled with hopping frequencies (in hops/s) in graph for *subject 1*; PF, preferred frequency (2.2 hops/s). For other subjects, the same frequencies are represented and preferred frequency is designated with an arrow. Thicker lines represent landing (muscle-tendon springs being stretched); thinner lines represent takeoff (muscle-tendon springs recoiling). *A*, normal hopping; *B*, maximum height hopping.

ground and their vertical stiffness was higher when they hopped as high as they could (Figs. 6 and 7). Despite these differences in the spring properties, the body behaved equally like a simple spring-mass system during normal and maximum height hopping at each frequency between the preferred and highest frequencies (Fig. 5).

The maximum vertical stiffness (achieved at the highest frequency during hopping in place and at the highest speed during forward hopping) was similar during maximum height hopping in place (49.5 ± 1.8 kN/m), normal hopping in place (45.7 ± 1.5 kN/m), and forward hopping (45.0 ± 4.5 kN/m) (Figs. 4 and 6).

Behavior of the muscle-tendon spring system during hopping in place at low frequencies. When the subjects hopped at frequencies below their preferred frequency, they did not behave as much like simple spring-mass systems. The force was not dependent on the displacement in a way that is typical of a simple spring (Fig. 5). During landing at the lowest frequency, force increased to a peak while the center of mass was moving downward (i.e., the muscle-tendon springs were being stretched) and then decreased while the center of mass continued its downward path. In some subjects, this pattern was repeated twice during landing, once at the beginning of the ground contact phase and once as the center of mass approached its lowest point. This is a clear deviation from the behavior of a simple spring-mass system because, in a simple mechanical spring, the force never falls while it is being stretched. Another clear deviation from springlike behavior was that in some subjects the force increased as the center of mass began to move upward and the muscle-tendon springs recoiled. In a simple mechanical spring, the force would never increase as it recoiled.

As hopping frequency increased from the lowest to the preferred frequency, the muscle-tendon spring system gradually behaved more like a simple spring-mass sys-

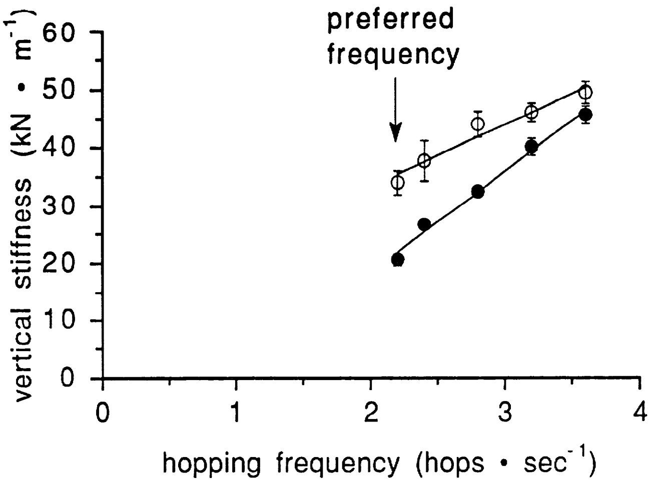

FIG. 6. Vertical spring stiffness (k) increased as a function of hopping frequency. Spring was stiffer both when subject hopped normally at high frequencies and when subject hopped higher at the same frequency. Closed symbols, normal hopping; open symbols, maximum height hopping. Each point is mean of all subjects; error bars, SE. Stiffness of spring was only calculated at hopping frequencies at which system resembled a spring-mass system (≥2.2 hops/s). Lines are linear least-squares regressions (normal hopping: $k = -16.6 + 17.5 \cdot \text{frequency}$, $r^2 = 0.990$; maximum height hopping: $k = 11.9 + 10.7 \cdot \text{frequency}$, $r^2 = 0.951$).

tem (Fig. 5). The shape of the landing force-displacement curve became more like that of a simple spring being stretched. At the preferred frequency, the landing and takeoff force-displacement curves followed almost identical paths, as they would in a simple spring being stretched and recoiling.

DISCUSSION

Our initial hypothesis, that the body behaves most like a spring-mass system at the preferred frequency, needs to be modified. We find that the system behaves like a simple spring-mass system over a wide range of frequencies extending from the preferred to the highest frequency possible during both normal and maximum height hopping. As frequency increases, stiffness is adjusted so that the body can still rebound from the ground in a springlike manner. Below the preferred frequency, the system does not behave like a simple spring-mass system. As the body moves downward and the muscle-tendon spring system is stretched, the force rises and falls at least once before the body reaches its lowest point. This pattern would never occur in a simple spring-mass system. However, a two spring-two mass system would have this force-displacement pattern if one spring were much stiffer than the other (1). When people hop at low frequencies, it is conceivable that there is one spring that is much stiffer than the rest of the muscle-tendon spring system and that this stiff spring stretches and recoils in a fraction of the time of the rest of the system. If this is the case, the points where the force decreases during landing correspond to the recoil of the stiff spring. In addition, during takeoff at low frequencies, the force-displacement curve does not resemble that of a simple spring-mass system. In some of the subjects, the force actually rises as the center of mass moves upward and the muscle-tendon spring system presumably recoils. This observation suggests that the muscles are actively adding mechanical energy to the system during takeoff to make up for elastic energy that was dissipated during landing.

Our refined hypothesis is that people choose the frequency at which they rebound from the ground in a springlike manner and at which the time available for force generation (the ground contact time) is maximized. Recent experiments have shown that metabolic rate during running is inversely proportional to the ground contact time over a range of speed and size (18). Cost triples as a horse, dog, or kangaroo rat increases speed, and the ground contact time is cut to one-third. When the ground contact time is shorter (at higher speeds), muscular force must be generated faster, requiring faster fibers with cross-bridges that cycle and consume ATP at higher rates (15, 23). At the preferred frequency during both normal and maximum height hopping, the ground contact time is longer than at higher frequencies and, presumably, the cost of generating muscular force is lower.

The stride frequencies used by running, trotting, galloping, and hopping animals are strongly dependent on body mass (14, 24). A galloping or hopping animal uses a stride frequency similar to a human hopper of similar size. These observations suggest that fundamental properties of the muscle and tendon system, such as muscle cross-bridge cycling rate and tendon stiffness, are setting stride frequency. They also suggest that the findings of this study may be general to all animals that use bouncing gaits.

We predict that the frequency selected by any running or hopping animal is the one at which the metabolic cost of operating the springs is the lowest. We have not measured metabolic energy consumed in the experiments reported here because hopping cannot be sustained long enough to make steady-state measurements over a wide enough range of speeds or frequencies. However, it is

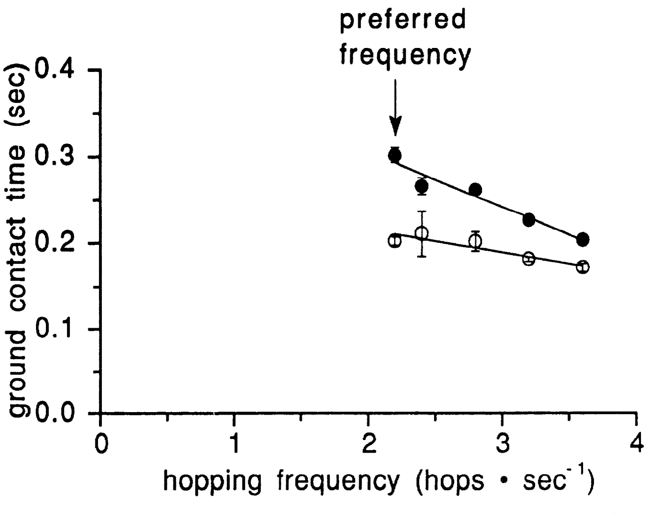

FIG. 7. Ground contact time (t_c) decreased between preferred frequency and highest frequency during both normal and maximum height hopping. Subjects spent less time on the ground at each frequency during maximum height hopping. Closed and open symbols, normal and maximum height hopping, respectively. Each point is mean of all subjects; error bars, SE. Lines are least-squares regressions (normal hopping: $t_c = 0.436 - 0.045 \cdot \text{frequency}$, $r^2 = 0.945$; maximum height hopping: $t_c = 0.267 - 0.026 \cdot \text{frequency}$, $r^2 = 0.858$).

known that running humans select the frequency at each speed at which the cost is lowest (11). Our refined hypothesis offers an explanation for why there is a stride frequency that minimizes the metabolic rate during running. We predict that metabolic rate will increase at lower frequencies because the body does not behave in a springlike manner and elastic energy is dissipated. Metabolic rate will increase at higher frequencies because the ground contact time is shorter.

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