

1. Supplementary Methods

Detailed description of the mechanical design and function of the custom clutch

The clutch comprises three sub-assemblies: the clutch frame, the pulley-ratchet and the pawl (cf. Fig. 1c). Detailed drawings and CAD models are provided as Supplementary Data 1 and Supplementary Data 2. These sets of components interact with each other during a clutching cycle that corresponds to a single stride of walking (cf. Fig. 2, bottom; Supplementary Video 2).

The clutch frame connects to the exoskeleton and supports the pulley-ratchet bearings, the pawl bearings and the pawl detent pin. The clutch frame is attached to the exoskeleton frame (Extended Data Fig. 2) using a single large screw, which provides a degree of self-alignment to the loads generated by the synthetic rope. Ball bearings are set into the clutch frame on either side of both the pulley-ratchet shaft and the pawl shaft, providing stable, double-shear, revolute joints. The spring-loaded pawl detent pin (whose role is described below) screws into a threaded hole in the frame, allowing pin force to be adjusted. The clutch frame is made from four parts for ease of manufacture and assembly. Two primary frame elements extend around the pulley-ratchet and pawl, connected at the top via three screws and a set of indexing surfaces for part alignment. These components experience substantial stress during clutch loading and were machined out of 7075-T6 aluminum. An additional component bridges the main components at the bottom of the assembly, further improving alignment and allowing the detent pin to be located below the pawl. This component has internal threads and was machined from 7075-T6 aluminum. Finally, a thin carbon steel rod bridges between the two main components to one side of the pawl, limiting the excursion of the pawl when it is in the disengaged position.

The pulley-ratchet sub-assembly (blue assembly in cf. Fig. 1c) rotates in the clutch frame, wraps up the rope, ratchets against the pawl, and causes pawl engagement and disengagement. The pulley shaft connects to bearings in the clutch frame, allowing the sub-assembly to rotate. The synthetic rope is tied to the pulley at a hole in its side. The rope wraps onto a cylindrical surface on the pulley, which is set in a groove to prevent the rope from slipping off. A small coil spring inside the pulley (visible as item 17 in the exploded assembly view on page 2 of Supplementary Data 1) provides a small torque in the opposite direction from that produced by tension in the rope. This ‘tensioning spring’ prevents the rope from going slack by wrapping it onto the pulley surface. A custom ratchet surface is attached to the pulley, coaxial to the pulley and shaft, via a permanent spline socket joint that provides distributed load transfer. The ratchet

has asymmetric teeth, each tooth having: (a) a curved side that allows the pawl tip to slip past during rotations that cause the rope to wrap onto the pulley and (b) a flat side that engages the pawl tip to prevent the rope from unspooling under tension. The flat side of the ratchet is angled such that the reaction force between the pawl and ratchet is primarily normal to the surface, with a small component that drives the pawl into the inside corner of the ratchet. Pins that engage and disengage the pawl are provided by the ‘pawl control’ component. Parallel pins offset from the center of this part make contact with either the outer or inner surface of the pawl as the pulley rotates, thereby moving the pawl into the engaged or disengaged position, respectively. The pawl control component is attached to the pulley through the spline joint, which allows adjustability of the pulley angles at which the pawl is engaged and disengaged. The pulley and pawl-control component experience substantial stresses and were machined from 7075-T6 aluminum. The ratchet surface experiences high stress at the contact point with the pawl and was machined from 17-4 PH stainless steel.

The pawl sub-assembly (red components in cf. Fig. 1c) rotates with respect to the clutch frame and is kept either engaged or disengaged with the ratchet by the detent pin. A shaft running through one end of the pawl connects to ball bearings, allowing rotational motion. The pawl extends towards the ratchet surface and, when engaged, has a small flat surface on its tip that locks against a matching surface on the ratchet tooth to prevent pulley rotations in one direction. The alignment of the pulley and ratchet were chosen to balance the force at the contact, which is reduced by a more tangent configuration, against ratchet tooth size and positional resolution, which are improved by steeper contact angles. The pawl is kept engaged with or disengaged from the ratchet by a spring-loaded detent pin that presses on a triangular feature at the base of the pawl. The detent pin consists of a ball-bearing-like pin element pressed onto the pawl by a small spring. The detent pin pushes on one of the sloped surfaces of the triangular feature of the pawl, such that part of the normal force induces a torque on the pawl in one direction. When the pawl is moved by the pawl-control pins of the pulley, the detent pin slips up and over the peak of the triangular feature, thus flipping the direction of torque generated. When the pawl is engaged with the ratchet and the pulley is rotated in the free-spinning direction, torque from the detent pin keeps the pawl engaged with the ratchet surface, leading to up and down motions and a clicking sound (Supplementary Video 2). When the pawl is in the disengaged configuration it presses steadily on the steel frame pin, which keeps it positioned for eventual re-engagement by the pawl control pin of the pulley.

The clutch engages at the beginning of the stance phase of walking, ratchets during early stance, holds the rope during mid- and late stance, disengages the ratchet at the end of stance, and allows free rotation during swing (cf. Fig. 2; Supplementary Video 1). At the end of the swing phase, just before heel contact, the ankle reaches its maximum dorsiflexion angle. This pulls the rope to its maximum extension, rotating the pulley to one extreme of its range, and causes one of the pawl-control pins to contact the outer surface of the pawl and flip it into the engaged configuration. The heel then contacts the ground, defining the beginning of stance, and the foot goes flat while the shank angle remains unchanged, corresponding to a plantarflexion of

the ankle joint. This allows the tensioning spring to take up slack in the rope while the ratchet teeth and pawl click past one another. The foot then remains flat on the ground while the shank progresses forward, corresponding to dorsiflexion of the ankle joint. This causes the ratchet and pawl to lock the pulley, building tension in the rope as the large exoskeleton spring is stretched. The heel then lifts off of the ground and, towards the end of the stance phase, the ankle begins to plantarflex again, eventually passing the maximum plantarflexion angle it reached during foot flat at the beginning of stance. This relieves tension from the rope, once again allowing the tensioning spring to wrap the rope up while the ratchet teeth and pawl slip past each other. At the end of the stance phase or the beginning of the swing phase, just as the toe leaves the ground, the ankle joint reaches its maximum plantarflexion angle. This allows the rope to reach its maximum retraction, with the pulley at the other extreme of its range, causing one of the pawl-control pins to contact the inner surface of the pawl and flip it into the disengaged configuration. During leg swing, the ankle joint dorsiflexes past the angle corresponding to foot flat at the beginning of stance (cf. Fig. 2d). The ratchet is disengaged, however, allowing natural ankle motions and adequate toe clearance. As the ankle reaches maximum dorsiflexion at the end of swing, the pawl is re-engaged and the cycle begins again.

2. Supplementary Discussion

In this section, we expand on the challenge presented by the ‘normal barrier’ of energy cost during walking, survey previous attempts to break it and expand on our interpretations of the underlying reasons the present device reduced metabolic rate.

The challenge: Why is it hard to reduce the energy cost of normal walking?

Humans are very skilled at normal walking. Over the past three to seven million years^{44,45}, we have evolved muscular¹, skeletal³ and neural⁴ structures that are well suited to walking. We learn and embed useful locomotion coordination strategies over our lifetimes⁵. We grow (or remove) muscle⁴⁶ and bone⁴⁷ in places it is useful (or unnecessary) for daily tasks such as locomotion over time scales of weeks and days, enabling more efficient movements (and saving energy that would be spent maintaining and carrying about unneeded tissues). We adapt to new environments during locomotion in minutes or seconds^{6,48,49}. We are exceptionally well-practiced at walking, taking about 10,000 steps per day⁷, or hundreds of millions of steps in a lifetime, thereby exceeding the 10,000 hour guideline for expertise⁸ by adulthood. Healthy, adult humans are expert at walking.

Metabolic energy use is an important aspect of walking performance. Over evolutionary time scales, with all other aspects of fitness being equal, it is advantageous to travel a given distance with as little energy use as possible^{1,41,50}. For example, an organism that uses less energy traveling between food sources will have additional stores with which to produce offspring or fight for territory. Perhaps as a result of selection pressure against wasting energy during

locomotion, people seem to choose energetically optimal coordination patterns. For example, people self-select step length^{9,51}, step width⁵², speed⁵³ (typically⁵⁴), and even arm motions¹⁰, that minimize energy cost during walking. If changes from self-selected values of these parameters are enforced, metabolic rate nearly always increases. Humans are expert at walking efficiently.

Definition of the normal barrier of energy cost

Because humans are already so well-tuned for locomotion, nearly any change to the human musculoskeletal system or its pattern of coordination increases metabolic rate. Therefore, the challenge has been to break the ‘normal barrier’ of energy cost:

Reduce the metabolic rate of healthy human walking under otherwise-normal conditions.

There are, of course, numerous ways to reduce energy cost without overcoming the same obstacles faced by a human trying to get from one point to another as efficiently as possible, and we would argue that these do not address the same challenge. For example, one can first make walking more difficult, then make walking easier by reducing the penalty. This would be the case if a load were added to the person’s body and then removed or otherwise made less onerous. As another example, one could exploit non-mobile devices connected to the ground, which could not travel with the human from place to place. This would be the case if a person were suspended over a treadmill using bungee cords. Another example would be to use machines that enable a non-walking form of locomotion, thereby not dealing with the difficulties of the original behavior. This would be the case if a person were to use roller blades or a bicycle. A final example would be to alter the task in some way such that the person is no longer expert and then to coach them or allow them to train and improve their skill. This would be the case if a person were to be made to walk on a balance beam, then given coaching and practice. Note that the use of a treadmill is not cheating, since walking on an ideally-operating treadmill is mechanically identical to walking over normal ground⁵⁵.

There are three qualitative ways to break the normal barrier, each with different implications: with a tethered powered device; with an autonomous powered device; and with an autonomous unpowered device. Although it might seem a simple thing based on conservation of energy (Extended Data Fig. 1), high-powered devices tethered to off-board actuation and control hardware have only recently demonstrated reduced metabolic energy consumption during normal walking². These devices overcome the substantial challenge of coordinating assistance usefully with the human neuromuscular system, but not the challenge of carrying actuation, control and energy storage hardware onboard. The normal barrier has also recently been broken with an autonomous powered device¹⁶, using similar control strategies as used by tethered devices, but with the additional engineering feat of lightweight packaging.

To break the normal barrier with an unpowered device, one cannot simply replace, or greatly exceed, biochemical energy use with synthetic energy input, but rather must reduce the energy

used by the system as a whole (Extended Data Fig. 1). Improving system efficiency in this way is equivalent to changing the human body such that it is more energy-effective at locomotion. The altered physical structure plays by nearly all the same rules as the natural human, operating indefinitely and not requiring additional foraging for synthetic energy sources. The synthetic device would not necessarily be like the human in terms of materials, self-growth or self-healing. Nevertheless, breaking the normal barrier with an unpowered device represents the most difficult and (we think) interesting way in which to reduce the energy cost of walking.

Does steady walking matter?

People engage in many locomotor activities other than steady-state walking, like starting and stopping, turning, speeding and slowing, running, climbing stairs and even skipping. Given so many possibilities, it might not be clear how much time people spend walking steadily and therefore whether these conditions are important to the energetic cost of real people getting around in the real world. It turns out that the most common locomotor activity among modern humans is steady walking. It takes only about two steps to reach steady state, even among less capable individuals⁵⁶. Walking bouts lasting more than 100 steps, or longer than two minutes, comprise more than 60% of steps taken in a day⁵⁷. Even including very short walking bouts of just a few steps, 70% of all walking *bouts* comprise more steady-state steps than transient ones. The vast majority of walking therefore occurs during steady gait, making it the most relevant and logical starting point for improving the energy economy of getting about. For these reasons, and for practical reasons related to experimental protocols, nearly all tests of the energetics of locomotion are conducted under such conditions^{2,16,17,18,42}.

In context: A survey of previous attempts to break the unpowered normal barrier

Over the past century, many machines intended to assist human locomotion have been invented and tested. Here we provide a sample of some illustrative designs.

Earliest attempts

People have tried to reduce the energy cost of walking with unpowered wearable devices since at least the 1890's. Beautiful examples of many common ideas for assistance are provided by the Yagn patents^{12,58,59}. These designs include long, curved leaf springs in parallel with the legs, intended to assist body weight support and provide a bounce during running; rubber bands connected between the ankles, intended to assist leg swing; various harnesses and frames to apply loads to the legs and the torso; and inflatable bladders beneath the heels, apparently intended to pump energy from one leg to the other during double-support. Another common idea for assistance is provided by the Beach patent (1891), which depicts a cowboy boot with a coil spring beneath the heel⁶⁰. Similar designs persist today⁶¹, with advertisements found in popular

in-flight magazines. Although compelling in theory and elegant in design, we have only anecdotal accounts of their effects on the effort of walking, and not the rigorous studies that would be required to firmly test whether these designs might break the normal barrier.

Recent attempts

Designs of unpowered, or effectively unpowered, devices intended to reduce the energy cost of walking and running from the past decade have many similarities to those of more than a century ago. Grabowski and Herr (2009) report a design with long, curved leaf springs in parallel with the legs, intended to assist with body weight support and to imitate spring-like behavior of the legs¹³. A similar design intended to assist running⁶² was not directly powered, but had computer-controlled clutches that engaged the exoskeleton at different times in the gait cycle. Although the energy cost of hopping in place was reduced by these structures, the metabolic cost of running was increased. A similar design is reported by Cherry *et al.* (2009), with similar effects on the energy cost of running⁶³. The increased energy cost of running may be due to costs associated with accelerating the inertia of these structures during leg swing⁶⁴. van den Bogert (2003) proposed a design using a single spring running across all the joints of the leg with carefully-chosen pulley diameters at each, intended to reduce muscle forces associated with body weight support, ankle push-off and leg swing⁶⁵. This ‘exotendon’ design was implemented by van Dijk *et al.* (2011), but caused metabolic rate to increase during walking, possibly because of the mass of the frame structure or difficulties human users may have had in controlling it¹⁴. Charalambous and Dean (2012) developed an exoskeleton with coupled hip and knee springs intended to reduce energy use associated with leg swing⁶⁶. Although this approach reduced activity in some thigh muscles, it led to a significant increase in metabolic rate. These and many other clever attempts to reduce metabolic rate with a passive device illustrate the difficulty of effective cooperation with the human neuromuscular system during locomotion and the importance of lightweight structures that do not produce a large initial energy penalty.

The cost of cushioning: An accidental near-miss at breaking the normal barrier for running

Perhaps unintentionally, Franz *et al.* (2012) nearly broke the normal barrier for running with an unpowered device simply by having subjects wear unusually lightweight, cushioned shoes⁶⁷. Although the result was not statistically significant, they found that athletes who were trained in barefoot running expended 2.1% less metabolic energy when running with low-mass (0.140 kg) shoes compared to running with bare feet. When the weight of the shoes was added to otherwise bare feet, the difference in metabolic rate increased to 3.4% and was statistically significant. The reasons for this difference are unclear, but were accompanied by an increase in stride length in shod conditions. It is not likely that this result owes to elastic energy storage and return in the shoe, given the low coefficient of restitution of foam rubbers at high impact speeds, leading the investigators to the concept of a ‘cost of cushioning’. Extrapolating, one might expect that a shoe

with even lower mass but the same cushioning properties might lead to about a 3% reduction in metabolic rate compared to barefoot running.

Reducing energy cost, but not breaking the normal barrier

Many researchers have demonstrated ways of reducing the metabolic energy consumption of walking that do not constitute breaking the normal barrier (see *The Challenge* above). Supporting a portion of body weight during walking using springs attached to the ceiling^{68,22} or inflatable balloons that encompass the ground and legs⁶⁹ can reduce metabolic rate during treadmill walking, but require non-mobile elements to do so. Springs that attach from a person's waist to the walls off to their sides can also reduce metabolic rate during treadmill walking^{70,71,72}, through a combination of effects on balance and vertical angular momentum, but are similarly non-mobile. Mobile versions of such room-sized devices are theoretically possible, but would likely be limited by structure mass and difficulties rolling along the ground with the person. Peak running speed, closely related to energy cost at a fixed speed, can apparently be improved by 'tuning' the compliance of the running track⁷³, but also requires a fixed locomotion location. Hunter *et al.* (2010) demonstrated that the energy cost of downhill walking can be reduced by 16% simply by instructing subjects to relax⁷⁴. This must not be included because the energetics of downhill walking differ from level walking, humans are less expert at downhill walking, and the change in energy use indicates that self-selected behavior under these conditions was initially energetically sub-optimal. Spring-loaded backpacks can reduce the penalty for walking while carrying large loads¹⁷, but not (as yet) the energy cost of normal walking itself. Similarly, if trained from a young age, some humans can carry loads on their heads with a lower metabolic penalty than experienced by other individuals carrying the same load in a backpack¹⁸. This represents a reduction in the penalty, rather than the cost of normal walking, and might derive from comparisons between individuals inexperienced and expert at this task. Harvesting energy during walking using a knee brace results in a lower metabolic penalty per Watt of electricity generated compared to other methods⁴², but this again is a reduction on a penalty rather than the initial task of walking (although the approach could, in theory, reduce the initial cost, as explained in Extended Data Figure 1). Many other human-powered devices, such as bicycles, can be used to reduce the metabolic energy expended during travel from one place to another⁴¹, but do so by enabling an alternate mode of locomotion.

Extended interpretation: Candidate explanations for observed trends in metabolic rate

The human neuromuscular system is highly complex, and many aspects of the interactions between neuromuscular electrical activity, molecular-scale muscle cross-bridge activity, fascicle-scale muscle mechanics, joint-scale biomechanics, whole-body dynamics and whole-body metabolic energy expenditure are not yet understood in detail. Measurements of these outcomes typically contain significant noise, rely on approximate models of the body and exhibit large

variability due to differences between individuals. These factors make it difficult to isolate the mechanisms responsible for moderate changes in metabolic rate. In this supplementary discussion section, we expand on our interpretations of the underlying data and the factors most likely responsible for changes in metabolic rate observed in the present study.

Reduced cost of muscle force production

Reductions in metabolic energy cost associated with force production by muscles at the assisted ankle joints provide the most consistent explanation of reduced metabolic energy expenditure with low and intermediate stiffness exoskeleton springs. Although not required by conservation of energy, muscles do consume metabolic energy to produce force, even when their length does not change (isometric conditions) and no mechanical work is produced. With the intermediate exoskeleton springs, the biological component of ankle moment was reduced during early and mid-stance (cf. Fig. 2b). The biological component of joint moment is produced by muscle forces at this range of joint motion. Reduced joint moments are therefore consistent with reduced force production in ankle plantarflexor muscles. Reduced joint moments can also be the result of increased force in antagonist muscles, or ‘co-contraction’, in this case by the ankle dorsiflexors. However, we observed reductions in electrical activity of the major plantarflexor muscles (soleus, cf. Fig. 2c) during early and mid-stance and did not observe increased dorsiflexor activity (tibialis anterior, Extended Data Fig. 4k) during this period with low and intermediate stiffness springs. Reduced electrical activity corresponds to reduced neural stimulation and muscle activation, which, all other things being equal (e.g. fascicle length and contraction velocity), leads to lower muscle force production and associated energy use.

The reduction in metabolic rate with the intermediate stiffness spring is quantitatively consistent with explanations based on reduced muscle activity primarily associated with force production. Simulation models of walking suggest that plantarflexor energy consumption occurs primarily during early and mid-stance and accounts for about 27% of total metabolic energy use during walking²⁷. This activity is primarily associated with force production, because muscle fascicles are nearly isometric, and therefore perform little or no mechanical work, during early and mid-stance²⁴. With the intermediate stiffness spring, the biological component of average ankle moment was reduced by 17% during early and mid-stance and 14% overall compared to normal walking. Similarly, soleus activity was reduced by 22% during early and mid-stance and 12% overall compared to normal walking. Extrapolating from these values, one would expect a reduction in overall metabolic rate of between 3% and 6%, similar to the observed 7% reduction. Reductions in mechanical and electrical signals associated with muscle force production are therefore both qualitatively and quantitatively consistent with the observed decrease in metabolic rate with low and intermediate stiffness exoskeleton springs.

Phenomenological models relating muscle electrical and mechanical state to metabolic energy use often include terms related to muscle activation, force and power⁷⁵⁻⁷⁸. These models use familiar ideas from physics and correspond well to most^{21,75}, although not all²⁹, empirical

data from experiments with muscles and individual muscle fascicles. Because concepts of force-related and work-related energy use are widespread in the biomechanics literature, and because they are intellectually accessible, we have used this decomposition in explaining the observed trends in metabolic rate. Researchers have also begun building models of muscle energy use from a molecular-level understanding of their constitutive elements⁷⁹, an approach with strong long-term prospects. We do not mean to imply from our use of terminology that the production of force in muscle has a direct, established metabolic requirement in all cases in the way that, for instance, the laws of thermodynamics bound the energy input required to produce net positive mechanical work. In this experiment, however, decreases in metabolic rate were primarily associated with decreases in muscle activity and mechanics that are primarily related to isometric force production.

Unchanged or increased cost of muscle fascicle work

The connection between ankle joint work and work done by muscle fascicles is complicated by the presence of elastic tendons in series with muscle. Tendons are compliant and can stretch, absorbing energy, and recoil, returning energy to the body at high efficiency, without tendon tissue consuming metabolic energy. If muscle fascicles in series with the tendon remain isometric during tendon stretch and recoil, the positive and negative components of joint work can each be substantial without muscle fascicles themselves performing any mechanical work. Muscle fascicles must, however, bear the same force as the tendon, since the two are in series. Joint power is therefore more removed from muscle fascicle work than joint moment is from muscle fascicle force, as are the metabolic energy consumptions associated with each. During normal walking at typical speeds, the positive and negative components of ankle joint work are largely, or wholly, the result of elastic tendon stretch and recoil^{23,24,80}.

Counterintuitively, external torque from an exoskeleton that reduces the biological component of joint moment and joint work can actually *increase* the work performed by muscle fascicles. If joint displacement remains the same over a step, the excursion of the entire musculotendon (or ‘muscle-tendon unit’) must also be the same. Musculotendon displacement is equal to the sum of the stretch of the tendon and the excursion of the muscle fascicles. Reducing the biological component of joint moment reduces the force experienced by the tendon, thereby reducing its stretch. If muscle fascicles were isometric in the unassisted cycle and joint angular displacements remain constant, an external moment will cause the fascicles to undergo an excursion. Mechanical work is the product of force and displacement. Even though fascicle force has been reduced, fascicle displacement has increased from zero to a finite value, meaning that muscle fascicles that did not perform mechanical work in the unassisted cycle now perform some work in the assisted cycle. If muscle fascicles were not perfectly isometric, but instead underwent some lengthening followed by some shortening in the unassisted cycle, a similar effect occurs, with changes in fascicle force and displacement leading to offsetting effects on fascicle work. Muscle fascicle work can therefore increase or remain unchanged with external

moment assistance from a spring, despite spring contributions to joint work leading to reduced muscle-tendon contributions to joint work. This phenomenon has been explored in detail in simulation models of locomotion⁸¹ and has been observed experimentally using ultrasound imaging of the ankle plantarflexor muscles during hopping with an ankle exoskeleton²⁸.

Most frustrating to the purposes of attributing changes in metabolic rate to changes in mechanical work by muscles, it has recently been experimentally demonstrated that in at least some stretch-shorten cycles, net work, rather than positive work, predicts force-specific metabolic energy cost. It has long been understood that performing positive work with muscle fascicles is energy-intensive compared to isometric contractions⁷⁵ and that performing a task requiring net positive power output results in similar whole-body metabolic rate as would be predicted by extrapolating from isolated fascicle efficiencies^{82,83}. Costs associated with isometric force production or over complete cycles with no net work, as can be the case in steady-state locomotion (Extended Data Fig. 1), have been less well understood. In a recent study of isolated muscle²⁹, isometric contractions consumed equal energy per unit force as contractions in which muscles were stretched and then shortened in such a way that they absorbed and produced equal amounts of mechanical work over the cycle. That is, in stretch-shorten cycles with zero net work, costs were better predicted by force than by the positive component of fascicle work. Level walking at steady speed requires no net energy input in theory, and during normal walking at moderate speeds the ankle joint produces little or no net work⁸⁴. A passive exoskeleton, such as one using a spring at the ankle joint, also produces no positive net work. This recent improved understanding of zero-net-work stretch-shorten cycle energetics may therefore apply to the current experiment.

These phenomena make it unlikely that reductions in muscle fascicle work were responsible for the reductions in metabolic rate observed with low and intermediate stiffness exoskeleton springs in the present study. Net joint work was nearly zero in the No Exoskeleton condition (Extended Data Fig. 5d), compatible with nearly all joint work being the product of elastic tendon stretch and recoil as observed in prior studies²⁴. Angular displacement of the ankle joint changed little across conditions (cf. Fig. 2d), indicating that total musculotendon excursion also changed little. The biological component of joint moment was lower with the intermediate stiffness spring (cf. Fig. 2b), indicating reduced musculotendon force and reduced tendon stretch. It is therefore likely that muscle fascicle excursion increased, thereby slightly increasing both the negative and positive components of fascicle work. Even if these components had, somehow, instead decreased by equal amounts, this would not imply a reduction in energy cost independent of force-related cost²⁹. The exoskeleton had no active components that could add mechanical work to the system, meaning that it could at best produce no change in net joint work. Instead, the exoskeleton seems to have dissipated a small amount of mechanical energy over each step cycle (Extended Data Fig. 5h). This seems to have resulted in a small increase in net positive work performed by musculotendons with the intermediate exoskeleton spring (Extended Data Fig. 5l). Unlike joint work that sums to zero on net, which could arise from tendon stretch and recoil, the net positive portion of joint work can only be derived from net positive work by muscle fascicles. While stretch-shorten cycles with zero net work seem to have cost best

predicted by force production, producing net positive work is still more expensive than isometric contractions^{75,29}.

In other words, rectified muscle fascicle work was likely minimal to begin with and likely increased with exoskeleton support, although this likely did not change metabolic energy use. Meanwhile, net muscle fascicle work assuredly increased slightly, likely increasing metabolic energy use associated with positive mechanical work. It is therefore most likely that costs associated with muscle fascicle work were equivalent or greater with the intermediate stiffness exoskeleton spring than during normal walking. This would not explain the observed reduction in whole-body metabolic rate.

Co-contraction of ankle muscles with high-stiffness exoskeleton springs

Increases in net metabolic rate with high stiffness exoskeleton springs may be due in part to increased dorsiflexor activity counteracting exoskeleton torque during early and mid-stance (Extended Data Fig. 4i,k). Humans seem to select coordination patterns with similar total ankle moments across a range of exoskeleton torque contributions^{2,30}. In this study, peak total ankle moment changed little across conditions (Extended Data Fig. 3a,d), despite increased contributions from the ankle exoskeleton (Extended Data Fig. 3e,h). Increased tibialis anterior activity during early and mid-stance might have reduced changes total joint moment, but increased metabolic energy used by this ankle dorsiflexor muscle group, which would have offset presumed benefits of consistent ankle moment elsewhere in the body.

The effects of altered ankle mechanics on knee muscle activity

Knee activity to counteract exoskeleton torque during mid and late stance may also have contributed to the upward trend in net metabolic rate with higher spring stiffness. Assistive torques that plantarflex the ankle also extend the knee. A joint torque is actually a set of equal and opposite moments applied to sequential body segments. An ankle plantarflexion moment therefore comprises a moment on the foot that rotates the toes downwards and a moment on the shank that rotates the knee backwards. This second moment is equivalent to one component of a knee joint extension moment and can have a similar effect on the knee. Perhaps to counteract this effect and avoid hyper-extension, subjects exhibited increased knee flexion moments during late stance with high-stiffness exoskeleton springs (Extended Data, Fig. 6a,d). These moments were likely due to increased activity in knee flexors, although measurements to verify such activity were not taken during this experiment. A similar effect on knee moment has been implicated in a study in which effective foot length was greatly increased⁸⁵.

The need for muscle-generated knee flexion torques may have been made more severe by reductions in forces produced by the biarticular gastrocnemius muscle group. The gastrocnemius acts both to plantarflex the ankle and to flex the knee. With ankle exoskeleton moment assistance, gastrocnemius activity was reduced during mid-stance compared to the No

Exoskeleton condition (Extended Data, Fig. 4e-g), before and during the period of increased knee flexion moments. Gastrocnemius muscles therefore contributed less to the biologically-generated knee flexion moment, meaning that the observed increase in moment must have been the result of even greater increases in activity of thigh muscles that flex the knee. One of the primary knee flexors is the biceps femoris, a biarticular group that also extends the hip, and such an increase might have caused further (unmeasured) compensations in hip muscles.

Unfavorable priming of muscle fascicles for push-off in late stance

Exoskeleton moment support with high-stiffness springs may have left plantarflexor muscle fascicles poorly positioned for work production during the ‘push-off’ phase at the end of stance, leading to less efficient performance of mechanical work by the body as a whole. The peak biological component of ankle joint moment was reduced with high-stiffness exoskeleton springs compared to normal walking (Extended Data Fig. 3l). Reduced biological contributions to ankle moment, without substantial changes in joint velocity, led to reduced biological contributions to ankle joint power during push-off (50-65% stride, Extended Data Fig. 5j). The exoskeleton absorbed net work over the step (Extended Data Fig. 5h) and did not replace the lost push-off work from ankle musculotendons. This led to reduced total ankle push-off work with high-stiffness exoskeleton springs (Extended Data Fig. 5b).

Decreased biological ankle push-off occurred despite maintained or increased ankle plantarflexor muscle electrical activity during this period. While soleus muscle activity during early and mid-stance was decreased with increasing exoskeleton spring stiffness (cf. Fig. 2c), soleus activity during late stance was unchanged (Extended Data Fig. 4d). In the gastrocnemius muscle group, activity during early and mid-stance was lower than normal walking in all exoskeleton conditions (Extended Data Fig. 4g), but during late stance increased to levels above normal walking with high-stiffness exoskeleton springs (Extended Data Fig. 4h). Energy cost associated with muscle activation⁷⁶ therefore seems to have increased during push-off with increasing exoskeleton spring stiffness, despite possible decreases in mechanical work.

The decrease in biological push-off work despite increased plantarflexor muscle activity may have been due to unfavorable musculotendon contractile state at the beginning of the push-off phase. Increased moment support from the exoskeleton with high-stiffness springs indicates reduced peak Achilles tendon force, and stretch, at the time of the onset of positive ankle push-off power (50% stride, Extended Data Fig. 5i). To increase musculotendon force, the muscle fascicles would have had to increase tendon stretch, since the tendon is spring-like and the muscle and tendon are in series. Stretching the tendon quickly to increase force at the beginning of push-off would have required high muscle fascicle velocity. The force produced by muscle fascicles is dependent on their velocity⁷⁵, with higher contraction velocity leading to a precipitous decrease in muscle force. This effect would be somewhat offset by an increase in fascicle length, which also affects force per unit activation⁷⁵, with opposite effects but to a lesser degree under these conditions⁸¹. To produce the same musculotendon forces during push-off as

in normal walking, subjects would therefore have had to activate their plantarflexor muscles more at the onset of push-off in the exoskeleton conditions. One might consider this a problem of inadequate ‘priming’ of the musculotendon to be in a suitable state for high-force, high-power activity at the end of stance. A similar effect was recently observed at higher torque levels in a powered exoskeleton⁸⁶. The small increase in plantarflexor activity during late stance and the decrease in total ankle push-off work in this study may reflect a balance between costs of increased activation and consequences of reduced push-off work elsewhere in the body.

The effects of high-stiffness springs on center-of-mass work

Reduced trailing ankle push-off work was accompanied by increased center-of-mass work during the ‘rebound’ phase of the ensuing step. As total ankle push-off work decreased, whole-leg center-of-mass push-off work also decreased (Extended Data Fig. 8e). At the same time, positive work during the rebound phase increased substantially, especially with the highest stiffness springs (Extended Data Fig. 8c). There is thought to be a mechanical coupling between trailing limb push-off work and leading-limb ‘collision’ dissipation, predicted by simple dynamic models of walking⁸⁷⁻⁸⁹, and between collision mechanics and those of the ensuing rebound phase^{19,25}. Reductions in push-off work, primarily associated with ankle activity, are expected to increase collision dissipation, thereby requiring even more positive work to be performed during rebound, thought to be associated with increased hip activity²⁵. In the present study, reduced push-off was accompanied by increased work during rebound. This increase in positive work was not accompanied by an increase in negative work during the collision phase, meaning that it could have signified a shift toward net positive muscle fascicle work during rebound in early and mid-stance. This change was not apparent in joint mechanics measurements, however, making attribution to a particular muscle group difficult (Extended Data Fig. 8).

Simple dynamical model interpretations must be tempered by the fact that decreased trailing limb push-off did not increase leading limb collision work, which is the cause of the coupling between ankle stiffness and overall mechanical work in prior simulation models^{19,25}. While work attributed to the trailing ankle during push-off might have been shifted to work attributed to the stance hip during mid-stance, this did not increase mechanical work on the center-of-mass overall. A similar lack of correlation between the magnitudes of push-off and collision has been observed in experiments with boots that fix the ankle joint⁹⁰ or prostheses with controlled whole-joint push-off work⁹¹. It should also be noted that such models predict trends in mechanical work, which, as we have described, is only indirectly related to metabolic energy use.

Alternate explanations

There are likely additional ways to explain observed changes in metabolic rate based on observed mechanics data or speculation on possible trends in unmeasured data. For example, tibialis anterior activity was elevated during the swing phase with stiffer springs (Extended Data

Fig. 4i), which might be related to coupling between stance phase ankle mechanics and toe clearance during swing. Muscle activity from thigh and hip muscle groups, which were not measured in this experiment, might provide additional insights into reasons for changes in metabolic rate. Direct measurement of muscle fascicle length, using ultrasound imaging, or of tendon force, using invasive techniques such as buckle transducers, would provide direct evidence for the interpretations above, or might indicate alternate explanations. These ideas could also be explored in musculoskeletal simulations. We expect future work with exoskeleton systems and simulation models to provide deeper insights into these underlying mechanisms.

First, do no harm: Why didn't energy cost increase when using the exoskeletons with no spring?

Although the exoskeletons used in this study were very light, they did add mass to the legs. Adding any mass to the limbs typically causes an increase in metabolic rate, particularly when added near the ankles⁵⁴, but we did not observe a measurable increase. This may simply be the result of measurement noise masking a small increase caused by the added exoskeleton mass. It might also be that other effects of the exoskeleton offset this cost, even without the spring. For example, the constraint imposed by the exoskeleton might have reduced biological contributions to inversion-eversion or internal-external rotation moments. These moments can have a significant impact on energy cost during human walking¹⁰.

The sweet spot: Is there a special meaning to the stiffness of the optimal spring?

The intermediate stiffness spring was special in that it minimized metabolic energy cost, but the reasons for this minimization are complex, reflecting the complexity of the human neuromuscular system being assisted. We had no theoretical reason to predict this particular stiffness would minimize energy cost. Instead, based on our prior modeling work²⁵, other models¹⁹ and intuition, we expected that very low stiffness springs would not change metabolic rate, a very high stiffness spring would interfere with natural motions of the ankle and increase metabolic rate, and that an intermediate stiffness spring could provide a benefit. Based on similar reasoning, we might expect optimal stiffness to depend on body characteristics, such as weight and height, and on walking speed.

Further reducing the energy cost of human walking using exoskeletons

It should be noted that this is only one variation of unpowered ankle exoskeleton design and that it is likely possible to achieve larger improvements in energy economy. Nonlinear springs, for example stiffening springs that have a greater ratio of change in torque to change in angle at higher torque, might provide additional benefits. Alternate engagement points, or engagement points that are altered on a step by step basis to aid balance⁹², might also be beneficial. Coupling of exoskeleton ankle joints to knee joints might allow energy normally dissipated at the knee

during late swing to be captured³⁸ and used to augment ankle push-off^{2,93}. Different ways of attaching to the body could improve load transfer and reduce dissipation. This is a small sample of the many possible related designs that could result in improved performance. Appropriate passive assistance at other joints, particularly the hip⁶⁶, might provide similar benefits. In the future, we expect such devices to surpass the level of unpowered assistance set in this study.

The addition of active power might lead to further improvements. Our findings with respect to muscle activity suggest that better exoskeleton performance would be obtained by combining early-stance ankle torque support with late-stance ankle work input. Torque support during early stance would reduce costs associated with muscle force production, but might leave ankle muscles poorly positioned for beneficial push-off work at the end of the step. Exoskeleton work assistance during push-off would make up for lost muscle work, avoiding negative consequences elsewhere in the body. This approach remains to be tested.

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