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Proprioceptive Feedback and Preferred Patterns of Human Movement

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Abstract

During cyclical tasks, humans often prefer stereotyped movement patterns. Although minimization of metabolic energy expenditure commonly is proposed as an underlying motor control goal, the mechanism by which humans choose their preferred movement pattern is not clear. We hypothesize that humans use proprioceptive feedback, which provides information about body mechanics in the identification of the preferred pattern of movement.

Keywords

metabolic energy; motor adaptation; motor control; optimization; resonant frequency; sensory feedback

INTRODUCTION

Proprioception commonly is defined as the sense of the body's motion or position. Decades of research have revealed the workings of various proprioceptive sensors and their importance during functional movement tasks (for detailed review, see Windhorst (34)). For example, proprioceptive feedback seems to be used to calculate error signals between the movement predicted by the brain's internal model of the body and the actual movement (34). Feedback from proprioceptive sensors also can directly contribute to muscle activity through reflexive loops to motor pools, potentially helping to maintain postural stability during body sway and shaping the timing of rhythmic muscle activity during cyclical tasks (34).

Recently, there has been an increasing call for neuroscience research to consider biomechanical factors (32). Behavior requires movement or forceful interaction with the environment (32), which are mechanical events that involve the mechanical properties of the body. Therefore, the central nervous system must account for body mechanics to effectively interact with the environment. Proprioceptive feedback provides a neural representation of body mechanics to the central nervous system. This suggests an additional role of proprioception during movement, namely, to allow the nervous system to identify the optimal mechanical pattern of movement during performance of a task.

The purpose of this review is to propose the hypothesis that proprioceptive feedback contributes to the choice of the preferred movement pattern during cyclical tasks. The proposed hypothesis is based on our recent work that has systematically investigated the preferred and optimal movement patterns during a bouncing task designed to allow experimental manipulation. This review will describe these experiments and address the importance of future testing of the proposed hypothesis.

MINIMIZING METABOLIC ENERGY EXPENDITURE

Humans often seem to prefer stereotyped movement patterns when performing cyclical tasks. Typically, the mechanical demands of a task can be met through many possible kinematic movement patterns. For example, when instructed to repetitively hop in place, humans have the ability to do so at a wide range of frequencies. However, they typically prefer to hop at a specific frequency that is relatively consistent whether hopping in place or hopping forward (7). During locomotion, humans prefer to walk at relatively slow speeds and to run once speed crosses a certain threshold. Adding a task constraint by controlling walking speed reveals a predictable relationship between step length and step frequency, both of which increase at faster speeds (9). This preference for specific movement patterns commonly has been attributed to the goal of minimizing metabolic energy expenditure (Joules) or metabolic rate (Watts) for both locomotion (2) and other cyclical tasks (28).

The strongest evidence for a movement strategy based on minimizing metabolic energy comes from experiments in which metabolic energy expenditure was quantified experimentally while movement pattern was varied. For a constant walking speed, enforcing a step frequency substantially higher or lower than the preferred step frequency increases the metabolic rate (35). Similarly, enforcing a step width either narrower or wider than preferred increases the metabolic rate (6). Easily prescribed deviations away from the preferred gait pattern seem to consistently increase metabolic rate, suggesting that this preference may be based on metabolic energy minimization.

Despite the apparent rationality of minimizing metabolic energy, this principle alone does not always explain observed human behavior. Although it has long been known that the metabolic energy expenditure of walking a certain distance is minimized at a speed of about $1.25 \text{ m}\cdot\text{s}^{-1}$ (24), humans can and do choose to walk at a wide range of speeds in various contexts (4). Even at a specific walking speed, humans do not always prefer the gait pattern that would minimize metabolic rate. When walking downhill, humans instead seem to prefer a more cautious, and costly, gait pattern (11,21). In addition, the preferred gait pattern seems to be influenced by strategies learned through previous experience, which may prevent humans from preferring the least costly pattern (22,27). Therefore, the choice of the preferred movement pattern, even for the well-studied example of human walking, is not entirely explained by the simple direct minimization of the metabolic rate.

POSSIBLE BASES FOR THE PREFERRED MOVEMENT PATTERN

Perhaps the simplest method by which humans could choose their preferred movement pattern would be to follow a preprogrammed motor plan. The organization of the central

nervous system itself, as developed during the lifespan, could promote certain muscle activation patterns during performance of a task. Theoretically, the choice of the preferred motor plan could be made in a feedforward manner, without need for feedback at all. Alternatively, humans could use feedback to select an appropriate preprogrammed motor plan (22,27). This mechanism would allow humans to rapidly choose a motor plan that could be varied in response to changes in the environment or state of the body but would require humans to appropriately respond to available sensory feedback.

During human movement, many physiological pathways provide the central nervous system with information about the state of the body. The most familiar source of this feedback is proprioception (34). Briefly, muscle spindles provide information about muscle length and velocity, Golgi tendon organs provide information about muscle force, and assorted other sensors provide additional mechanical information, including feedback of joint angle, pressure, and vibration. Humans also receive feedback of the metabolic energy expenditure of a task both through central chemoreceptors in the bloodstream (1) and peripheral metabotropic receptors in the active muscles (12). Less well understood is sense of effort feedback, which provides information related to the descending command required to accomplish a task (18).

These sources of feedback could play a more involved role in motor control than simply helping humans decide which preprogrammed motor plan to use. The theory of optimal feedback control proposes that feedback is an essential element of functional motor control (31). This theory suggests that humans must be able to predict the outcome of their descending motor commands, compare these predictions with sensory feedback, and use this information to optimize some aspect of task performance (26). Typically, the optimal movement pattern is identified by minimizing a cost function that includes an error term related to movement accuracy and an effort term related to the energy requirements (26). Surprisingly, given the importance often attributed to its minimization, metabolic energy only recently has been measured experimentally during the type of reaching task often used to investigate optimal feedback control (10). Instead, investigators often have approximated the energy requirements of a task using mechanical measures, including joint stiffness, movement kinematics, or mechanical energy.

The existence of multiple feedback sources has the potential to enhance performance during human movement. Individual feedback sources are inherently noisy. By combining information from each of these sources and a prior estimate of the body's state, humans can reduce the error in this estimate, improving movement accuracy (8). Thus, humans could use multisensory integration to minimize the error term described in optimal feedback control theory. Similarly, humans also may take advantage of all feedback sources that could provide information relevant to the goal of minimizing the energy requirements of a task (Fig. 1). For example, if humans want to minimize metabolic energy expenditure for a given task, it would seem logical for them to monitor feedback from central chemoreceptors. They also likely would monitor feedback from peripheral metabotropic receptors, an additional source of information that potentially could be used to directly minimize metabolic expenditure. Less obviously, it may be beneficial to monitor the sense of effort because the descending command required to adequately activate muscular actuators is likely related to

the subsequent metabolic demand. Finally, and of primary interest for this review, humans may indirectly monitor metabolic expenditure, or other indicators of energy requirements, by using proprioceptive feedback to sense the mechanical state of the body. A benefit of using proprioceptive feedback to approximate cost would be the rapid time course with which this feedback becomes available (29) in comparison with directly sensing metabolic energy expenditure (1,12).

Proprioceptive feedback, thus, could influence the preferred pattern of movement in several ways. Most simply, proprioception provides information about the mechanical state of the body, which could itself affect how humans prefer to move. For example, feedback from muscle spindles or cutaneous receptors of the feet could contribute to the sense of instability during downhill walking, preventing humans from preferring the gait pattern with minimal metabolic expenditure (11,21). In addition, proprioceptive feedback could be used as a correlate for metabolic expenditure during some tasks, potentially allowing more rapid identification of the approximate metabolic optimum.

In summary, proprioception could influence the preferred movement pattern by providing feedback relevant to the mechanical demands of a task or by serving as a correlate for metabolic energy. To test the hypothesis that proprioception contributes to the choice of the preferred movement pattern, we must be able to independently identify the mechanically optimal movement pattern and the metabolically optimal movement pattern. We also must be able to experimentally quantify the actual mechanical and metabolic costs that may be minimized and how these costs change with altered patterns of movement. To definitively state that proprioception influences the preferred movement pattern, experiments must demonstrate that humans prefer the mechanically optimal movement pattern, even at an increased metabolic rate. We also must be able to experimentally distinguish between the physiological sources of feedback that could underlie the optimization process, possibly through an understanding of the time scales of these feedback sources.

IDENTIFYING A MECHANICAL OPTIMUM

The mechanical properties of the human body influence the performance of movement tasks. In turn, proprioceptive feedback provides information about the mechanical state of the body to the central nervous system with a relatively short time delay (29). Therefore, proprioception has the potential to provide humans with rapid feedback directly relevant to their performance. Unfortunately, the possible link between proprioception and optimization of task performance is difficult to investigate experimentally. In part, this is caused by an inability to identify a movement pattern that could be considered mechanically optimal and, thus, could be indicated by proprioceptive feedback. For example, it has become clear that gait mechanics play an important role in determining the economy and stability of walking (14). However, as a result of the many involved joints and muscle groups, it still is not possible to analytically identify a mechanically optimal gait pattern.

Identification of the mechanically optimal movement pattern for a task requires appropriate experimental design and analytical methods. To avoid the complexities inherent to gait and other multiple joint movements, we recently investigated a simple bouncing task that

involved movement only at the ankle joint and was powered solely by the plantarflexors (Fig. 2A). In contrast to hopping, our bouncing task did not include an aerial phase because the subject's feet remained in contact with the environment throughout the movement. The mechanically optimal frequency of the bouncing task was identified for individual subjects through a combination of noninvasive experiments and simple mechanical models; the resonant frequency was calculated as the frequency with the maximal gain from plantarflexor muscle activity to output ground reaction force (Fig. 2B), with an average value across subjects of just above 3 Hz (5). By bouncing at the resonant frequency, subjects maximally took advantage of the body's mechanics such that a minimal amount of plantarflexor activity was required to produce a given output force. In addition, both ultrasound experiments (30) and model simulations (5) have revealed that bouncing at the resonant frequency allows the muscle to remain nearly isometric while the tendon stores and returns energy. Therefore, proprioceptive feedback from muscle spindles has the potential to identify the mechanically optimal frequency by determining the movement frequency at which muscle velocity is minimized.

Moving at the resonant frequency has metabolic benefits in addition to being mechanically optimal. Metabolic energy expenditure was minimized when subjects bounced near the resonant frequency (Fig. 2C) (5). Maintaining the same rate of positive mechanical work required more metabolic energy when bouncing either faster or slower than resonance. Importantly, the mechanically optimal frequency and the metabolically optimal frequency were identified entirely independently, without relying on the assumption that the preferred movement pattern is optimal. The physiological basis for the metabolic benefits of bouncing at resonance is the variance in energetic demand of skeletal muscle. In general, producing larger muscle forces requires more metabolic energy. However, the mechanical state of the force-producing muscle also strongly influences metabolic expenditure. For matched force levels, concentric (shortening) muscle actions are more costly than either isometric (constant length) or eccentric (lengthening) muscle actions (25). Therefore, by bouncing at resonance and allowing the plantarflexors to produce force isometrically, rather than concentrically, metabolic energy can be conserved.

The close relationship between mechanics and metabolic energy expenditure suggests that proprioceptive feedback has the potential to provide information used to determine the preferred movement pattern for cyclical tasks. As an example, for a simple bouncing task, humans could monitor feedback from muscle spindles to determine how changes in movement frequency affect the velocity of the plantarflexors. By voluntarily varying movement frequency until plantarflexor velocity is minimized, subjects could arrive at the resonant frequency. In turn, this would minimize the metabolic rate. A possible benefit of monitoring proprioceptive feedback, in addition to directly sensing metabolic energy expenditure, is the substantially faster time course with which proprioceptive information becomes available to the central nervous system.

IS OPTIMAL ALWAYS PREFERRED?

Although moving at the resonant frequency to minimize metabolic rate would seem to be a reasonable motor control strategy, humans do not automatically exhibit this behavior. During

short trials (30 s) of a reclined bouncing task (Fig. 3A), humans consistently preferred to bounce at a frequency slower than resonance (23). In longer trials (6 min), metabolic rate was not minimized when subjects were free to bounce at their preferred frequency but rather when a frequency near resonance was prescribed using auditory feedback (20). One possible explanation for this apparently nonoptimal behavior is that humans may simply choose their preferred bouncing frequency based on a preprogrammed motor plan without regard to feedback of any type. Alternatively, bouncing is likely an unfamiliar task, and humans may not have previously generated an appropriate preprogrammed motor plan that they could choose based on the available feedback. Finally, the preferred bouncing frequency may reflect optimization of some cost function but not one that is dominated by either mechanical factors (*e.g.*, muscle velocity) or metabolic energy.

Modifying the mechanics of the bouncing task altered behavior, providing evidence for the importance of feedback. The mechanical properties of the moving body were modified by either adding mass or parallel stiffness (Fig. 3A) (23). As would be predicted for a simple sprung mass, adding mass decreased the resonant frequency, whereas adding stiffness increased the resonant frequency (Fig. 3B). The addition of mass or stiffness also influenced the preferred frequency, which changed in the same direction as resonant frequency (*e.g.*, with a lower resonant frequency, subjects preferred to bounce more slowly) (Fig. 3C). However, for all mechanical conditions, the preferred frequency was significantly lower than the resonant frequency (Fig. 3D). The mechanics-dependent change in preferred frequency demonstrates that the preferred bouncing pattern is not simply caused by an unchanging preprogrammed motor plan that is insensitive to feedback. However, this finding does not differentiate between a feedback-dependent choice of a preprogrammed motor plan and a feedback-dependent optimization process. Neither does this result provide insight into the physiological source of feedback responsible for this change (*e.g.*, proprioceptive or metabolic feedback).

The rapid onset of mechanics-dependent changes in the preferred bouncing frequency provides indirect evidence that these changes are not a response to metabolic feedback. The effects of mechanics were present nearly immediately once subjects began bouncing, as the altered preferred frequency was apparent within the first 2–4 s of the trials (Fig. 3C). In comparison, the availability of metabolic feedback to the central nervous system is thought to take substantially longer, with peripheral metabotropic afferents reported to have initial latencies of 5–30 s (12) and central bloodstream receptors reported to exhibit a time constant of approximately 100 s (1). It would be unlikely for feedback with such a long time course to cause the observed rapid response. In contrast, the rapid mechanics-dependent changes could potentially be modulated by feedback with a shorter time scale, such as proprioceptive feedback or sense of effort. These sources of feedback potentially could be used either to form a cost function to be minimized or to identify an appropriate motor plan based on previous experience with the task (22,27).

Further experiments have demonstrated that the mechanics-dependent changes in preferred frequency likely are not modulated by sense of effort. Peripheral ischemia, a neurophysiological technique commonly used in motor control studies to disrupt sensory feedback from muscle spindles, was applied to the lower legs of subjects by inflating cuffs

around the thighs (23). While ischemia was applied, the sensory feedback available from muscle spindles was substantially reduced. In this physiological state, subjects did not alter their preferred bouncing frequency in response to altered mechanics (Fig. 4). Because peripheral ischemia would not be expected to influence the cortical representation of a descending command, sense of effort alone apparently is insufficient to cause the observed response to altered mechanics. These results, in combination with the findings previously described, are consistent with our proposal that proprioceptive feedback contributes to the choice of the preferred movement pattern during cyclical tasks. However, our results do not provide support for an automatic optimization process based on a simple plausible source of feedback because in none of the described experiments did subjects immediately prefer to bounce at either the resonant or metabolically cheapest frequency.

OPTIMIZING ADAPTATION

Humans have the ability to modify their movement patterns over time, in part, through a motor adaptation process based on error reduction (13). This type of adaptation has been investigated carefully for reaching tasks (13) and for walking (3). However, recent work has suggested that error reduction is not solely responsible for driving changes in the observed movement pattern over time (3). Instead, once humans are able to perform a task with a given level of skill or accuracy, they then may begin to improve the efficiency of the task, suggesting a link between adaptation and optimal feedback control. Investigations of this process, hereby termed “optimizing adaptation,” have been limited thus far by an inability to identify the optimal movement pattern of a task *a priori*, instead often depending on the assumption that the preferred or steady-state movement pattern is optimal for some cost function.

The presence of optimizing adaptation has been demonstrated experimentally for a simple bouncing task. For this task, the mechanically optimal frequency (*i.e.*, resonant frequency) can be identified for individual subjects before asking them to choose their preferred frequency (5,23). Previous work has revealed discrepancies between the resonant and the preferred frequencies during short bouncing trials (23). However, when subjects were allowed to bounce for a longer time period, the preferred frequency gradually increased, approaching resonance over time (Fig. 5) (20). Therefore, subjects adapted their preferred pattern of movement toward the bouncing frequency predicted to be both mechanically and metabolically optimal.

The adaptation of the preferred frequency toward resonance could be driven by proprioceptive feedback. To successfully perform the bouncing task, subjects must first meet the target mechanical power (Watts) requirements (indicated through visual feedback) by cyclically activating the plantarflexors. The initial choice of movement frequency for this presumably unfamiliar task could be the result of several processes: the frequency could be chosen arbitrarily; the frequency could be based on a preprogrammed motor plan for a more familiar task (*e.g.*, upright hopping (7)); or the frequency could be the result of muscle activation timing caused by stretch reflexes. Once the mechanical power requirements were met, a process that was complete within a few seconds, subsequent changes in the preferred movement pattern that occurred during a period of minutes can be attributed to optimizing

adaptation. Subjects could use muscle spindles to monitor length changes and velocity of the plantarflexors, while varying the frequency of plantarflexor activation, with the goal of driving this velocity to zero. The long time course of this process could be caused by the many iterations of feedback required to arrive at the optimum, despite the relatively short delay of proprioceptive feedback becoming available to the central nervous system. A similar mechanism could explain the long time course observed for some aspects of adaptation during walking (22,27). Importantly, whereas rapid changes in behavior can be used to rule out contributions from feedback sources with a slow time course (27), slow changes in behavior cannot be used to rule out contributions from feedback sources with a fast time course.

Alternatively, the gradual adaptation of bouncing frequency could be explained by direct optimization of the metabolic rate, which is minimized by bouncing near the resonant frequency (5,20). The long time course of the observed adaptation could be conceivably a result of the relatively slow feedback from either peripheral metabotropic receptors or central bloodstream chemoreceptors. However, it is unclear whether such slow feedback would allow an iterative optimization process to occur during the observed period. As evidence against the direct optimization of metabolic rate during rhythmic movement, humans do not prefer the pedaling cadence that minimizes metabolic rate during submaximal cycling (17). This finding could be explained by the mechanical characteristics of cycling, for which muscles cannot remain isometric and proprioceptive feedback, thus, may be unable to serve as a correlate of metabolic rate.

Optimizing adaptation based on proprioceptive feedback also could play an important role in other functional tasks, including walking. Recent experiments using ultrasound to quantify musculotendon mechanics during walking have revealed that the plantarflexors stay near isometric for much of the stance phase, allowing the Achilles tendon to store and return energy in a catapult-like fashion (16). When walking up or down slopes, humans dramatically alter their plantar-flexor activation patterns, but the isometric behavior is retained (16). Therefore, in addition to using feedback during walking to trigger the choice of a preprogrammed motor plan (22,27), humans also could use proprioceptive feedback from muscle spindles to optimize their plantarflexor muscle activation patterns. Such an optimization process could reduce the metabolic demands of generating plantarflexor power during walking but would not necessarily be evident from relatively gross spatiotemporal measures of step length or frequency.

Although the findings previously presented are consistent with the hypothesis that proprioceptive feedback can contribute to adaptation of the preferred movement pattern, we still have no direct evidence to differentiate between the effects of various feedback sources. Based on previous investigations of sensory feedback and motor control (8), it seems likely that humans will take advantage of every available source of feedback that provides information relevant to the goals of the task. The specific role of proprioceptive feedback could be clarified by designing experiments in which the mechanically optimal movement pattern and the metabolically optimal movement pattern differ. Ideally, these optima could be identified independently, the actual mechanical and metabolic costs could be quantified, and moving with the mechanically optimal movement pattern would cause a substantial

increase in metabolic energy expenditure. Under these conditions, adaptation toward the mechanically optimal movement pattern clearly would indicate a primary role of proprioceptive feedback.

CLINICAL IMPLICATIONS

Proprioceptive feedback can be disrupted by neurological disease or injury. For example, deficits in proprioception accuracy have been reported for populations with peripheral neuropathies caused by diabetes (33) or Charcot-Marie-Tooth syndrome (19), as the signals from the peripheral receptors are degraded. Such deficits in proprioception are known to influence the performance of functional tasks that require knowledge of where the body is in space, including the maintenance of postural balance (33).

Disruption of proprioceptive feedback in clinical populations also could prevent optimizing adaptation. Experiments involving these populations could potentially overcome some of the inherent difficulties of isolating the effects of proprioception in participants with an intact uninjured nervous system. For example, patients with a reduced ability to accurately sense and interpret feedback from plantarflexor muscle spindles may be unable to effectively activate these muscles such that they contract near-isometrically while bouncing or during the stance phase of walking, even if plantarflexion strength is retained. Activating muscles concentrically rather than isometrically would be expected to increase the metabolic energy required to walk at a given speed, a factor that can reduce functional mobility. Future work could directly test whether clinical proprioceptive deficits are associated with an inability to adapt the preferred movement pattern toward the mechanical or metabolic optimum.

An improved understanding of the potential links between proprioception, optimizing adaptation, and functional mobility may allow the development of more effective rehabilitation techniques. For example, patients with diabetic neuropathy exhibit abnormal patterns of plantarflexor muscle activity during stance (15), whereas Charcot-Marie-Tooth syndrome patients have increased energetic expenditure per unit of distance, even when no clinical gait deviations are apparent (19). These gait performance changes in clinical populations could be partially caused by a reduced ability to optimize behavior using proprioceptive feedback. Function, thus, may be improved through rehabilitation methods designed to enhance residual proprioceptive feedback or to provide alternative forms of feedback through auditory or visual pathways.

SUMMARY

Proprioceptive feedback has characteristics that may allow it to be used for the optimization process proposed to underlie the choice of the preferred movement pattern. This source of feedback is relatively fast and is predictably related to metabolic energy expenditure for some cyclical tasks. Recent experiments have demonstrated that the preferred movement pattern is dependent on both the mechanical state of the body, which can be indicated by proprioceptive feedback, and the availability of sensory feedback during performance of a task. Humans do not always automatically prefer the mechanically optimal movement pattern but can gradually adapt their preference toward optimum over time when relevant

proprioceptive feedback is available. These results have led to the hypothesis proposed in this review — that proprioceptive feedback contributes to identification of the preferred movement pattern. Future experiments designed to directly test this hypothesis hold promise for advancing the understanding of human motor control in both healthy and clinical populations.

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Figure 1.

Multiple physiological sources of feedback can provide humans with information related to the energy required to perform a task. This simplified schematic figure is intended to illustrate several potential sources of this feedback and is not intended to represent any specific anatomical structures. A. Direct feedback of metabolic energy expenditure is available from both central chemoreceptors and peripheral metabotropic receptors. During voluntary movement, changes in metabolic expenditure are largely attributable to the costs of muscle activation. B. Sense of effort feedback provides humans with information about the magnitude of the descending command required to perform a task. This descending command is likely closely related to the subsequent muscle activation and the related metabolic demand. C. Proprioceptive feedback provides humans with information about the body's mechanical state, including muscle length, velocity, and force. These mechanical factors will influence muscle activation patterns, the relationship between muscle activation and muscle force, and the metabolic demand of the muscular activation driving movement.

Figure 2.

Human subjects performed a simple bouncing task at a range of prescribed frequencies while the rate of positive mechanical work was held constant. A. Subjects bounced vertically while standing on a frame designed to reduce the mechanical demands of the task. Ground reaction force (*GRF*) and plantarflexor electromyography activity (*EMG*) were measured and used to characterize the parameters of a simple mechanical model using system identification. The mechanical model included a contractile element (*CE*), damper (*B*), and parallel elasticity (*K_{PE}*) in series, with series elasticity (*K_{SE}*) acting on the mass of the body (*M*). B. The resonant frequency was calculated from the *GRF* and *EMG* data fit to the simple model, as illustrated for a single subject. C. Across subjects, the metabolic rate was minimized when subjects bounced at approximately 3 Hz, quite similar to the calculated resonant frequency. Metabolic rate was significantly ($*P < 0.05$) lower than that expected from muscles performing positive work (*dashed horizontal line*) for intermediate frequencies. [Adapted from (5). Copyright © 2011 American Physiological Society. Used with permission.]

Figure 3.

Humans performed a reclined bouncing task that allowed easy manipulation of mechanics. A. Subjects bounced while reclined on a moving sled. In some trials, mass or parallel stiffness was added. B. Adding either mass or stiffness predictably altered the resonant frequency, as illustrated for a single subject. C. Mechanics-dependent changes in preferred frequency paralleled changes in resonant frequency. These effects were apparent within the first 2–4 s of bouncing. Frequency is not plotted for the first 2 s of bouncing because subjects had not consistently reached the prescribed task demand. D. The preferred frequency was significantly ($*P < 0.05$) lower than the resonant frequency for all mechanical conditions. [Adapted from (23). Copyright © 2011 The Company of Biologists. Used with permission.]

Figure 4.

Disruption of sensory feedback eliminated the mechanics-dependent changes in preferred frequency. Both before application of ischemia (left group of columns) and after the effects of ischemia had dissipated (right group of columns), the addition of mass significantly ($*P < 0.05$) decreased the preferred frequency. However, during ischemia (center group of columns), while sensation was disrupted, subjects did not vary their preferred frequency in response to the added mass. [Adapted from (23). Copyright © 2011 The Company of Biologists. Used with permission.]

Figure 5.

Humans gradually adapted their preferred bouncing frequency toward resonance over time. Preferred frequency was significantly ($*P < 0.05$) less than resonance for the first 110 s of bouncing. The preferred frequency approached resonance with an exponential time constant of 136 s (group data $R^2 = 0.97$). [Adapted from (20). Copyright © 2012 American Physiological Society. Used with permission.]