Loading the Limb During Rhythmic Leg Movements Lengthens the Duration of Both Flexion and Extension in Human Infants

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Musselman KE, Yang JF. Loading the limb during rhythmic leg movements lengthens the duration of both flexion and extension in human infants. J Neurophysiol 97: 1247–1257, 2007. First published December 6, 2006; doi:10.1152/jn.00891.2006. Sensory input is critical for adapting motor outputs to meet environmental conditions. A ubiquitous force on all terrestrial animals is gravity. It is possible that when performing rhythmic movements, animals respond to load-related feedback in the same way by prolonging the muscle activity resisting the load. We hypothesized that for rhythmic leg movements, the period (extension or flexion) experiencing the higher load will be longer and vary more strongly with cycle period. Six rhythmic movements were studied in human infants (aged 3–10 mo), each providing different degrees of load-related feedback to the legs during flexion and extension of the limb. Kicking in supine provided similar loads (inertial) during flexion and extension. Stepping on a treadmill, kicking in supine against a foot-plate, and kicking in sitting loaded the legs during extension more than flexion, whereas air-stepping and air-stepping with ankle weights did the opposite. Video, electrogoniometry, surface electromyography, and contact forces were recorded. We showed that load-related feedback could make either the duration of flexion or extension longer. Within the tasks of stepping and kicking against a plate, infants who exerted lower forces showed shorter extensor durations than those who exerted higher forces. Because older babies tend to step with greater force, we wished to rule out the contribution of age. Eight babies (>8 mo old) were studied during stepping, in which we manipulated the amount of weight-bearing. The same effect of load was seen. Hence, the degree of loading directly affects the duration of extension in an incremental way.

INTRODUCTION

Animals, including humans, display many forms of rhythmic leg movements, such as kicking, cycling, swimming, crawling, walking, and hopping. This is also true of human infants, who show stepping (Yang et al. 1998), kicking (Thelen 1985), and air-stepping (Yang et al. 1998) behaviors within the first year of life. Sensory input modifies and molds many of these rhythmic behaviors to adjust them to physiological and environmental conditions (Pearson 1993; Rossignol et al. 2006). For example, rapid responses are needed when a cat unexpectedly steps in a hole in the ground. Leg muscles compensate quickly so that the animal does not fall (Gorassini et al. 1994). Many of these rapid responses are carefully controlled by the nervous system so that they are expressed only when it is appropriate for the successful completion of the task (Buford and Smith 1993; Lam et al. 2003). Slower changes are also needed, for example, to accommodate growth as animals and humans mature.

Are there environmental constraints common to all these rhythmic behaviors that require similar coping strategies? Gravity is a ubiquitous force imposed on most movements and might be dealt with in a similar way by the nervous system regardless of the movement. In this paper, we study how young infants respond to load during rhythmic leg movements. For simplicity, we will use the word load to encompass inertial and other loads that might be sensed by proprioceptors, cutaneous, and other receptors.

Load-related sensory input has a powerful influence on the motor output in walking. Direct or indirect activation of extensor muscle afferents that detect stretch and load during the extension period of walking enhances the amplitude of the muscle activity, prolongs ipsilateral extension and inhibits the transition to flexion (Conway et al. 1987; Duyens and Pearson 1980; Guertin et al. 1995; Ivanenko et al. 2002; Pang and Yang 2000; Pearson et al. 1992; Whelan et al. 1995). A similar phenomenon is seen when the period of flexion is loaded during walking. The amplitude and duration of flexor muscle activity can be increased in walking decerebrate cats by mechanically resisting flexion during swing (Lam and Pearson 2001) or by direct activation of group I afferents from hindlimb flexors (Hiebert et al. 1996; Lam and Pearson 2002). Intracellular recording from motoneurons during fictive locomotion in cats suggest excitatory pathways from group I muscle afferents to flexor and bifunctional motoneurons (Perreault et al. 1995; Quevedo et al. 2000; Stecina et al. 2005), very similar to those found to extensor motoneurons. Interestingly, qualitatively similar results were found during fictive scratching in cats (Stecina et al. 2005).

The load-related response during walking may be partly responsible for the phenomenon that the duration of stance (extension) is generally longer than swing (flexion) and varies more with the speed of walking. We will call this an extensor-dominated pattern as proposed by Yakovenko et al. (2005). Virtually every animal walks in this way, including insects (Delcomyn 1971), reptiles (Williams 1981), birds (Jacobson and Hollyday 1982), rodents (Cohen and Gans 1975), carnivores (Arshavskii et al. 1965; Halbertsma 1983), and primates (Wilkens 1983) as well as humans (Grillner et al. 1979).

Perhaps gravity imposes greater load-related feedback during extension, resulting in its prolongation. This seems likely because when afferent input is small or absent, the invariant duration of swing (flexion) is more labile (Baker et al. 1984;

Other rhythmic movements that impose greater loads during flexion, such as air-stepping in the cat and chick (Johnston and Bekoff 1992, 1996; Vilensky et al. 1989) or air-scratching in the cat (Deliaagna et al. 1975), have sometimes been reported to be flexor-dominated. Interestingly, real scratching in intact cats incorporates a period when the limb makes contact with the body during extension, which correspondingly shows a shortening of the duration in extension (Kuhta and Smith 1990). Additional anecdotal evidence indicated that when a limb inadvertently hits an obstacle during scratching either during extension or flexion, the strength and duration of the muscle activity is enhanced (turtle, Stein and Grossman 1980; cat, Kuhta and Smith 1990).

We explored the idea that the human, like other living beings, may have developed a common way to respond to load during rhythmic movements. We studied human infants under the age of 1 yr prior to the development of independent walking. Our hypothesis is that the response to load during different rhythmic leg movements would be similar. The prediction is that loading the extensors will lengthen the period of extension, and loading the flexors will lengthen the period of flexion. Preliminary results have been reported in abstract form (Musselman and Yang 2005).

METHODS

Subjects

Sixty-four healthy infants aged 3–10 mo were recruited through parent/infant groups at public health clinics in Edmonton. Infants and their parents attended one testing session lasting ~1 h. Informed, written consent was obtained from a parent at the time of testing. Ethical approval was obtained from the Health Research Ethics Board of the University of Alberta and Capital Health, Edmonton.

Experimental procedures

Six rhythmic movements were studied in which three provided greater loads to the legs during extension, two provided greater loads during flexion, and one provided similar loads during flexion and extension. Rhythmic leg movements in infants are more easily elicited when arousal level is high (Thelen 1985); therefore a researcher and/or parent attempted to excite the infant through play. One or two trials (each lasting 1–2 min) of each rhythmic movement were attempted. Short rests of 1–2 min were taken between trials. The infant’s body weight was measured at the end of the experiment. The six movements studied were as follows, separated into three categories.

The first category was movement that provided approximately equal load during flexion and extension. The movement involved kicking in a supine posture: infants kicked while lying supine on a play mat. The loads experienced by hip and knee muscles during flexion and extension were estimated to be about equal by Jensen et al. (1994) based on inverse dynamics to estimate the joint torques.

The second category contained movements that provided more load during extension. Three movements were tested. 1) Stepping on a treadmill—a researcher held the infant under the arms over a treadmill, allowing the infant to support as much of his/her weight as possible without the infant’s knees collapsing into flexion. The researcher’s forearms were supported by a platform to minimize imposing movements on the infant. The loads experienced by the legs during extension (stance phase) of stepping were dominated by body-weight, which was far greater than the loads experienced during flexion (swing phase) to lift the leg. This can be seen from the magnitude of muscle moments generated in the lower limb during adult walking (Winter 1983). 2) Kicking against a surface—The infants kicked in a supine position with their feet contacting a firm surface during extension of the leg. For this rhythmic movement, the loads experienced by the leg muscles was greater during extension when the feet exerted force against a firm surface, compared with flexion when the feet were removed from the surface. The surface against which the infants kicked was either a hard piece of Styrofoam stabilized by a researcher (3 infants) or a Plexiglas plate instrumented with a force transducer (5 infants). 3) Kicking in sitting—The infants were seated at the edge of a small bench allowing their legs to hang over the edge. Kicking in this position consisted of alternate knee flexion and extension, with little hip movement. Knee extension in this posture consists of lifting the leg against gravity, while knee flexion is assisted by gravity.

The third category included movements that provided more load during flexion. 1) Air-stepping—Air-stepping is a stepping-like movement elicited when infants are held upright under their arms with their feet suspended. In this movement, gravity resists flexion and assisted extension. The flexor muscle torque at the hips is four times greater in air-stepping compared with kicking in supine (Jensen et al. 1994). 2) Weighted air-stepping—Air-stepping was also attempted with the infants wearing 0.5 or 1.0 lbs weights on each ankle, to provide additional loads to the flexor muscles during flexion of the limb. The ankle weights were estimated to be 24–56% of the leg weight. Leg weight was estimated to be 10.9% of body weight (Schneider et al. 1990).

Control for effect of age on stepping

We found that older infants tended to support a greater percentage of their body weight than younger infants during stepping. To rule out the possibility that the extensor-dominated pattern is an effect of age rather than load, an additional condition was tested. Eight older infants (aged 8–10 mo) stepped on the treadmill while the amount of weight-bearing was manipulated by the researcher holding the infant. These infants stepped under two conditions: normal weight, in which the infants were encouraged to support as much of their body weight as possible, with support provided only as needed for safety, and low weight, in which the researcher provided consistent force upward, to support more of the infant’s body weight. The manipulations were applied for 20-s periods while the infants were stepping.

Instrumentation

Surface electromyograms (EMGs) were obtained from the quadriceps and hamstrings bilaterally for all infants and from the gastrocnemius-soleus or tibialis anterior bilaterally in some infants. EMG recordings from the gastrocnemius-soleus and tibialis anterior were not collected from all infants because preliminary data showed that these muscles were not consistently used in the rhythmic movements studied. Pairs of infant-sized silver-silver chloride recording electrodes (Kendall, Chicopee, MA) were placed on the skin over the above-mentioned muscles, after the skin was cleaned with alcohol. The signals were conditioned with an AMT-8 amplifier (Bortec Biomedical, Calgary, Canada), band-passed from 10 Hz to 1 kHz. Black leotards covered the electrodes and corresponding wires to prevent movement artifact, and provided good contrast to the skin markers for videotaping.

All trials were videotaped (Canon Elura 50, Canon, Mississauga, Canada) in the sagittal plane. The leg fully visible in the video was the reference leg. White adhesive markers were applied to the midline of the trunk above the iliac crest, the greater trochanter, the lateral knee joint line, the lateral malleolus and the head of the fifth metatarsal on the camera side. Markers were also applied to the medial knee joint.
line, the medial malleolus and the medial aspect of the great toe of the contralateral leg.

Twin-axis electrogoniometers (Penny and Giles, Biometrics, Blackwood Gwent, UK) were placed over the right and left knee joints. The knees were chosen rather than the hips because preliminary data showed knee flexion/extension to be characteristic of all 6 rhythmic movements in contrast to hip flexion/extension, which was minimal when the infants kicked in sitting. The arms of the goniometers were aligned with the long axes of the femur and tibia.

A split-belt treadmill, described in an earlier study (Yang et al. 2005) was used in this study because it is equipped with separate force plates for the right and left legs, allowing accurate measurement of vertical forces for each limb (model INFSBT-FP, designed and built by R Gramlich and S Graziano, University of Alberta, Edmonton, AB). A Plexiglas partition between the right and left treadmill belts helped to keep the legs on separate belts. The two belts were always run at the same speed, between 0.1 and 0.6 m/s depending on the infant’s ability.

The Plexiglas foot-plate (2 cm thick, 26 cm high, 34.5 cm wide) was attached to an instrumented uniaxial force transducer (model 60001A50-1000, Intertechnology, Toronto, ON, Canada) that was securely mounted to a wall. The custom-made plate was tested to ensure accurate readings regardless of the position on the plate at which force was exerted.

A custom-made digital counter synchronized the video and analog signals at a rate of 1 Hz. The EMG signals were high-pass filtered at 10 Hz and full-wave rectified. All signals (rectified EMG, goniometer, force plate and foot-plate) were low-pass filtered at 30 Hz and converted from analog to digital form at 250 Hz (Axoscope, Molecular Devices, Foster City, CA). The raw signals were recorded on videotape with a PCM encoder (A.R. Vetter, Redersburg, PA) for back-up.

**Analysis**

The video recordings were reviewed to identify sequences of rhythmic movements. The data were included for analysis if the following criteria were met: 1) the infant performed sequences of leg movements, defined as at least two sequential knee flexion-extension movements in both legs (with no pauses > 1 s and a change in knee angle ≥ 20° in both directions), in at least one of six rhythmic movements, and 2) the total number of flexion-extension cycles from these sequences was eight or more for any one rhythmic movement.

Video records of the reflective markers on the limb were digitized with an automatic tracking system (Peak Motus, Vicon, Los Angeles, CA), and hip and knee angles obtained for the sagittal plane. The extended (i.e., straight) knee and hip were defined as 0°. Positive angles represent flexion. A customized software program (Matlab, MathWorks, Natick, MA) was used to calculate average hip and knee angles for a full cycle of each rhythmic movement performed by each infant. A subset of subjects (n = 17) was randomly selected for this analysis from a pool of subjects (n = 30) who provided ≥2 forms of rhythmic movements.

The durations of the cycle, flexion, and extension were estimated from the knee goniometer signals, using a customized software program (Matlab, MathWorks). This was the preferred method instead of the digitized video data because of the ease with which large sets of data could be analyzed. Cycle period was defined as the onset of knee flexion to the onset of the subsequent knee flexion (solid vertical lines in Fig. 1 mark the onset of knee flexion). Onset of knee extension

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**FIG. 1.** Raw data from a few cycles of kicking against a surface (A), kicking in sitting (B), stepping on a treadmill (C), and air-stepping (D) are shown for infant MPL (5.2 mo old; A, C, and D) and infant MKL (5.5 mo old, B). Hip (solid line) and knee (dashed line) joint angles from the video data (top), and quadriceps (Quads) and hamstrings (Hams) electromyographic (EMG) activity are shown for the 4 behaviors. Increasing angles represent flexion. Solid vertical lines mark the onset of knee flexion. Dotted vertical lines in C mark the onset of knee extension. Solid horizontal lines under joint angle traces mark the time of contact of the foot with the foot-plate (A) or treadmill (C). The stick figures beside each graph show the flexion and extension motion for one cycle of each type of movement. The marker position for the trunk, hip, knee, and ankle are indicated by T, H, K, and A, respectively, in the stick figures.
is indicated with vertical dotted lines (Fig. 1C). The durations of the cycle, flexion and extension were also estimated using the hip angle in the 17 subjects for whom video data were fully analyzed. All except two infants contributed eight or more cycles to each movement type; the two infants contributed six cycles each of hip angle data to air-stepping.

Some infants performed rhythmic leg movements in an alternate manner (i.e., 1 leg flexes while the other extends), and others preferred synchronous movements (i.e., both legs flexing or extending at the same time). In the weight-bearing position, synchronous movements resembled hopping on the treadmill. A customized software program (Matlab, MathWorks) was used to determine the phase lag between the two legs. Phase lag was defined as the onset of a cycle in the contralateral limb expressed as a percentage of the cycle of the reference limb. A synchronous movement was defined as one in which the phase lag was 0–20 or 80–100%, whereas an alternate movement was a phase lag of 20.1–79.9%. Both forms of coordination were included for analysis.

EMG data were used for descriptive purposes only. This is because of the small number of data sets in which we could be sure the cross-talk from other muscles was small (see Statistics). An infant’s EMG data were included if there was clear EMG from ≥10 movement cycles, from at least one of the four muscles.

The peak force (in Newtons) exerted by the infants during the extension movement of every step and kick (against the foot-plate) was measured. The average peak force across cycles was expressed as a percentage of the infant’s body weight. If an infant kicked synchronously against the foot-plate, the peak force of each leg was estimated by dividing the observed peak force in half.

Statistics

A one-way ANOVA was used to compare the following across rhythmic movements: the durations of flexion and extension, cycle period, knee and hip joint range of motion, and maximum and minimum joint angles for the knee and hip (Bonferroni correction used for post hoc analyses). Angle-angle plots (hip vs. knee) were produced for each rhythmic movement performed by the infants. Linear regression analyses were used to quantify the relationship between hip and knee angles. The significance of the regression (i.e., slope not equal to 0) was assessed with an F-test (Pedhazur 1982). For each infant, the slopes of the regression lines for the different rhythmic movements were compared using Welch’s t-test, which is appropriate for comparing data sets differing in sample size or variability (Glass and Hopkins 1996). Slopes of the regression lines were compared only if the regressions were significant. Independent t-tests were used to compare the duration of the cycle for alternate and synchronous forms of a rhythmic movement. Linear regression analyses were used to determine the relationship between the durations of flexion or extension, and the cycle period for each rhythmic movement. Like the analysis of the angle-angle plots, the significance of the regression was assessed with an F-test. A paired t-test was used to compare the slopes of the regression lines for the flexion and extension durations within each movement. Welch’s t-test was used to compare regression line slopes from alternate and synchronous forms of a movement and also across movements. Pearson’s Product-Moment correlation coefficients were used to determine if there was crosstalk between recordings of antagonist muscles. If the correlation coefficient exceeded 0.3 for any pairs of EMG recordings, those recordings were not included for analysis. Significance was set at P < 0.01 for all statistical tests due to the large number of tests performed. All mean values reported are accompanied by 1 SD.

RESULTS

Of the 64 infants tested, 44 (aged 3.2–10.1 mo) provided useful data for at least one rhythmic movement. For each rhythmic movement studied, details of the number of infants and the number of cycles are shown in Table 1.

Description of rhythmic movements

Of the 17 infants included in the kinematic analysis of hip and knee motion, 10 provided data for kicking in supine, 2 for kicking against a surface, 4 for kicking in sitting, 15 for stepping on a treadmill generating greater activity than kicking in sitting or air-stepping. Figure 1 shows the time course for the hip and knee movements, and muscle activity from the quadriceps and hamstrings during a sequence of kicking against a surface (A), kicking in sitting (B), stepping (C), and air-stepping (D). Data in Fig. 1, A, C, and D, are from the same baby. Stick figures beside each graph show the motion for one cycle. The hip (solid lines) and knee (dashed lines) angles are superimposed at the top of the graph to allow inspection of the timing of movements between the two joints. The thin vertical lines indicate the beginning of a cycle. The thick horizontal lines below the angles indicate the time the foot is in contact with a surface during kicking against a foot-plate (A) and stepping on a treadmill (C). Note that with the exception of kicking in sitting, the hip and knee joints flex and extend at roughly the same time.

The timing of quadriceps activity was similar in all the movements. Quadriceps activity began around the time of peak knee flexion and continued until the time of peak knee extension (Fig. 1). The amplitude of quadriceps activity varied between behaviors with kicking against a surface and stepping on a treadmill generating greater activity than kicking in sitting or air-stepping. Hamstrings activity was more variable across MOVEMENTS.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Movement</th>
<th>Number of Infants</th>
<th>Number of Cycles</th>
<th>Range: Cycles/baby</th>
</tr>
</thead>
<tbody>
<tr>
<td>Load-extension</td>
<td>Stepping/hopping</td>
<td>25</td>
<td>797</td>
<td>12–71</td>
</tr>
<tr>
<td></td>
<td>Kicking against a surface</td>
<td>8</td>
<td>131</td>
<td>10–35</td>
</tr>
<tr>
<td></td>
<td>Kicking in sitting</td>
<td>5</td>
<td>141</td>
<td>10–55</td>
</tr>
<tr>
<td></td>
<td>Stepping (normal weight support)</td>
<td>8</td>
<td>210</td>
<td>18–38</td>
</tr>
<tr>
<td></td>
<td>Stepping (low weight support)</td>
<td>8</td>
<td>165</td>
<td>8–31</td>
</tr>
<tr>
<td>Load-flexion</td>
<td>Air-stepping</td>
<td>11</td>
<td>196</td>
<td>12–33</td>
</tr>
<tr>
<td></td>
<td>Weighted Air-stepping</td>
<td>4</td>
<td>67</td>
<td>10–35</td>
</tr>
<tr>
<td>Neutral</td>
<td>Kicking in supine</td>
<td>27</td>
<td>669</td>
<td>10–89</td>
</tr>
</tbody>
</table>

The number of infants and the total number of movement cycles included for analysis for each rhythmic movement are listed. In addition, the number of cycles contributed by each baby varied (range shown in last column). Seven of the 8 infants who kicked against a surface also kicked in supine. All 4 of the infants who air-stepped with weights also air-stepped without weights.
behaviors. For kicking against a surface, stepping and air-stepping, hamstrings activity began shortly after the onset of quadriceps activity, and persisted longer than quadriceps activity (Fig. 1, A, C, and D). Sometimes this hamstring activity appeared as a double burst, whereas at other times it was a continuous longer burst.

Group data indicate that the cycle period and the flexion and extension durations varied between movements. The average cycle period of stepping and kicking against a surface were longer than the average cycle period of most other movements (all comparisons \( P < 0.001 \), except \( P = 0.129 \) for kicking against a surface versus kicking in supine). Stepping and kicking against a surface were also characterized by longer periods of extension (\( P < 0.001 \)). These two movements typically consisted of knee flexion followed by slower extension of the knee, and/or a plateau in maximal knee extension prior to the onset of flexion (Fig. 1, A and C). A plateau in maximal knee flexion was frequently seen in the air-stepping behaviors (Fig. 1D). There was no statistically significant difference in knee range of motion, nor minimum or maximum knee angles, across behaviors (\( P > 0.01 \)).

All behaviors involved near synchronous movements at the hip and knee with the exception of kicking in sitting. For this rhythmic movement, hip motion relative to that of the knee was more variable. In one infant the hip appeared to move in the direction opposite that of the knee (Fig. 1B), whereas in other infants, the hip moved in unison with the knee (not shown). Also, hip motion was smaller for kicking in sitting compared with the other movements, although this difference did not reach statistical significance. There was no difference in minimum or maximum hip angles across behaviors. Hip range of motion was smaller than knee range of motion for all rhythmic movements tested.

Four babies performed four types of rhythmic movements in a single session. We show the angle-angle plots of the hip and knee for two of these babies in Fig. 2. Linear regression was significant (\( P < 0.01 \)) and the slope positive for 85% (35/41) of hip-knee angle plots, reinforcing the observation that the hip and knee move in unison during the rhythmic movements tested. The regressions found not to be significant (6/41) were from four different movements in five infants. Thus there was not one particular infant or movement that did not show simultaneous hip and knee flexion/extension overall. Even though hip movement is constrained during kicking in sitting, the hip and knee still moved together more often than not, as three of the four regressions for kicking in sitting were found to be statistically significant with positive slopes. Interestingly, for each infant, the slopes of the regression lines were similar across all movements (\( P > 0.01 \) for all within-subject comparisons).

**Comparison of alternate and synchronous forms of movement**

The alternate and synchronous forms of rhythmic movements were compared to determine if it was appropriate to combine the two types of coordination for analysis. Because our primary interest was the relationship between the duration of a period (flexion or extension) with the duration of the cycle, we focused on this relationship. The durations were estimated from the knee angle (as outlined in Methods). A linear regression between the duration of flexion and the duration of the cycle was estimated for the synchronous and alternate forms of the same movement in turn. The slopes of the regression lines were then compared between the synchronous and alternate forms of the same behavior. The same procedure was used for the extension duration of the movement. No differences were found in the slope of the relationship for either the flexion or extension period in five of the six movements (Fig. 3 shows 4 examples). A comparison was not performed for the sixth movement, weighted air-stepping, because of the small number of infants that showed this behavior (i.e., 1 alternate and 3 synchronous). The cycle periods for the alternate forms of the movements were longer than the synchronous forms (\( P < 0.01 \), except \( P = 0.02 \) for air-stepping). In spite of the differences in cycle period, the relationship between durations of flexion/extension and cycle was identical. Hence, the data for alternate and synchronous forms of a movement were pooled for subsequent analyses.

**Relationships among durations of flexion, extension, and cycle for the knee**

The relationship between the durations of flexion/extension and cycle were examined for each type of movement, by fitting
the data to a straight line. Linear regression lines obtained from each individual baby (Fig. 4, gray lines) are shown superimposed on the regression lines obtained from the group (Fig. 4, dark dashed lines). In general, the data from individuals were reflected in the regression line of the group. All regressions performed on the group data were statistically significant (i.e., the slope of the relationship was different from zero). The durations of extension and flexion were very similar for kicking in supine. Identical slopes were found for the regression lines between flexion/extension and cycle period (Fig. 4A). Movements that loaded the limbs more during extension (Fig. 4B: stepping, kicking against a surface, and kicking in sitting) showed a longer duration of extension, and a stronger relationship between cycle period and extension. Movements that loaded the limbs more during flexion (air-stepping and weighted air-stepping) showed the opposite (Fig. 4C).

FIG. 3. Alternate and synchronous forms of the movements show the same relationship for flexion and extension with cycle period. Each data point represents 1 cycle from an infant. Slopes of the regression lines for alternate and synchronous forms of a behavior were the same ($P > 0.01$). The regression line for alternate and synchronous forms is — and - - - , respectively.

FIG. 4. Regression lines describing the relationship between flexion or extension duration with the cycle period are shown for individual subjects (gray lines). Superimposed is the regression line for all the subjects (black, dashed lines). The slope of the regression line for flexion ($b_f$) and extension ($b_e$) are shown. The durations were based on the motion of the knee. The movement conditions included those in which the loads were similar between flexion and extension (A), greater in extension (B) and greater in flexion (C). Refer to Table 1 for the number of infants included and the range of movement cycles obtained from each infant for each rhythmic movement.
The relationships between duration of flexion/extension and cycle period at the hip were also analyzed because previous work in other animals have shown differences between the joints (rostral scratch in turtles, Robertson et al. 1985; Stein and Daniels-McQueen 2004; walking in chicks, Johnston and Bekoff 1992, 1996). Only stepping and airdropping were analyzed here because average \( r^2 \) values for the hip and knee angle-angle diagrams were lower for these rhythmic movements compared with the others (\( r^2 \) values were as follows: stepping = 0.51 ± 0.29, air-stepping = 0.58 ± 0.29, kicking in supine = 0.88 ± 0.14). Note that the subject in Fig. 2A showed high \( r^2 \) values even for stepping and air-stepping, which was more common among younger infants. Lower \( r^2 \) suggests that the hip and knee do not always move in unison, and one might suspect that the hip may not show the same flexion/extension durations compared with the knee. As hip movement is minimal during kicking in sitting, this movement was not analyzed. Linear regressions were statistically significant for the relationships between duration of flexion/extension and cycle period at the hip for both stepping and air-stopping. Like the relationships seen at the knee, the duration of extension was longer and showed a stronger relationship with cycle period compared with flexion for stepping (Fig. 5A), whereas the opposite was found for air-stepping (Fig. 5B). The same trend was seen in both the individual and group data, and the same relationships were found for the hip and the knee.

**Fig. 5.** The durations of flexion and extension are plotted as a function of the duration of the cycle for the hip motion. The slope for extension (right) was significantly greater than that for flexion (left) in stepping (A). The slope for flexion was greater than that for extension in air-stepping (B), but this difference did not meet statistical significance. All conventions in the graph are the same as Fig. 4. Seventeen infants contributed a total of 353 cycles of stepping (range: 8–48 cycles/infant), and four infants contributed 32 cycles of air-stepping (range: 6–12 cycles/infant).

Changes in load affect the durations of flexion and extension in the same movement

All comparisons up to this point have been across different movements that require the infant to use different amounts of load during flexion and extension. To examine the effect of load on the same movement, the data from stepping and kicking against a surface were re-plotted as follows. The average peak force exerted by the infants during stepping on the treadmill ranged from 17.9 to 46.9% of their body weight. So the relationship between duration of flexion/extension and cycle period was plotted for the three infants who stepped with the lowest average forces of the group (17.9–22.3%, low-force group) and the three infants that showed the greatest average forces (38.4–46.9%, high-force group; Fig. 6A). The high-force group showed durations of extension that were longer and varied more strongly with cycle period compared with the low-force group. The average ages of the high- and low-force groups were 9.0 ± 1.2 and 5.1 ± 1.3 mo, respectively. To rule out age as a potential confounding factor, eight older infants (mean age = 9.4 ± 0.8 mo) were tested while stepping on the treadmill under two load conditions: stepping with normal weight (averaged 59.4 ± 6.6% body weight) and stepping with low weight (averaged 20.1 ± 3.5% body weight). There was a considerable change in the relationship between duration of flexion/extension and cycle period under the 2 stepping conditions (Fig. 6B). Again, the slope of the regression line for extension was greater with the higher load, but the difference was not statistically significant.

A similar relation was seen in kicking. There was a trend for the extensor-dominated pattern to be greater in infants who exerted >20% of their body weight (\( n = 3 \), mean = 31.4 ± 13.6% body weight) than those who exerted <20% of their body weight (\( n = 2 \), mean = 15.8 ± 3.0% body weight; Fig. 6C) although the slopes of the relationships were not significantly different.

**Muscle activity during rhythmic movements**

Twenty-one babies provided EMG data from the hamstrings and quadriceps. Of these, cross-talk was suspected in eight of them. Muscles from the lower leg were more susceptible to cross-talk, probably because of the proximity of the recording electrodes in a small child. Of the 16 infants from whom we had gastrocnemius–soleus and Tibialis anterior records, cross-talk was suspected in 13. Thus quantitative comparisons were only made for the quadriceps muscle for infants who performed two movements that involved different amounts of extensor load. Pair-wise comparisons between kicking supine and stepping showed no significant differences in the amplitude of the quadriceps burst (\( n = 11 \)). No differences were found between kicking supine and kicking against a surface (\( n = 5 \)).

**Discussion**

We demonstrate that infants respond to load-related feedback in the same way in a variety of rhythmic leg movements. The period (flexion or extension) that experiences the greatest load is longer in duration and more important in determining the cycle period. As we will discuss in the following text, this
were unable to record from the important hip flexor muscles between extensor- and flexor-dominated patterns. Second, we were unable to manipulate the load sufficiently to induce a switching to fat tissue overlying the muscles and the high possibility of crosstalk between muscles. Hence, we relied on kinematic data to define the durations of flexion, extension and cycle, an indirect measure of the motor output.

Load-related sensory feedback affects the timing of both flexion and extension

We showed that altering load, either through minor changes in the task or changes in the degree of load experienced in the same task, could cause either the flexion or the extension periods to be longer (or dominant). Previous work has focused on the importance of load-related proprioceptive signals for controlling both the timing and amplitude of extensor muscle activity during walking in mammals (reviewed in McCrea 2001; Duyens et al. 2000). More recently, similar findings have been reported for flexor muscle activity in cats during walking (Lam and Pearson 2001, 2002; McVeal et al. 2005; Perreault et al. 1995; Quevedo et al. 2000; Stecina et al. 2005) and scratching (Stecina et al. 2005). Our results support both these ideas and extend the findings to rhythmic leg movements in human infants.

Load is also important in determining the duration of flexion and extension during other rhythmic movements besides upright walking. Inverted walking in insects and primates is interesting because the flexor muscles are used for the period of support (equivalent to the period of stance in upright walking), whereas the extensor muscles are used for reaching (equivalent to the period of swing) (cockroach, Larsen et al. 1995; Loris, Jouffroy and Stern 1990). Because the period of support bears the greater load, it is longer and more strongly correlated with the walking speed than the period of swing (cockroach, Larsen et al. 1995; Ateles or woolly monkey, Turnquist et al. 1999) in spite of the fact that flexor muscles are used during support.

A rhythmic movement that has been reported to be flexor-dominated is scratching in the cat (Deligianna et al. 1975). Most of the early work, however, was done in decerebrate cats during air-scratching or paralyzed animals with no movement (Berkinblit et al. 1978a, b; Deligianna and Feldman 1981; Deligianna et al. 1975), so in both cases, there was no contact with a substrate. During air-scratching, the flexion period likely encounters more resistance as the arm flexes against gravity, compared with the extension period that would be assisted by gravity. In intact cats, scratching involves contact with the body (i.e., increased load) during the extension period of the movement. In agreement with our hypothesis, the period of extension is lengthened compared with air-scratching, resulting in an approximately equal period of flexion and extension (Kuhta and Smith 1990).

There are sporadic reports in the literature for which the duration of flexion is longer than the duration of extension during locomotor-like movements of behaving animals. For example, the duration of hip flexion (Johnston and Bekoff 1992) and ankle flexor activity (Johnston and Bekoff 1996) during air-stepping in chicks are longer than extension and show a strong relationship with cycle period. Air-stepping in neonatal monkeys also shows a similar phenomenon (Vilensky et al. 1989). These results are in agreement with our findings.

**Methodological issues**

First, we were unable to measure the load experienced by the various sensors directly. Instead, indirect estimates were made based on the vertical ground reaction during stepping and the contact forces during kicking against a plate for loads applied during extension. Loads applied during flexion were indirectly estimated by the limb load (Schneider et al. 1990) and the extra weights. The load experienced during free kicking in supine was obtained from the literature (Jensen et al. 1994). Although we did not have exact measures of the sensory input, we were able to manipulate the load sufficiently to induce a switching between extensor- and flexor-dominated patterns. Second, we were unable to record from the important hip flexor muscles because they are not accessible from the surface. Moreover, good EMG data are difficult to obtain from human infants due to fat tissue overlying the muscles and the high possibility of crosstalk between muscles. Hence, we relied on kinematic data to define the durations of flexion, extension and cycle, an indirect measure of the motor output.

**FIG. 6.** The effect of load on the duration of flexion and extension within the same movement condition. A: data from infants who showed low (left) and high (right) weight support during treadmill stepping. B: data from 8 infants when they were stepping under normal conditions (right) and low load conditions (left). Load in this case was manipulated by the experimenter supporting the baby. C: data from infants who showed low (left) and high (right) loads when kicking against the kick plate. Linear regression lines for extension (---) and flexion (——) are shown, together with the slope of those lines (b<sub>f</sub>, flexion; b<sub>e</sub>, extension).

A general principle appears to apply to many rhythmic leg movements across vertebrate species.
Air-stepping in spinal kittens and adult spinal dogs, however, were less clear. Some showed longer extension durations (Giuliani and Smith 1985; Naito et al. 1990), opposite to what we would predict. The reason for these inconsistencies is unknown.

Movements in which load-related feedback has not been quantified

For scratch behaviors of the turtle, the powerstroke was defined as the period when the limb rubs against the body (reviewed in Stein 2005). By this definition, we would expect the duration of the powerstroke to be longer than the return stroke, but this was not always the case. Based on analyses of the movements, one might expect all scratches to be extensor-dominated because the contact phase in all cases is coincident with extension in both the hip and knee (Mortin et al. 1985). Yet rostral scratch in behaving animals showed a balanced period of flexion and extension, whereas pocket scratch was flexor-dominated and caudal scratch was extensor-dominated (Earhart and Stein 2000). Because load has not been quantified in these movements, it is difficult to know whether the behavior is truly an exception to our hypothesis or whether other loads during the scratching, such as the resistance provided by the water, are also substantial. Nevertheless, it is clear that sensory feedback associated with real scratching movements alters the relative durations of the flexion and extension because the period that is dominant is not always the same for fictive compared with intact preparations (compare fictive Robertson et al. 1985, with intact Mortin et al. 1985).

In swimming, the durations of flexion and extension are similar and both vary with cycle period (chicks, Johnston and Bekoff 1992, 1996; turtles, Earhart and Stein 2000). Because the load experienced by the limbs during swimming is largely viscous, the load depends on the speed of the movement. We would predict that the durations of flexion and extension would depend on the speed of the movement in each phase. Thus future work to quantify the load would be helpful to determine if our hypothesis holds true for swimming and scratching.

Dominance patterns may not be the same across joints

Whether a flexor or extensor period is dominant during rhythmic movements can also differ across joints within a limb. For example, the period of stance during walking is characterized by hip and ankle extension and knee flexion in the chick (Johnston and Bekoff 1992, 1996). Correspondingly, walking in chicks is extensor-dominated at the hip and ankle and flexor-dominated at the knee. To determine if such patterns exist in our infants, we analyzed the motion of the hip and knee in a subset of infants during stepping and air-stepping because these movements showed the greatest differences in motion between the hip and knee (i.e., lower \( r^2 \) in hip versus knee movement). The hip and knee showed the same dominance patterns in all cases (Fig. 5).

Other forms of afferent feedback

Afferent feedback besides load may also influence the duration of phases in rhythmic movements. Stretch of hip flexor muscles is clearly one variable that influences when the stance phase ends during walking (Grillner and Rossignol 1978; Hiebert et al. 1996; Pang and Yang 2000). Sensory signals associated with hip flexion may also control the termination of the swing phase (McVea et al. 2005). In the behaviors we studied here, however, the maximum and minimum hip angles reached were not significantly different between behaviors. Cutaneous input may also be involved. The duration of flexor (tibialis anterior) activity was prolonged during air-stepping when tape was applied to the paw of a spinal cat, resulting in a stronger duration-period relationship for flexion (Giuliani and Smith 1985). Clearly, other afferent input not specifically tested here could also control the duration of a phase and could be explored in the future.

Functional and clinical implications

Our findings suggest that during many forms of rhythmic limb movements, animals and humans use a similar strategy to overcome the load experienced during the movement. When load is encountered, whether during the flexion or the extension period of the movement, muscle activity to counter the load is reinforced and prolonged to overcome the load. Similar responses are seen during the extensor period of walking in individuals with spinal cord injury, including those with clinically complete lesions (Harkema et al. 1997). Indeed, the manipulation of load on extensors has been used successfully to improve walking after injury to the nervous system (Barbeau and Blunt 1991; Dobkin et al. 2006; Wernig et al. 1995). Whether similar responses can be elicited in these individuals by manipulating load on the flexors during walking remains to be seen.

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