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Marching to the beat of the same drummer: the spontaneous tempo of human locomotion

Hamish G. MacDougall and Steven T. Moore
Human Aerospace Laboratory, Department of Neurology, Mount Sinai School of Medicine, New York, New York

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MacDougall, Hamish G., and Steven T. Moore. Marching to the beat of the same drummer: the spontaneous tempo of human locomotion. *J Appl Physiol* 99: 1164–1173, 2005. First published May 12, 2005; doi:10.1152/japplphysiol.00138.2005.—Laboratory studies have suggested that the preferred cadence of walking is ~120 steps/min, and the vertical acceleration of the head exhibits a dominant peak at this step frequency (2 Hz). These studies have been limited to short periods of walking along a predetermined path or on a treadmill, and whether such a highly tuned frequency of movement can be generalized to all forms of locomotion in a natural setting is unknown. The aim of this study was to determine whether humans exhibit a preferred cadence during extended periods of uninhibited locomotor activity and whether this step frequency is consistent with that observed in laboratory studies. Head linear acceleration was measured over a 10-h period in 20 subjects during the course of a day, which encompassed a broad range of locomotor (walking, running, cycling) and nonlocomotor (working at a desk, driving a car, riding a bus or subway) activities. Here we show a highly tuned resonant frequency of human locomotion at 2 Hz (SD 0.13) with no evidence of correlation with gender, age, height, weight, or body mass index. This frequency did not differ significantly from the preferred step frequency observed in the seminal laboratory study of Murray et al. (Murray MP, Drought AB, and Kory RC. *J Bone Joint Surg* 46A: 335–360, 1964). [1.95 Hz (SD 0.19)]. On the basis of the frequency characteristics of otolith-spinal reflexes, which drive lower body movement via the lateral vestibulospinal tract, and otolith-mediated collic and ocular reflexes that maintain gaze when walking, we speculate that this spontaneous tempo of locomotion represents some form of central "resonant frequency" of human movement.

locomotor; vestibular; step frequency; cadence; otoliths

AS WE MOVE AROUND OUR ENVIRONMENT, the linear movement of the head is coupled to trunk linear motion by the cervical spinal column, and head and trunk movement in turn reflect the kinematics of the lower limbs (18, 30). During the swing (flexion) phase of walking, the trunk moves upward, reaching a peak as it passes over the single supporting foot, and is at its lowest point during the double-limb support phase as the body transitions from the conclusion of the current swing phase to the initiation of the swing phase of the other leg. Consequently, the vertical linear movement of the entire body exhibits a dominant component at the frequency of stepping. Laboratory studies of over-ground human walking (32) have shown that, on average, preferred cadence is close to 120 steps/min, equivalent to a step frequency of 2 Hz; on a treadmill, however, step frequency varies considerably with belt speed from 1.5 Hz for slow walking (0.6 m/s) to 2.4 Hz for fast walking (2.2 m/s) (18). The vertical linear movement of the head exhibits a clear dominant peak at the frequency of stepping (18, 19, 30, 31), and vertical head acceleration is critical in maintaining posture and gaze via spinal and ocular reflexes mediated by the otoliths, which are located in the peripheral vestibular labyrinth of the inner ear and transduce linear acceleration (18, 19, 30, 31, 37).

Whether the cadence of walking determined in the laboratory can be generalized to all human locomotor activity in a natural setting is not known and was the primary goal of this study. Locomotion studies conducted in a laboratory setting are restricted by the physical limitations of the available space and the measurement volume of the motion-capture device. The seminal study by Murray et al. (32) was limited to locomotion over 4.9 m [approximately the same distance as a more recent study (19)], and subjects first practiced walking along this path in pace with a metronome at 112 steps/min (1.87 Hz). Subjects may not reach a "steady state" of locomotion over such short distances, and there is the possibility that having subjects walk a predetermined path may cause an adjustment of stride length to accommodate the available distance. Treadmills have commonly been utilized to overcome space limitations and to allow an "unlimited" walking path, but the fact that subjects move to maintain a relatively static position in space on a moving belt, rather than actively locomote over ground, generates treadmill-specific patterns of gait. For example, vertical body movement is smaller on a treadmill than with over-ground walking (18), and step frequency is linearly related to height for a given belt speed (30), whereas there is no correlation between cadence and height during over-ground locomotion (32).

Determining cadence and the related frequency characteristics of linear head movement during natural locomotion is critical in understanding head-eye coordination. Recent treadmill studies have demonstrated a compensatory pitch of the head in response to vertical head translation (i.e., as the head translates upward it pitches down, and vice versa) that acts to point the nasooccipital axis at a distance of ~1 m in front of the subject (the "head fixation distance") (18, 30, 31), likely an otolith-mediated linear vestibulocollic reflex. The frequency characteristics of this putative reflex are unknown, but compensatory head pitch develops only at step frequencies >1.7 Hz (18). This is consistent with the high-pass nature of the linear vestibuloocular reflex, which generates vertical eye movements compensatory for head translation for visual targets between the subject and the head fixation distance during walking (30, 31). This ocular reflex exhibits an increasing sensitivity at >1 Hz and has a significant response at ~2 Hz (3, 33, 34). Moreover, the compensatory pitch of the head during

Address for reprint requests and other correspondence: S. T. Moore, Mount Sinai School of Medicine, Dept. of Neurology, Box 1135, 1 East 100th St., New York, NY 10029 (E-mail: steven.moore@mssm.edu).

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locomotion is degraded in patients with bilateral vestibular deficits (15, 36) and astronauts returning from spaceflight (1, 28), which may be due to a deconditioning of otolith function, and/or a decreased cadence that reduces the frequency of vertical head acceleration such that it is below the operational range of the linear vestibulocollic reflex. In either case, the net result for the individual is significant oscillopsia and reduced dynamic visual acuity.

The finding of a preferred step frequency at 2 Hz during over-ground walking in the laboratory (32) is consistent with the notion of spontaneous tempo, a popular field of study of the Gestalt psychologists in the first half of the 20th century. Spontaneous tempo, as determined from subjects freely tapping out a rhythm with their finger, was found to average ∼2 Hz (4, 7, 11, 21, 27), as did the preferred tempo of metronome beats (10, 26, 45). The spontaneous tempo was also closely correlated with the cadence of walking (17, 25). A predilection for a 2-Hz frequency of movement has also been observed in music; a study of the tempi of >74,000 pieces of modern Western music from beats-per-minute lists used by disc jockeys, random radio selections, and compact disc compilations of popular music from 1960 to 1990 demonstrated a peak at a frequency of 2 Hz (27) (see Fig. 3*B*).

The aim of this study was to determine whether humans exhibit a preferred cadence during extended periods of natural activity and whether this step frequency is consistent with that observed in laboratory locomotion studies (32) and spontaneous tempo (4, 7, 10, 11, 21, 26, 27, 45). Previous studies of daily activity have utilized pedometers and, to a lesser extent, single-axis accelerometers to assess the number of steps per day (40–43), but these devices are incapable of providing information on cadence and frequency characteristics of linear body motion. Here, we utilize a lightweight, self-contained activity monitor to measure triaxial linear head acceleration at 40 Hz in normal subjects over a 10-h period, which allows a detailed frequency analysis of cadence and linear head movement during periods of natural locomotion.

METHODS

Subjects. Twenty healthy subjects (10 men and 10 women), with no history of vestibular or gait abnormalities, participated in this experiment. Age, height, and weight were as follows: 22–62 yr [37 (SD 12)], 152–182 cm [167 (SD 9)], and 40–100 kg [64 (SD 18)], respectively. The study was approved by the Institutional Review Board at the Mount Sinai School of Medicine and was performed in accordance with the ethical standards of the 1964 Declaration of Helsinki. Subjects gave informed consent before their inclusion in the study.

Activity monitor. Human movement was recorded using a self-contained activity monitor mounted on the rear of a baseball cap (Fig. 1, *inset*). Linear acceleration of the head in space along the nasooccipital (forward-backward), interaural (side-to-side), and dorsoventral (up-down) axes was acquired at a rate of 40 Hz over a period of 10 h. The device was programmed to start data collection when the subject awoke and was worn throughout the day as the subject performed his/her normal daily activities. The activity monitor was lightweight (48 g), about the size of a pager (76 × 51 × 16 mm), and contained a triaxial linear accelerometer with an analog-to-digital converter and flash memory (DigiTrac, IM Systems, Baltimore, MD). The weight of the unit was ∼1% of the typical head mass of 4,200 g (32a), which would not significantly affect head movement. The device was designed to monitor leg activity in sleeping subjects with restless leg syndrome; to our knowledge, this was the first time it was used to measure acceleration of the head.

The quoted accuracy of the accelerometers was 5%, with cross talk between measurement axes limited to <10%. This was independently verified by the authors with a direct comparison with an industry-standard accelerometer (model ADXL150EM-3, Analog Devices). In addition, the DigiTrac was placed on a servo-driven linear sled and oscillated at 2 Hz with amplitude of 1 cm, and the measured linear acceleration was well within 5% of the actual value of 0.16 g. The frequency response (3-dB cutoff) of the device is 0.46–14.1 Hz; thus the static gravitational component of acceleration is filtered out. Although heel strike generates frequency components up to 100 Hz (9, 16), most of the power is below 10 Hz (16). Results of previous locomotion studies (5, 18, 30) demonstrated negligible power for head movement at frequencies >6 Hz due to attenuation of the shock waves by the musculoskeletal system (44) (Fig. 1). Thus the frequency range of the DigiTrac was ample for the task at hand.

A fitted baseball cap provided a stable platform for mounting the DigiTrac activity monitor on the subject because of the large contact area with the head. This was verified in two subjects by comparison of head acceleration during treadmill locomotion at 100 m/min measured with the DigiTrac and with a video-based motion analyzer (Optotrak 3020, Northern Digital) (30). There was no significant difference in the linear acceleration measured with the two devices. Another advantage of utilizing a fitted baseball cap was the consistency in placement. A subject comfortably positioned the baseball cap on the head. We then placed the DigiTrac on the cap, such that the vertical (z) axis of the DigiTrac was approximately orthogonal with the stereotaxic horizontal plane, as determined from four external landmarks: the left and right tragion (a point in the depth of the notch just above the tragus of the ear) and the left and right orbitale (the inferior point of the lower margin of the orbit). For example, in the subject photograph in Fig. 1, the DigiTrac z-axis was tilted 1.2° with respect to the head dorsoventral axis (Fig. 1, *inset*). The subject was asked to remove the cap, wait 30 s, and then place the cap on the head in the same orientation. This was repeated 10 times. There was little variability in cap position, with a standard deviation of the orientation of the DigiTrac z-axis of 2.1° relative to the head vertical axis. This would introduce a minimal measurement error of 0.06% in the measured vertical linear acceleration. In practice, the DigiTrac could be tilted in pitch with respect to the dorsoventral (z) head axis by up to ±19° and still induce an error in vertical linear acceleration of <5% [i.e., cosine(19°) = 0.95].

Placement of the DigiTrac exposes the unit to tangential and centripetal accelerations during rotation of the head. Inasmuch as we did not measure angular head movement, it is not possible to dissociate linear acceleration due to head translation from the components generated by a simultaneous head rotation. This is most critical during high-frequency head movement, as linear accelerations generated by low-frequency (<0.46-Hz) head rotation (tilts) would be filtered out. To estimate an upper bound for the error induced by head rotation, we utilize data from our locomotion studies (30). During fast (100 m/min) treadmill walking, a pitch of the head occurs at 2 Hz in conjunction with a robust vertical linear acceleration of the head of 0.5-g peak amplitude. The peak pitch angular velocity and acceleration of the head are 13°/s and 161°/s^2, respectively. The DigiTrac was positioned on the back of the head ∼8 cm from the pitch rotation axis (29) at the level of the interaural axis (Fig. 1, *inset*). The centripetal acceleration sensed by the DigiTrac would be negligible, with a peak magnitude of 0.0004 g directed toward the head rotation axis (along the nasooccipital axis). The peak tangential component sensed by the activity monitor would be 0.02 g parallel with the head dorsoventral axis, introducing a maximum error of 4% in the measured vertical linear acceleration of the head. These errors are less than the accuracy of the DigiTrac accelerometers (5%). Generation of vertical linear (tangential) acceleration at a frequency of 2 Hz with magnitude comparable to that observed during walking (0.5 g) with head rotation alone would

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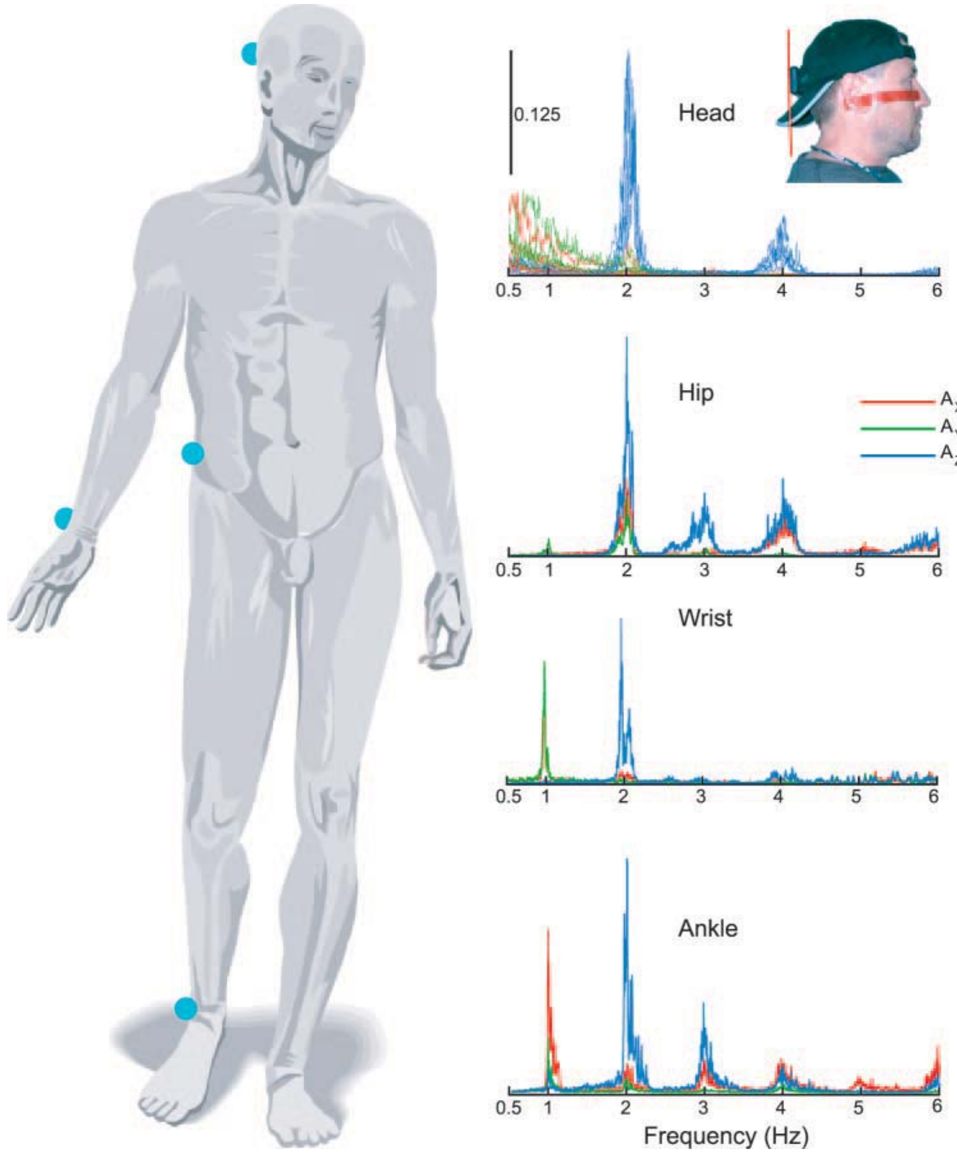

Fig. 1. Power spectra of linear acceleration from a subject wearing the activity monitor on the head (data from 5 separate days are overlaid), wrist, hip, and ankle. For the head: A_x, linear acceleration along the nasooccipital (x) axis; A_y, linear acceleration along the interaural (y) axis; A_z, linear acceleration along the head-vertical or dorsoventral axis (z). For the hip, wrist, and ankle: A_x, linear acceleration along the dorsoventral (x) axis; A_y, linear acceleration along the mediolateral (y) axis; A_z, linear acceleration along the body-vertical or rostrocaudal axis (z). Magnitude of acceleration was represented using a relative scale; vertical scale bar shows 12.5% (0.125) of the power of a pure 2-Hz sine wave with amplitude of 0.3 g over 1 h. This metric was chosen because it represents an acceleration and frequency of head movement associated with typical walking speed of adult humans. There was little variability in the pattern of head acceleration over the five 10-h epochs, with the dominant vertical component at 2.05 Hz (SD 0.03). Power spectra of the lower body exhibited the same 2-Hz dominant peak in vertical movement that was passed up from the ankle, through the trunk, and to the head. The 1-Hz peak (stride frequency) and higher frequency harmonics observed at the ankle were attenuated by the musculoskeletal system before reaching the head. *Inset*: positioning of activity monitor on the rear of a fitted baseball cap worn by a subject. Red line illustrates tilt of the vertical (z) axis of the accelerometer relative to the head, which in this instance was pitched back 1.2° from the head dorsoventral (vertical) axis. Red tape shows the line through the right tragion and orbitale, used to define the stereotaxic horizontal plane.

require a head pitch acceleration of 3,500°/s^2, which is beyond the physiological limits of movement (29). Thus the impact of high-frequency head rotation on the linear acceleration measures of the head in space was negligible.

During the 10-h epoch, subjects indicated changes in activity by pressing an event button on the DigiTrac, which inserted a flag in the data trace. In addition, subjects provided a log of daily behavior that was cross-referenced with the event markers to identify periods of locomotor activity.

Data processing. The linear acceleration data were processed using Labview's advanced analysis package (National Instruments, Austin, TX). The power spectra were calculated using fast Fourier transforms. The magnitude of head acceleration in the power spectra shown in Figs. 1–3 and 7 is represented relative to the power of a pure 2-Hz sine wave with amplitude of 0.3 g over 1 h [0.021 (m/s^2)^2/Hz]. The scale bar (vertical bar labeled 0.125) included on all the spectral plots shows 12.5% of this value. For example, the power spectrum of head acceleration over 10 h of natural activity for a single subject (Fig. 1, *top plot*) demonstrates that the peak vertical linear acceleration at 2 Hz (blue trace) had a relative magnitude of ~20% of the power of a pure 2-Hz sine wave with amplitude of 0.3 g over 1 h. This metric was chosen because it represents an acceleration and frequency of head movement associated with the typical walking speed of adult humans (18).

A "moving" root-mean-square (RMS) trace of the 10-h activity waveform was calculated using a sliding window of 2-s width, which was chosen to incorporate all measured frequencies within the window (the frequency response of the accelerometers rolls off below 0.46 Hz). The RMS value of the linear acceleration component along a particular axis was calculated at a point in the center of the window from 1 s of data either side. The window then slid one data point later in time, and the process was repeated, generating RMS values over the entire 10-h epoch. To determine periods of locomotor activity from the 10-h traces, the dorsoventral (vertical) acceleration data were divided into 60-s intervals, and the power spectrum was calculated for each interval. Periods of activity where the dorsoventral head acceleration exhibited a dominant peak in the range 1.5–2.5 Hz were defined as locomotor on the basis of previous treadmill (18) and over-ground (32) walking studies in the laboratory.

RESULTS

Power spectra of head linear acceleration over 10 h from a typical subject are shown in Fig. 1. To demonstrate repeatabil-

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ity, the subject wore the activity monitor on 3 consecutive weekdays and over a weekend (separated by 2 wk), for a total of five 10-h epochs. The power spectra were very consistent over the five test sessions (Fig. 1, *top plot*), with a dominant peak of vertical head acceleration at 2.05 Hz (SD 0.03). The frequency spectra of linear movement of ascending body segments was obtained from a single subject to demonstrate the causal relation between step frequency and the dominant frequency of vertical head acceleration during locomotion in a natural setting. The same subject wore the device for 10 h on 3 consecutive days on the right ankle, hip, and wrist, respectively (Fig. 1). The power spectra exhibited the same 2-Hz dominant peak in vertical movement (i.e., step frequency) that was passed up from the ankle, through the trunk, and to the head, as previously observed in treadmill studies in the laboratory (18, 30, 31). The power spectra of ankle movement also exhibited a large component at 1 Hz (i.e., stride frequency) and had significant high-frequency harmonics, which were attenuated by the musculoskeletal system before reaching the head (44). The wrist also exhibited a dominant vertical acceleration at 2 Hz, as well as a large component parallel to the mediolateral (*y*) axis at 1 Hz, reflecting the lateral movement of the body at the stride frequency.

A broad variety of activities were undertaken by the 20 subjects over the course of a day. Head linear acceleration data over 10 h for three subjects is shown in Fig. 2. The first subject (Fig. 2*A*), a 23-yr-old woman vacationing in New York City, walked and rode the subway around Manhattan, visited the Museum of Modern Art, shopped, visited the authors' laboratory, and then walked back to the apartment where she was staying, stopping at the supermarket on the way, and promptly fell asleep. The second subject (Fig. 2*B*), a 62-yr-old male university professor in Sydney, Australia, rode his bicycle in the morning, caught a bus into town and shopped, and then spent the rest of the afternoon gardening at home. The third subject (Fig. 2*C*), a 34-yr-old postgraduate student, walked to

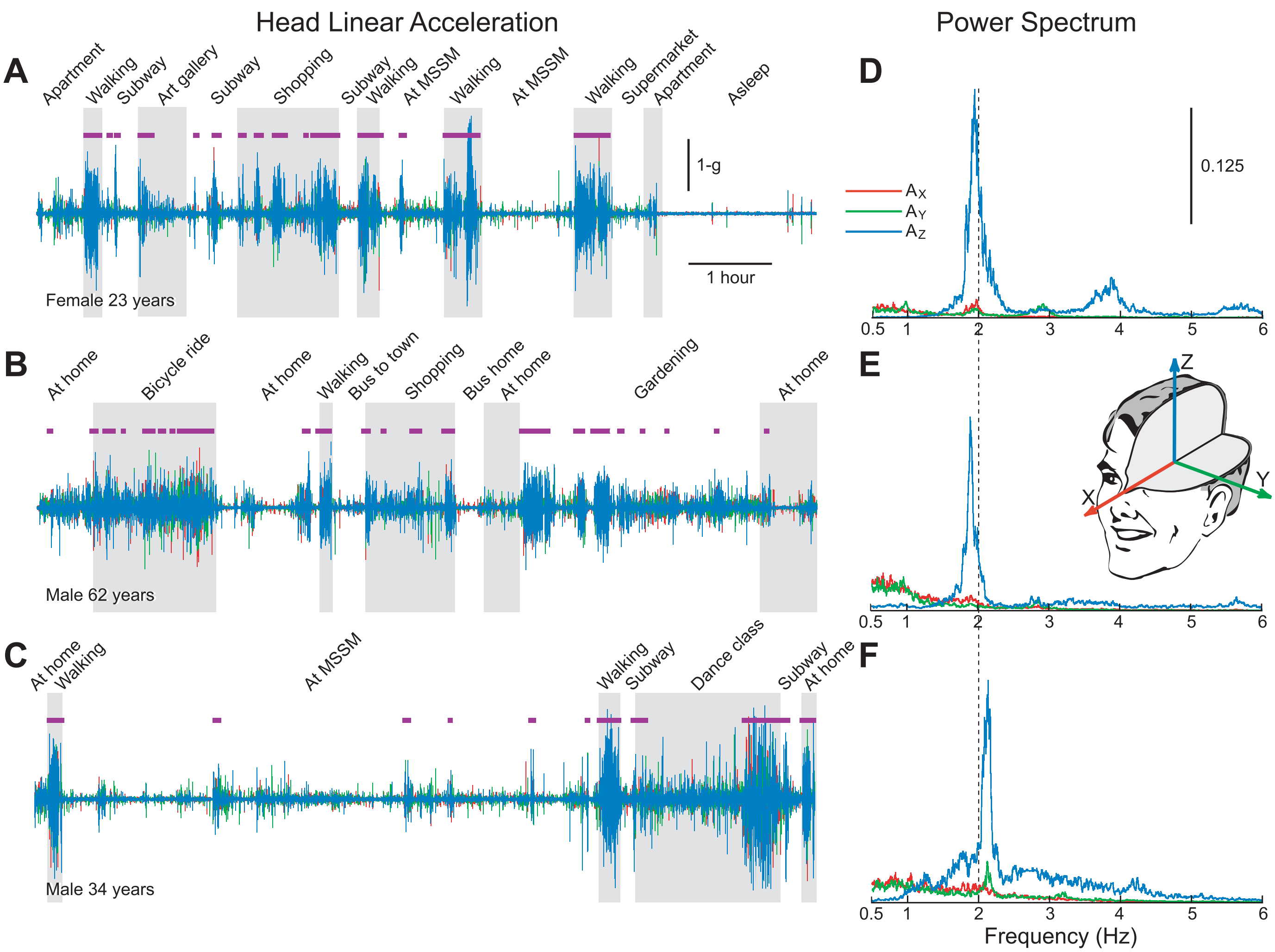

Fig. 2. Linear acceleration of the head over a 10-h period for 3 subjects. *A*: 23-yr-old woman sightseeing in Manhattan. *B*: 62-yr-old male university professor enjoying the weekend. *C*: 34-yr-old male postgraduate student working in a laboratory and attending a dance class in the evening. Purple bars, significant vertical linear acceleration of the head in the frequency range 1.5–2.5 Hz, which was defined as signifying locomotor activity. MSSM, Mount Sinai School of Medicine. *D–F*: despite the varied nature of physical activity, power spectra of head linear acceleration over 10 h for the 3 subjects were almost identical, with a large dorsoventral (*z*) acceleration component with a dominant peak close to 2 Hz. Magnitude of head acceleration was represented using a relative scale; vertical scale bar (*D*) shows 12.5% (0.125) of the power of a pure 2-Hz sine wave with amplitude of 0.3 g over 1 h. This metric was chosen because it represents an acceleration and frequency of head movement associated with typical walking speed of adult humans.

Mount Sinai School of Medicine, where he spent the day working at a desk with intermittent periods of locomotion, and then walked and rode the subway to a dance class. There was significant linear acceleration of the head during locomotor activity (Fig. 2, *A–C*), particularly along the dorsoventral (z) axis, with peak amplitude of ~1 g. Despite the differences in age and daily activity of the three subjects, the frequency spectra of the entire 10-h data set exhibited a clear peak at ~2 Hz for the vertical (z) component of head movement (Fig. 2, *D–F*).

This result was remarkably consistent across all 20 subjects (Fig. 3*A*). There was a clear dominant peak of vertical head movement at 2.0 Hz (SD 0.13) (range 1.70–2.16 Hz) in the frequency spectra of the entire 10-h epoch, with no evidence of correlation with age, height, weight, or body mass index [P (2-tailed) $>$ 0.1, Pearson's correlation analysis; Fig. 4]. ANOVA revealed no significant difference ($P = 0.46$) between the dominant vertical frequency of male [2.0 Hz (SD 0.15), $n = 10$] and female [2.0 Hz (SD 0.12), $n = 10$] subjects. Furthermore, the observed frequency of vertical head acceleration [2.0 Hz (SD 0.13)] was not significantly different from the step frequency of 1.95 Hz (SD 0.19) observed in the laboratory study of Murray et al. (32) [$t(138) = 1.08$, P (double-sided) $= 0.28$] or the spontaneous tempo [2.01 Hz (SD 0.4)] of subjects tapping a 4/4 beat with their finger (7) [$t(38) = 0.094$, P (double-sided) $= 0.93$]. The mean magnitude of the interaural (y) and nasooccipital (x) components of head acceleration was a factor of 10 lower than the dorsoventral (z) component. Interaural head acceleration exhibited a peak at 1 Hz with harmonics at 2 and 3 Hz, whereas the nasooccipital movement had a peak at 2 Hz (Fig. 3*B*).

The frequency characteristics of the averaged head linear acceleration (Fig. 3*B*) were similar to those observed during laboratory locomotion studies, where the dorsoventral and nasooccipital linear acceleration of the head are coupled to the vertical motion of the body at the frequency of stepping, and the interaural component reflects the lateral body sway at the stride frequency (i.e., half the step frequency) (18, 19, 30). The fact that interaural acceleration was significantly less than the vertical component of head acceleration has previously been

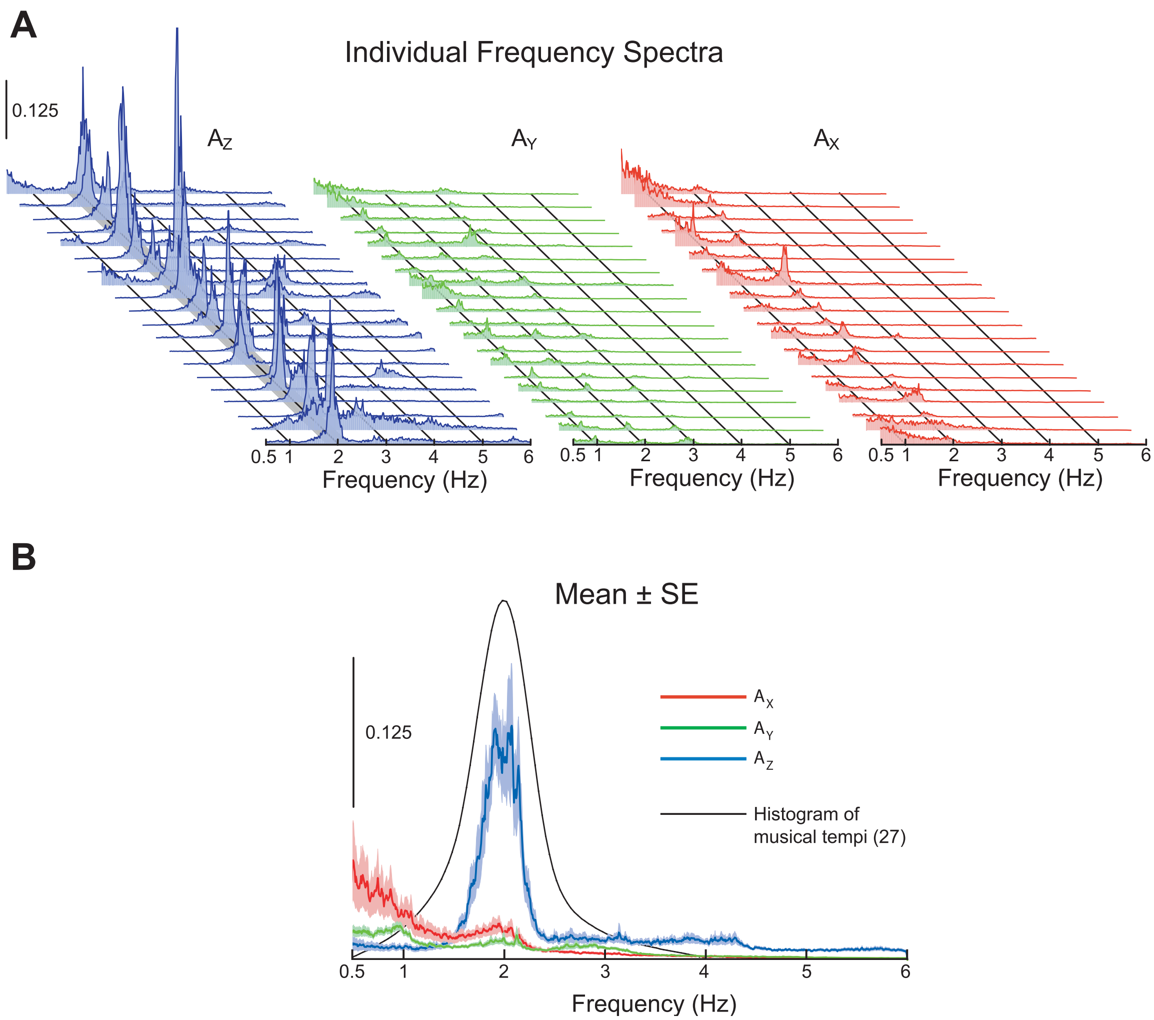

Fig. 3. *A*: power spectra of linear acceleration of the head over a 10-h period. Magnitude of head acceleration was represented using a relative scale; vertical scale bar shows 12.5% (0.125) of the power of a pure 2-Hz sine wave with amplitude of 0.3 g over 1 h. Each slice in the plots represents 1 of the 20 subjects. All subjects exhibited a clear dominant frequency of vertical (z) movement at ~2 Hz [2.0 Hz (SD 0.13); mean (SD) is shown as gray shaded region in A_z plot]. *B*: averaged power spectra (mean and SE of 20 subjects) demonstrated a highly tuned resonance of movement at 2 Hz. Black trace is adapted from a histogram of tempi from a large database of modern Western music (27) and demonstrates clear prevalence of rhythm equivalent to 2 Hz (120 beats/min).

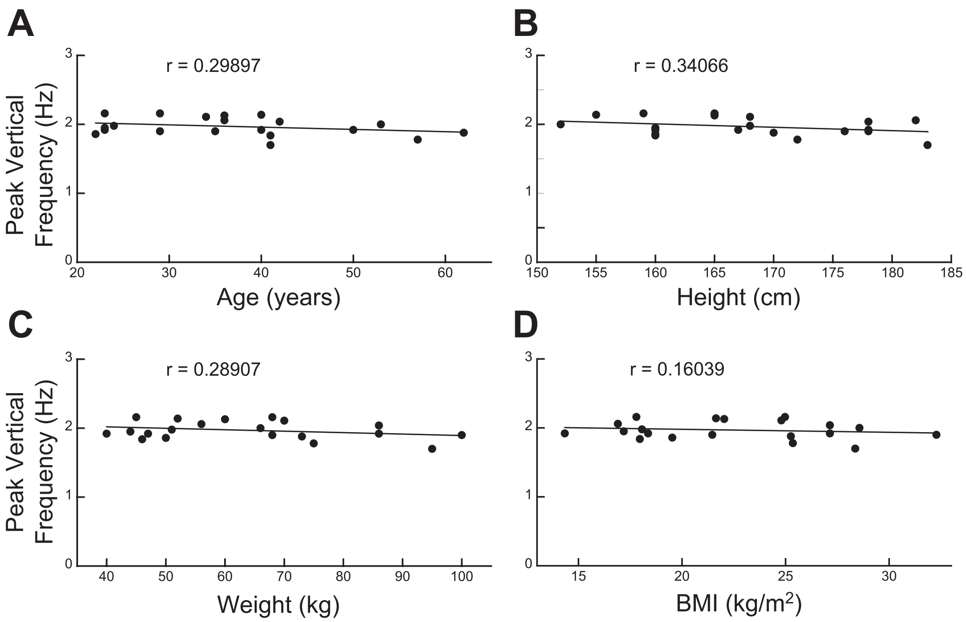

Fig. 4. Plots of the dominant frequency of vertical head acceleration vs. age, height, weight, and body mass index (BMI). There was no evidence of a systematic relation between peak frequency of vertical head acceleration and age, height, weight, or BMI.

observed in treadmill (31) and over-ground (19) locomotion studies. This is due to the lower magnitude (10-mm peak) and frequency (1 Hz) of lateral (19, 31) than vertical (20-mm peak and 2 Hz, respectively) translation (18, 19, 30, 31). The power of the interaural acceleration component is also smaller during over-ground walking than during treadmill locomotion. This may be due to the flexible properties of the treadmill platform, which generates more lateral body movement. Moreover, during locomotion in a natural setting, the head is often yawed relative to the trunk as the subject looks around the environment (e.g., when checking for vehicles while crossing a road); thus the interaural component of head acceleration would be reduced as a result of cross-coupling between the interaural (y) and nasooccipital (x) axes of the head-mounted three-dimensional accelerometer. In contrast, subjects typically maintained fixation on a target directly ahead during treadmill locomotion studies (18, 30, 31).

An analysis of head movement data during various activities confirms the similarity in the frequency spectra of head acceleration during unrestricted locomotion (Fig. 3*B*) to those obtained from laboratory treadmill studies (18, 30, 31). During periods of active locomotion (determined from event markers and subject reports of daily activity) such as walking, descending stairs, cycling (on a stationary ergometer and over ground), and cleaning an apartment, there was a highly tuned peak in the vertical acceleration of the head at ~2 Hz that reflected the linear movement of the lower limbs and trunk (Fig. 5). Note that the vertical head acceleration generated during activities such as shopping and visiting an art gallery (Fig. 2*A*), gardening (Fig. 2*B*), and cleaning an apartment (Fig. 5) was most likely due to the walking inherent in these endeavors. Nonlocomotor activities, such as driving a car, traveling as a passenger in a car, bus, or train, and working at a desk, generated minimal high-frequency linear acceleration of the head along all axes (Fig. 6).

Periods of activity in which the head vertical acceleration exhibited a dominant peak in the range 1.5–2.5 Hz were identified in each 10-h data set. The results demonstrated that significant power at ~2 Hz was highly correlated with active locomotion as determined from daily activity logs and event markers, such as walking, running, dancing, shopping, gardening, visiting an art gallery, and riding a bicycle (Fig. 2, *A–C,* purple bars above activity data). Across all 20 subjects, locomotor activity comprised 12.7% (SD 3.5) [76 min (SD 21)] of the 10-h epoch (Fig. 7*A*). Thus, of the 200 h of data collected, locomotor activities totaled 25.4 h: 6.1 h of cycling (24%) and 19.3 h (76%) generalized as pursuits involving some variation of bipedal locomotion (walking, running, dancing). Although locomotor activity comprised only 12.7% of each 10-h epoch, it accounted for over half of daily high-frequency vertical linear acceleration (Fig. 7*B*). The cumulative RMS acceleration along the three head axes during locomotor activity, expressed as a percentage of the total RMS over 10 h, was 53.7% (SD 7.9) for dorsoventral (z) acceleration, 35.5% (SD 7.4) for interaural acceleration (y), and 39.7% (SD 10.1) for nasooccipital (x) acceleration (Fig. 7*B*). Almost all the power of high-frequency linear head movement was generated during the 76 min of locomotor activity, the power spectra of which (Fig. 7*D*) were remarkably similar to those calculated from the entire 10-h data set (Fig. 3*B*). Nonlocomotor activities, such as riding the bus or a train, driving a car, or working at a desk, generated negligible high-frequency head acceleration (Fig. 7*C*).

DISCUSSION

The major finding of this study was that the vertical linear acceleration of the head (and, therefore, step frequency) exhibited a highly tuned dominant component at 2 Hz (SD 0.13) during daily locomotor activity. This cadence was consistent with the extensive laboratory study (utilizing a 5-m walking path) of Murray et al. (32) but extends this result to include a variety of activities in a natural setting over 10-h periods. This highly tuned frequency of locomotion was unrelated to subject age or height (Murray et al. also found no systematic relation between step frequency and these two parameters); moreover,

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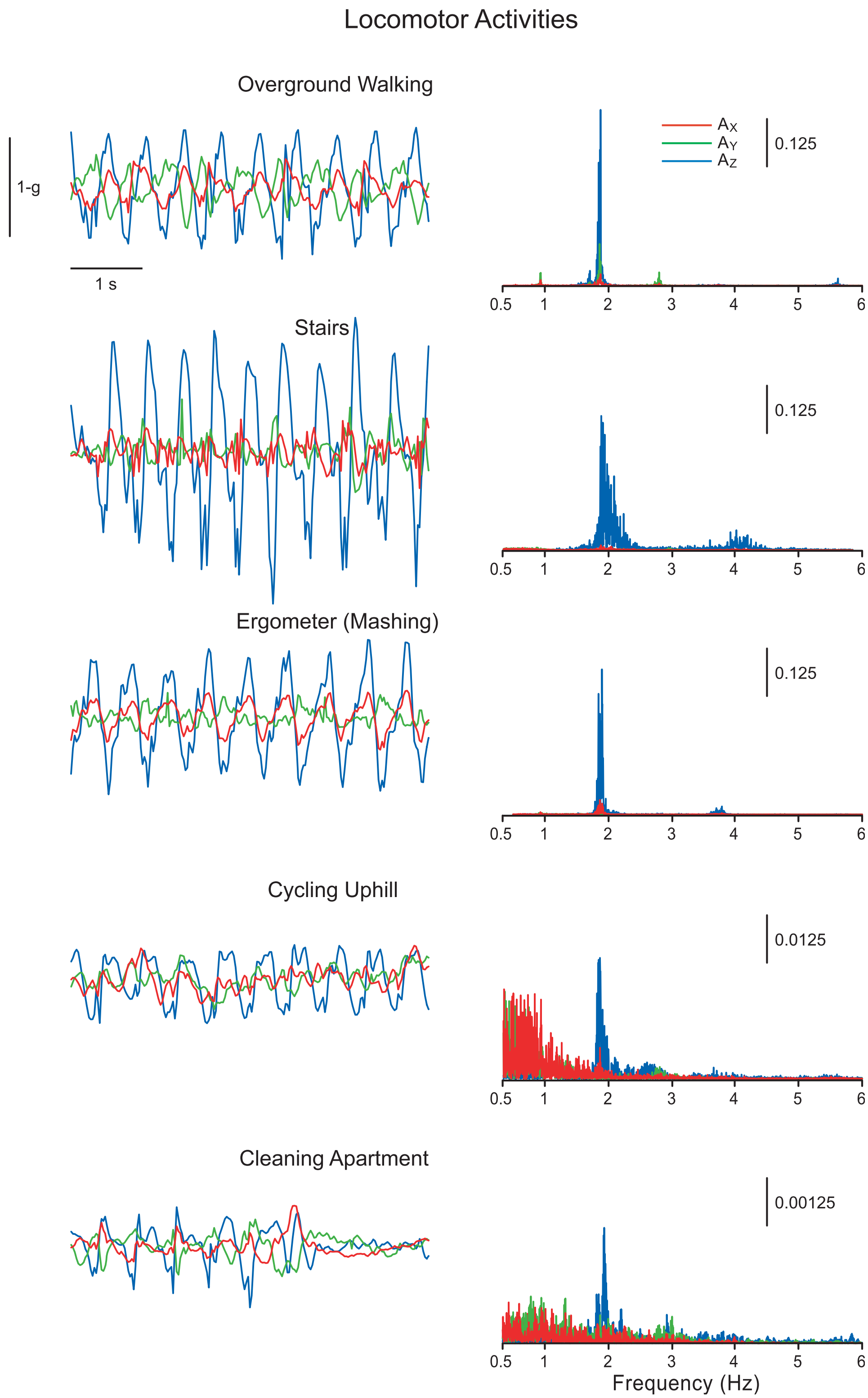

Fig. 5. Sample data (5 s) and power spectra (over 5 min) during various locomotor activities: over-ground walking, descending stairs, cycle ergometer (while "mashing," i.e., standing on pedals), over-ground (uphill) cycling, and cleaning an apartment. Power of the subject's head acceleration is shown relative to power of a pure 2-Hz sine wave with amplitude of 0.3 g over 5 min. During locomotion, there was a dominant peak in vertical head acceleration at ~2 Hz.

no evidence of a correlation with weight, body mass index, or gender was observed. Locomotor activity comprised only 12.7% of the 10-h epoch on average but accounted for the majority of head vertical linear acceleration during the course of the day.

The following question remains: What is the source for this intrinsic tempo? Mechanical resonance is unlikely given that the body mass index of our subjects was 14.3–32.2 kg/m^2. Alternatively, the stiffness and inertia of the head-neck complex may exhibit a resonance at 2 Hz, although this also appears doubtful given that the inertia of the head is negligible at <3 Hz (22, 23, 35), and the vertical movement of the head during locomotion reflects trunk (and lower limb) movement via the direct cervical spinal coupling (Fig. 1). In addition,

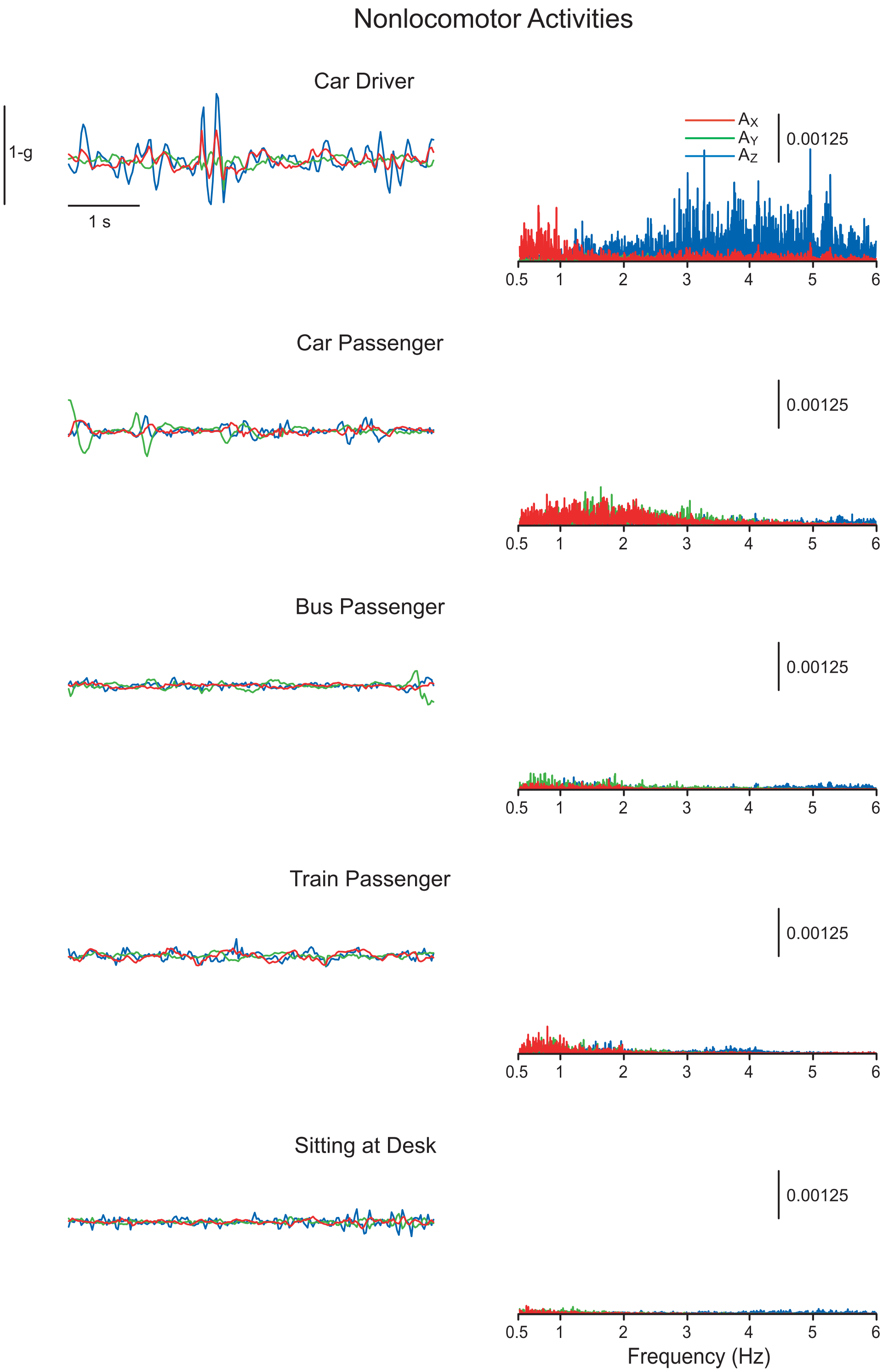

Fig. 6. Sample data (5 s) and power spectra (over 5 min) during various nonlocomotor activities: driving a car, car passenger, bus passenger, train passenger, and individual working at a desk. Power of the subject's head acceleration is shown relative to power of a pure 2-Hz sine wave with amplitude of 0.3 g over 5 min. During nonlocomotor activities, high-frequency acceleration of the head was minimal.

head oscillation was not apparent during passive movement of the body, such as when driving a car or riding in a train, bus, or car. Thus the vertical head movement observed in this study does not represent some form of passive head-on-body motion (such as that observed in a "bobble-head" doll).

Certainly, the characteristics of bipedal locomotion appear to be a factor. Oxygen cost is minimized at step frequencies of ~2 Hz (20, 46), and subjects walking on a treadmill over belt speeds of 0.8–1.8 m/s adjusted their stride length in an attempt to maintain this step frequency (18). However, the dominant 2-Hz frequency of movement observed in our subjects is not merely a result of the biomechanical restraints of bipedal locomotion. Vertical head movement frequency and, therefore, cadence ranged from 1.4 to 2.5 Hz in individual subjects at treadmill belt speeds equivalent to very slow to fast walking (18). Thus, although we can adapt our pattern of movement

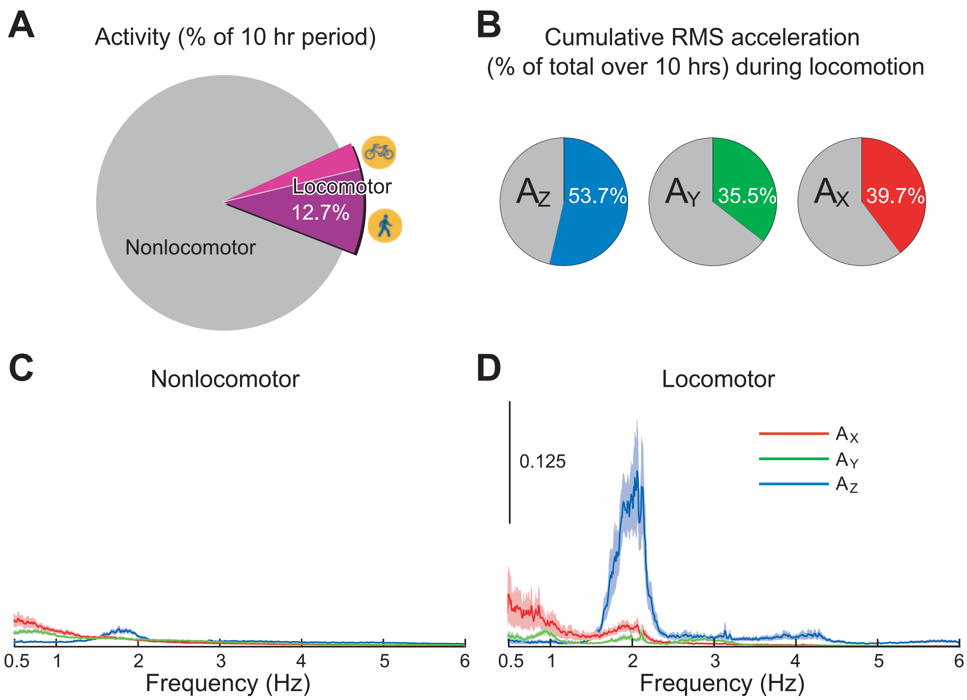

Fig. 7. *A*: locomotor activity, defined as periods when vertical head acceleration exhibited a dominant peak in the range 1.5–2.5 Hz, accounted for an average of 12.7% (76 min) of the 10-h epoch. Of these 76 min of activity, 24% (18.2 min) involved cycling, with the remainder related to pursuits associated with bipedal locomotion (e.g., walking and running). *B*: most of the vertical high-frequency acceleration of the head occurred during the 76 min of locomotor activity. Cumulative root-mean-square (RMS) acceleration along the 3 head axes during locomotion, expressed as percentage of total RMS over 10 h, was 53.7% (SD 7.9) for dorsoventral (*z*), 35.5% (SD 7.4) for interaural (*y*), and 39.7% (SD 10.1) for nasooccipital (*x*) acceleration. *C*: power spectra (mean and SE of 20 subjects) of head acceleration demonstrated negligible power during nonlocomotor activity, which comprised (on average) 87.3% of the 10-h epoch. *D*: power spectra during locomotor activity was almost identical to spectra from the entire 10-h epoch (cf. Fig. 3*B*); thus most high-frequency movement of the head occurred during locomotion.

over a wide frequency range to accommodate extrinsic drives such as a moving treadmill belt, the highly tuned 2-Hz frequency of movement exhibited by our 20 subjects represents a preferred tempo over a wide range of locomotor activities in a natural setting.

The frequency of locomotion observed in the present study is consistent with the spontaneous tempo of finger tapping (4, 7, 11, 21, 27) and preferred metronome beats (10, 26, 45), both of which were 2 Hz on average and closely correlated with the cadence of walking (17, 25). One possibility is that this preferred or spontaneous tempo and the highly tuned locomotor frequency observed in the present study reflect the intrinsic tempo of a spinal central pattern generator. Central pattern generators have been established as the basis for locomotor rhythmicity in invertebrates, primitive fish, and cats (12–14); however, their existence in humans can only be inferred from indirect evidence (6, 24).

A comprehensive study of Western music from the later half of the 20th century demonstrated a clear preference for musical tempi of ~120 beats/min (27), and recent observations suggest that vertical motion at this frequency (2 Hz) may indeed be perceived as pleasurable (the "saccular pleasure" hypothesis) (38). Step cadence is strongly reflected in the vertical linear movement of the head, generating peak linear acceleration of ~0.6 g (18, 30). The saccules, the portion of the otoliths that primarily sense acceleration along the vertical (dorsoventral) axis of the head, have a mechanical resonance at ~300 Hz (39), but electrophysiological studies in the squirrel monkey demonstrated a peak in the gain of irregular saccular afferents at 2 Hz (8). These irregular units provide descending signals to spinal interneurons and motoneurons that drive lower body movement via the lateral vestibulospinal tract. In addition, otolith-mediated linear vestibuloocular and vestibulocollic reflexes, which act to coordinate vertical head and eye movement during walking to maintain dynamic visual acuity, also exhibit an optimal response at ~2 Hz (3, 18, 30, 31, 33, 34). In fact, the linear vestibulocollic response that generates compensatory head pitch is absent when step frequency is $<$1.7 Hz (18). The highly tuned 2-Hz vertical acceleration of the head and body during active locomotion may represent some form of central "resonant frequency" of human movement. That is, within this narrow frequency band, otolith-mediated spinal, collic, and ocular reflex responses and gait biomechanics are optimized.

This finding may be of relevance to our study of locomotor deficits in returning astronauts. During extended periods in microgravity, astronauts are unlikely to generate significant 2-Hz vertical head acceleration because of the lack of bipedal locomotion. Crewmembers returning from the International Space Station report significant oscillopsia during postflight locomotion and exhibit erratic head pitch movements and a significant decrease in the coherence between head pitch and vertical trunk translation on a treadmill (1), indicative of an impaired linear vestibulocollic reflex (18, 30, 31). This may be due to an upregulation in sensitivity of high-frequency otolith-mediated reflexes in microgravity due to a lack of linear acceleration stimulation on orbit. Results from the Neurolab STS-90 mission support this hypothesis, with a postflight threefold increase in high-frequency (1.6-Hz) otolith sensitivity in oyster toadfish flown aboard the shuttle (2). A similar increase in otolith sensitivity at 2 Hz in humans would generate larger head pitch during locomotion and inappropriate linear vestibuloocular reflex eye movements at far target distances that may impair dynamic visual acuity.

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