Acquisition of operant-trained bipedal locomotion in young Japanese monkeys (*M. fuscata*): A longitudinal study

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Contents

Abstract

Locomotor learning involves a process consisting of both practice and experience, together with physical growth and neural maturation, resulting in an enduring ability to elaborate a behavior, in this study, bipedal (Bp) locomotion. This study addressed developmental aspects of the acquisition of operant-conditioned upright posture and Bp walking by the normally quadrupedal (Qp) juvenile Japanese monkey (*M. fuscata*) with a focus on physical growth and locomotor learning. Specific questions were 1) how do multiple motor segments establish coordination during Bp locomotor learning in physically maturing monkeys, and 2) how are postural adjustments and propulsive movements of the hindlimbs integrated during the execution of Bp locomotion? Four male monkeys (age: 2.8 to 3.5 years, body weight: 3.2 to 4.6 kg) were first motivated operantly to stand upright on a smooth floor and a stationary treadmill belt (width = 60 cm, walking length = 150 cm). They were then trained to walk bipedally on the moving treadmill belt (speed: 0.4-0.7 m/s). A regular training program (5 days/week; 30-60 min/day) was given to each monkey for the first 40 to 60 days, followed by a less intensive training. Upright postural stability and Bp walking capability were assessed kinematically for 592 days on monkey A and 534 days on monkey B after the beginning of locomotor training. Bp locomotion of monkeys C and D were kinematically analysed for about 200 days, and thenafter behaviorally. Side and back views of the walking monkey were photographed (10 frames/s) and videotaped (250 frames/s). Stick figures of the head, body, and hindlimbs were drawn with reference to ink-maked ear position and pivot points of hindlimb joints. All kinematic data were digitized and analysed using Image Express program (NAC). After sufficient physical growth and locomotor learning, all

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the monkeys gradually acquired: 1) a more upright, a more stable posture with a constant body axis during Bp locomotion; 2) a more stable and a stronger functional coupling between the body and hindlimb movements with a less antero-posterior fluctuation of a body axis, 3) a smaller left (L) to right (R) deflection of the pelvic point allowing the monkey to walk along a straight course, 4) a more coordinated relationship between hip-knee, knee-ankle, and ankle-mp joints. Such coordination progressed rostrocaudally over the period of long term locomotor training (thereby reflecting more constraint-free means of locomotion), and 5) the acquisition of well-coordinated Bp walking at relatively high treadmill belt speed (up to 1.5 m/s). All of these results illustrated the capability of the developing monkey to integrate the neural and musculoskeletal mechanisms required for sufficient coordination of upper (head, neck, trunk) and lower (hindlimbs) motor segments so that upright posture could be maintained and Bp locomotion elaborated.

Introduction

The study of locomotor behavior in non-human primates has been central to physical anthropologists since the early investigations conducted by Muybridge (1957). Anthropologists and biologists have historically conducted much of the research on non-human primate locomotion in an effort to elucidate the relationship between morphology of the locomotor system and species-specific locomotor behavior (Fleagle and Mittermeier. 1980; Ishida et al., 1985; Okada. 1985; Rollinson and Martin. 1981; Rose. 1973). More recently, neurophysiologists have become interested in non-human primate models of locomotion in an effort to better understand neural mechanisms associated with movement control (Eidelberg et al., 1981; Lawrence and Kuypers. 1968a, b). Whereas most non-human primates prefer quadrupedal terrestrial locomotion and branching, occasionally bipedal standing and walking is required due to environmental circumstance. The macaque monkey demonstrates Bp behaviors even though their physical features are not well suited for such posture and locomotion (Hildebrand, 1967; Okada. 1985; Snyder, 1967). Nevertheless, juvenile Japanese monkey *(M. fuscata)* in particular, demonstrates Bp standing and even walking when forelimbs are needed for getting and eating food (Iwamoto, 1985), and when trained over long periods (Hayama. 1986; Preuschoft et al 1988).

Although simple in appearance, locomotion is a complex motor activity that requires the integrated control of multiple body (motor) segments (Sherrington, 1906). Adequate control of each body segment such as the head, neck, trunk, and limbs is necessary for the execution of both Qp and Bp locomotion (Mori, et al. 1987; Mori et al., 1996a, b). Elaboration of Bp locomotion requires both the generation of propulsive force by the lower limbs and the generation of antigravity force to maintain upright posture and body equilibrium (McGraw,

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1940; Mori, 1997). To fully understand the critical components of Bp locomotion, it is important to have a model that can provide multiple systems-level observations including behavioral, physical, biomechanical, neural-anatomical, and neural-physiological activity. To this end, we have developed a non-human primate model that successfully elaborates both Qp and Bp locomotion on a moving treadmill belt (Nakajima, et al 2001).

One of our earlier studies demonstrated that young monkeys learn to walk quadrupedally with a diagonal gait pattern (Mori et al., 1996). During this investigation, we observed the occasional conversion from Qp to Bp locomotion when food rewards were presented at a higher orientation. In our recent studies, we have successfully employed operant training methods, using food rewards, to establish the skill of Bp locomotion in a series of young monkeys (Mori et al. 2000 a; Nakajima et al. 2001). With long-term locomotor training, these monkeys can adjust their Bp locomotor patterns to increases and decreases in moving treadmill belt speeds, and also can adjust to changes in inclination and declination of treadmill belt angles (Mori F. et al. 1999). Further, once these skills are achieved, these monkeys can successfully clear obstacles on the moving treadmill belt and adopt a defensive posture to compensate for stumbling similar to that observed in humans (Mori F. et al.; 2001).

Our observations reinforce the notion that with appropriate long-term locomotor learning, young Japanese monkeys, having acquired the capability to walk quadrupedally, consolidate *potential* neural mechanisms in the central nervous system (CNS) that are related to elaboration of Bp locomotion. The physical growth of the musculoskeletal system, in combination with CNS maturation and locomotor learning also appears necessary for successful emergence, refinement, and adaptation required for the elaboration of Bp locomotion. Progression through such developmental processes has already been described

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on a behavioral level from longitudinal observations of human infants during the attainment of an upright posture and Bp locomotion (Bril and Breniere. 1993: Gessel and Ames, 1940: McGraw 1940; Okamoto and Kumamoto. 1972; Thelen et al. 1994). Observations from these studies suggest rostro-caudal maturation of postural and locomotor control systems. Further, these studies have provided the foundation for investigations related to the development and integration of multiple motor segments necessary for an upright posture and locomotion.

The current study was designed to address the acquisition and refinement of Bp locomotion during what may be, a *sensitive period* for this skill, in the developing monkey. The aim of this study was to further describe this process using a longitudinal design to investigate how young Japanese monkeys acquire the skill of Bp locomotion as these monkeys developed physically over time and experienced various treadmill belt speed conditions. In this study, we addressed two major questions. First, how do multiple motor segments establish coordination during Bp locomotor learning in physically maturing monkeys? Second, how are postural adjustments and propulsive movements of the hindlimbs integrated during the execution of Bp locomotion? Preliminary results have been reported elsewhere (Tachibana et al. 2000, 2001).

Methods

Four young, male Japanese monkeys (*M. fuscata*: monkeys A, B, C and D, initial body weight 3.8 kg, 3.3 kg, 4.6 kg and 4.2 kg, respectively) were the subjects of this study. At the beginning of the study, age estimates of monkeys A, B, C, and D were 3.0, 2.8, 3.5 and 3.3 years, respectively. Age estimates were based on body weight and the appearance and shape of juvenile and permanent adult teeth (Gotoh, S, Primate Research Institute, Kyoto Univ, personal communication). All four monkeys accomplished Bp locomotion as a result of a daily training program ranging from approximately 30 to 60 minutes over a period of 434 to 592 days.

Training occurred in several stages. First, monkeys were unrestrained and allowed to acclimatize to the investigator, laboratory setting, and treadmill apparatus. Initial acclimatization took approximately 7 days. Second, monkeys were operantly trained (using food rewards) to stand upright on the floor. Rewards were presented at an appropriate height requiring Bp standing in order to grasp the food from the investigators. Monkeys were motivated to stand bipedally while extending one or both forelimbs to obtain food. During the training session, food rewards were only given when a Bp stance was achieved. At first, monkeys needed external support around the hip area. This support was typically provided from the rear of the monkey by way of the investigators' own legs, arms, or hands in the same manner as that done with young human children (Bril and Breniere 1993). Within a few days, monkeys could stand bipedally, unsupported, for approximately 1 to 2 minutes. Third, Bp standing was transferred to the stationary treadmill belt (width = 60 cm, walking length = 150 cm). The same reward procedures were employed to encourage the monkeys to stand bipedally on the treadmill belt surface. Within 14 to 21 days of training, all monkeys

accomplished a stable Bp stance on the stationary treadmill belt surface for several minutes. Fourth, monkeys were trained daily to walk bipedally on the surface of a moving treadmill belt.

All monkeys accomplished an *elementary* form of Bp locomotion during early training session. Gradually, monkeys were trained to increase the duration of Bp locomotion (2 to 4 minutes) within a training trial. Operant conditioning continued to employ the intermittent presentation of food rewards by the investigators positioned in front of the monkeys while they were standing or walking on the treadmill belt. During Bp locomotion, the monkeys were motivated to get food rewards from the investigators using forelimb digits. The presentation of rewards was height-adjusted for each monkey to ensure optimal upright posture, balance, and maintenance of the appropriate center of body mass. Once Bp locomotion was achieved, monkeys were required to perform between 10 and 15 trials of bipedal walking during each training session (4 to 5 minutes). Liberal use of rest breaks between trials was given to encourage good motivation throughout a training session. Treadmill speed was increased and/or decreased in a stepwise manner over a range of 0.4 to 1.5 m/s. Over time, the monkeys learned to walk bipedally at higher treadmill speeds.

Prior to all recording sessions, ink marks were placed on the monkey's left-side body skin surface of the ear, hip, knee, ankle, and metatarsophalangeal (mp) joints. Additional ink marks were placed on the monkey's back over the spinal column along its midline. One mark was placed over the thoracic spine at vertical midrange of the scapulae (T3-4; lower neck position) and the second mark was placed over the lumbar spine above the tail and slightly above the level of the hip joints (L7-S1: upper pelvic position) (Preuschoft et al. 1988).

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A total of 5 cameras were used to record the monkey's posture and Bp walking patterns. Two high-speed video systems (NAC HSV-500: 250 frames/s) were used for recording Bp locomotion. One camera was positioned to the monkey's left and recorded side-view kinematics. The other camera was positioned behind the monkey and recorded back-view kinematics. When necessary, the second camera was positioned to the monkey's right side and recorded side view kinematics. These two cameras were synchronized. In addition, two single lens reflex cameras were used to take serial photographs (*Canon EF*: 10 frames/s, shutter speed of 1/500 s) from both side-view and back-view positions. A digital video camera was used to take real-time recordings during locomotion. Data from monkeys C and D were kinematically analysed for about 200 days from the beginning of locomotor training, and then used principally for visual inspection of locomotor movements. Data obtained from monkeys C and D provided similar results to those of monkeys A and B. Detailed analyses of kinematic parameters were performed on digitized data from monkey A for 592 days and monkey B for 534 days.

Ruled grid squares of 5 cm served as a reference background during recording sessions. These grids were later used as a reference for the selection of locomotor samples that were: (a) free of extraneous movements, and (b) met criteria for body axis stability. Specifically, selected samples included those where 10 consecutive step-cycles were executed with antero-posterior body axis fluctuations of less than $\pm$ 10 cm. Early-stage locomotion samples were obtained when monkeys walked with a greater antero-posterior body axis fluctuation (criterion range: less than $\pm$ 20 cm). Samples meeting these criteria were considered representative of exemplary Bp locomotion for that particular recording days.

Kinematic measurements were taken using the body surface markings and tracking these

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across each frame of the videotape for the behaviors of interest. A digital imaging analysis system (NAC Image Express) was used to digitize and measure all step-cycles of interest. Digitizing parameters such as frame intervals and sampling rate (i.e., frames per second) were adjusted in accordance with the type of movements measured. A total of 6 general movement parameters were derived from step-cycles recorded over time and at various treadmill speeds. The parameters measured included: (1) body axis angles, (2) body axis vertical and lateral fluctuations, (3) step-cycle stance and swing phases, (4) lower-limb joint angles, (5) lower-limb joint and limb trajectories, and (6) joint movement relationships (in time-motion and motion-motion configurations).

Results

The longitudinal study period for monkeys A and B was 592 and 532 days, respectively. The results from data collected during the early stages of the study period reflect Bp locomotion on treadmill belt speeds of 0.4 and 0.7 m/s. Data from middle and later stages of the study period reflect Bp locomotion on treadmill belt speeds of 1.0, 1.3, and 1.5 m/s. Changes in treadmill speed condition were due to each monkey's ability to acquire faster walking rates over time. Kinematic parameters related to the acquisition and refinement of bipedal locomotion will be presented qualitatively in a series of selected figures. Data will be presented in data displays representing the 6 general parameters listed previously. Supportive quantitative analyses will be presented when appropriate and for specific variables of interest.

Physical growth patterns in monkeys A and B.

Fig. 1 shows an overview of the longitudinal scope of this study and overall changes in height and weight for monkeys A and B across the study period. The top graph depicts monkey A's weight change from training day 8 to 592 and his change in height from day 79 to day 592. The bottom graph depicts monkey B's weight change from training day 16 to 534 and his change in height from day 64 to 534. Body weight increased across the study period, from 3.7 to 5.5 kg, and from 3.3 to 4.8 kg, for monkeys A and B, respectively. Body height also increased across the study period, from 65 to 78 cm, and from 63 to 73 cm for monkeys A and B, respectively. The red vertical lines drawn at various time points (days) indicate when extensive kinematic analyses were made. Also depicted in the top graph are three heavy red arrows placed at days 31, 102 and 334 when serial photographs of monkey A in Fig 2 were

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taken.

Changes in body axis parameters associated with the acquisition of Bp locomotion.

Fig. 2 shows a series of side-view photographs representing changes in fluctuation of the body axis for monkey A at 3 separate time-points (see Figure 1). In frame 1 on day 31 (top row in Fig 2), the weight of monkey's body mass was supported by the L and R hindlimbs (*double-support phase*). The monkey then initiated a *swing phase* of the R hindlimb (frame 2 and 3) and resumed again the double support phase (frame 4). The monkey then initiated the swing phase of the L hindlimb followed by a *single support phase* by the R hindlimb (frame 5 to 6) ending again with double support phase (frame 7). This 7 frame series represents a single locomotion *step-cycle* of L and R hindlimbs. On training days 102 (middle row in Fig. 2) and 334 days (bottom row in Fig. 2) with higher treadmill speeds, similar locomotion cycles were exhibited and included both single and double support phases by the hindlimbs. However, changes in duration and limb placement during swing and stance phases changed across the study period. These changes are described in relation to limb and joint trajectories and postural parameters in the data displays presented later.

Stick-figure drawings displayed to the right of each photograph series, represent the superposition of all 7 individual yellow-lined stick figures, for that series of photographs. Cumulative stick figures allow us to examine the changes in postural stability and limb movements associated with physical growth of the monkey concurrently with the acquisition of Bp locomotion. Specifically, on day 31 (top row in Fig. 2), the monkey exhibited variable body axis (head to hip trajectories) postures across the series of sequential hindlimb movements. In addition, larger range of antero-posterior body axis movements was present.

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Data from day 102 (middle row Fig. 2) and day 334 (bottom row in Fig. 2) show less antero-posterior fluctuation of the body axis relative to the reference line indicating increased postural stability. As can be seen in this figure, the monkey is significantly taller at day 334 (74cm) than on days 31 (64 cm) and 102 (67 cm), respectively.

Changes in body posture and lower limb-joint trajectories.

To further examine the process of acquisition and refinement of Bp locomotion, we have compared cumulative stick figures taken during selected training sessions at the treadmill speed of 0.7 m/s. Figure 3 shows 12 graphs representing kinematic data obtained between 19 to 592 days for monkey A (top row graphs) and 25 to 534 days for monkey B (bottom row graphs). Red and black horizontal lines have been placed under each drawing and represent the sequential stride lengths for the L and R hindlimbs, respectively. These graphs allow us to examine the chronological changes in the dynamic relationship between head, body axis, hip, ankle, limb movements, and stride length within and across training sessions.

Generally, both monkeys exhibited similar fluctuation patterns in body axis and lower limb trajectories over the time period examined. The results obtained from early training sessions, shown in the left side of Fig. 3A and 3B (i.e., day 19 days for monkey A and day 25 for monkey B), indicate that both monkeys exhibited: (a) highly variable antero-posterior trajectories for all body and limb segments, (b) variable forward body axis orientation, and (c) variable relative foot placement and stride length. These drawings and associated stride lengths for each monkey show that antero-posterior fluctuation of the body axis was related to the variability in stride lengths within and across locomotion step cycles. On day 19 (monkey A) and day 25 (monkey B), the positions of the L and R foot placement (beginning

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of stance phase) and foot *lift-off* from the treadmill belt (end of stance phase) varied greatly in relation to the vertical reference line. In each locomotion step-cycle, the stride lengths of the L and R hindlimbs were variable indicating that their cyclic movements were not well coordinated resulting in associated variability in the other trajectories described previously. On day 79 (monkey A) and day 101 (monkey B), the stride lengths of the L and R hindlimbs became almost equivalent, but the beginning of stance phase in relation to the reference was not yet consistent. On day 592 (monkey A) and day 534 (monkey B), both the stride lengths of L and R hindlimbs were equivalent and foot placement on the moving treadmill belt became consistent.

Table 1 summarizes the means, standard deviations (SD), and coefficients of variation (CV) for stride length obtained from 10 selected days across the study period. Over this period of time, the stride lengths of the monkeys A and B increased by approximately 2.5 cm and 3.0 cm, respectively. On day 19, monkey A produced a mean stride length of 33 cm with CV values of 11.6 (L hindlimb) and 12.0 (R hindlimb). On day 25, monkey B, produced a mean stride length of 31 cm with CV values of 11.5 (L hindlimb) and 10.2 (R hindlimb). CV values decreased steadily for both monkeys. Data obtained for monkey A on day 164, resulted in CV values of 3.3 (L hindlimb) and 4.5 (R hindlimb) which were similar to values observed at day 592. Data obtained for monkey B on day 157 resulted in CV values of 6.9 (L hindlimb) and 4.5 (R hindlimb) which were similar to values observed at day 534.

Fig. 3 shows that vertical movement also was highly variable during early training periods. However, as can be seen by looking from left to right across the graphs, each monkey made significant refinements in antero-posterior and vertical body and limb trajectories across the

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study period. These changes are characterized as: (a) decreases in variability and subsequent range of motion in antero-posterior trajectories of all body and limb segments, (b) acquisition of a nearly upright body orientation, (c) acquisition of a stable head position, and (d) acquisition of stable foot placement and stride length. In addition, vertical head movements became smaller during the later training sessions. The data presented in Fig. 3 show that both monkeys exhibited refinements of the spatial and timing parameters involved in the movement of multiple motor segments associated with Bp locomotion. Both monkeys gradually acquired body and hindlimb coordination and L-R coordination in the hindlimbs. The results suggest that the monkeys moved towards an efficient execution of Bp locomotion.

Vertical fluctuations of body and limb positions.

The plots shown Fig. 4 illustrate the vertical fluctuation (in cm) of head, hip, and knee during Bp locomotion for 5 step-cycles obtained during each measurement session across the study period. The descriptive data associated with vertical fluctuations obtained from 10 selected days are summarized in Table 2 for monkeys A and B. This figure shows that vertical fluctuation of head position, as estimated from the ink marking at the ear, decreased steadily over time for the both monkeys. Specifically, data obtained from monkey A during an early session (day 19) had a mean ear height of 59.2 cm (SD = 2.2, CV = 3.7). In contrast, data obtained during the last training session (day 592) had a mean of 71.9 cm (SD = 0.5, CV = 0.5). Data obtained from monkey B at day 25 resulted in a mean of 57.4 cm (SD = 2.0, CV = 3.6). In contrast, data obtained from day 534 resulted in a mean of 68.1 cm (SD = 1.2, CV = 1.2).

Vertical fluctuation of hip position also decreased over time. However, as can be seen

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from Fig. 4 and Table 2, the extent of decrease in vertical fluctuation was smaller than that of

head position. Means obtained from monkey A were 25.3 cm (SD = 1.0, CV = 4.0) on day

19, and 28.6 cm (SD = 0.6, CV = 2.0) on day 592. Means obtained from monkey B were

24.3 cm (SD = 1.0, CV = 4.0) on day 25, and 27.4 cm (SD = 0.7, CV = 2.5) on day 534. In

contrast to the smaller fluctuation of ear and hip positions, vertical fluctuation of knee height

was considerably larger. Means obtained from monkey A were 15.3 cm (SD = 1.9, CV =

12.5) on day 19, and 18.1 cm (SD = 2.1, CV = 11.8) on day 592. Means obtained from

monkey B were 13.4 cm (SD = 2.0, CV = 15.3) on day 25, and 16.6 cm (SD = 1.6, CV = 9.6)

on day 534. Fluctuations in the knee were generally higher than the other body segments and

continued to exhibit vertical variability even at the end of the study period. Variability in knee

fluctuations may be related to the biomechanical factors involved in continuous Bp

locomotion. It is also possible that monkey's CNS mechanisms controlling distal limb

movements are not yet well developed during an early training period of Bp locomotion.

Lateral fluctuation of the body axis.

Fig. 5 shows a series of 8 photographs and 8 associated graphs representing leftward (L)

and rightward (R) movement of the body during Bp locomotion. The relative coupling

between the lateral movement deflections of the neck and pelvis demonstrates the overall

stability of the body axis during Bp locomotion. Several important observations were made as

follows. First, for example, in monkey A at day 79 and monkey B at day 101, the head and

neck movement patterns are variable. As can be seen from the photographs, lateral fluctuation

of the body axis is relatively large and with a lack of coupling between upper and lower trunk

segments. In both monkeys, sometimes the upper part of the body moves more than the

lower part and visa-versa. The photographs taken at day 164, 268 and 592 for monkey A, and those taken at days 194, 276 and 534 show a smaller degree of lateral fluctuation, reflecting tighter overall coupling between the neck and pelvic movements over the long term training period. Such results demonstrate the refinement and emergence of body axis stability.

A second set of observations can be derived from the lateral movement of the pelvic position (in cm). Fig. 5 shows that the waveforms of side to side deflections of the pelvic position are irregular at early training sessions as can be seen from the waveforms at days 79 and 164 for monkey A, and those at days 101 and 194 for monkey B. However, lateral oscillations of the pelvic signals around the center reference line gradually became symmetrical over the period of long-term locomotor learning. For monkey A, means of the L and R movement of the pelvic position on days 79, 164, 268, 592 were 2.5 cm (SD = 1.4, CV = 55.8), 2.3 cm (SD = 1.3, CV = 55.9), 1.9 cm (SD = 1.1, CV = 57.5) and 1.8 cm (SD = 0.6, CV = 32.0), respectively. For monkey B, means of the L and R movement of the pelvic position on days 101, 194, 276, and 534 were 1.4 cm (SD = 1.0, CV = 72.9), 1.6 cm (SD = 0.9, CV = 54.4), 1.2 cm (SD = 0.6, CV = 48.3) and 1.2 cm (SD = 0.3, CV = 26.5), respectively. Data obtained from selected 10 days are summarized in Table. 3, and waveform patterns of side to side deflections of the pelvic position are illustrated in Fig. 6 together with the range of $\pm$ 1 SDs. Fig. 6 shows clearly that side to side deflection of pelvic position becomes regular and smaller for both monkeys A and B.

Data from this analysis provide further evidence that monkey developed stable patterns of Bp locomotion by acquiring a novel capability ; (a) symmetrical weight bearing of the lower limbs against gravity, (b) symmetrical stance-swing cycles of the lower limbs, (c) overall balance control during forward locomotion, and (d) forward vs. lateral momentum during

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locomotion. The refinement of these skills is likely to be accompanied by the changes in physical ability, which allows the monkey to support his body weight against gravity. *Component skills* may include the development of musculoskeletal and associated joint-tendon structures. Other important factors include the development of: (a) balance and postural control, and (b) bilateral lower-limb motor control.

Changes in body axis angle during locomotion at different treadmill speeds.

Chronological changes in the body axis angle are plotted in Fig.7 for monkeys A and B during Bp locomotion at different treadmill speeds. During the early training sessions between days 13 and 45, monkey A could walk continuously only at a treadmill belt speed of 0.7 m/s. Between 45 to 145 days, he could walk at treadmill speeds of 0.7 and 1.0 m/s. After this period, this monkey could walk at treadmill belt speeds of 0.7, 1.0 and 1.3 m/s. Similarly, monkey B could walk continuously only at treadmill speed of 0.7 m/s during early training sessions between 25 and 83 days. Between 83 and 120 days, he could walk at treadmill speeds of 0.7 and 1.0 m/s. After this period, this monkey could walk at treadmill belt speeds of 0.7, 1.0 and 1.3 m/s. Two graphs in Fig.7 show that body axis angles increased over time in both monkeys. Body axis angles were initially variable and centered around 70 to 75 degrees for monkey A and 65 to 75 degrees for monkey B, indicating an inclined body axis posture during Bp locomotion. During the period between days 79 and 240, monkey A exhibited a steady increase in body axis angle until postural stability was reached in the later stages of the training period. In contrast, monkey B, exhibited a rapid increase in body axis angle between days 25 and 37 and then a steady increase until postural stability was reached in the later stages of the training period. Fig. 7 shows that both monkeys

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stabilized their walking patterns when their body axis angle reached approximately 80-85 degrees.

As expected, body axis angles were greater during the lowest treadmill belt speed (0.7 m/s). With higher treadmill belt speeds of 1.0 and 1.3 m/s, the body axis angle decreased by approximately 2 to 3 degrees. This indicates that slight increases in body axis inclination are necessary to achieve continuous Bp locomotion at higher treadmill belt speeds. Table 4 summarizes the means, SDs and CVs of body axis angles obtained during data collection sessions. It is apparent that both monkeys acquired stability of upright posture over the time periods examined. Interestingly, the most dramatic change in body weight of both monkeys occurred during the time when overall body axis stabilization was achieved. We can speculate that there is a dynamic relationship among musculoskeletal growth as represented by the increases in monkey's body weight and height, neural maturation, and locomotor learning.

Chronological changes in stance, swing, and frequency in relation to treadmill belt speed.

Fig. 8 shows 6 individual graphs representing longitudinal data for stance, swing, and step-cycle frequency from monkeys A and B during Bp locomotion at different treadmill belt speeds. These data allow us to examine the interaction between treadmill belt speed and the specific timing components of hindlimb movements. The data shown in this figure indicate that the swing phase remains relatively constant (approximately 0.2 sec) and is stable across all trained treadmill speeds and over time. Both monkeys adopted a relatively quick swing phase during relatively early periods of training (days 79 and 101 for monkeys A and B, respectively), which remained invariable throughout the study period. In contrast, the

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duration of the stance phase and step frequency systematically changed with changes in treadmill speed and physical growth of the monkeys. For example, at 3 selected days and at lower treadmill speeds (0.4 and 0.7 m/s), stance phase duration was longer than durations associated with higher treadmill belt speeds (1.0, 1.3 and 1.5m /s). As treadmill belt speeds became incrementally faster, stance phase durations became incrementally shorter.

Comparison of the data between days 79 and 215 for monkey A, at treadmill speeds of 0.7 and 1.0 m/s shows that mean stepping frequency is slightly larger at day 215 than day 79, although the durations of the swing and stance phase were similar. Comparison of the data between days 215 and 432 for monkey A, at the treadmill speeds of 1.0 and 1.3 m/s shows that mean stepping frequency is smaller at day 432 than day 215, although the durations of the swing and stance phase were similar. The changes in the stepping frequency and stance durations in the monkey B over the selected periods were similar to those of monkey A. Taken together, these results suggest that both monkeys adopted a strategy of hindlimb movements adequate for bipedal locomotion on selected days across the study period, thus reflecting the extent of physical growth and locomotor learning. The basic strategy seems to be the same as can be seen from systematic changes in the stance phase and stepping frequency.

Angular changes in hip, knee, ankle and mp joints.

Fig. 9 shows individual angular changes in the hip, knee, ankle and mp joints measured during selected training sessions at days 19, 29, 102, 268 and 432 for monkey A. It should be noted that the data for monkey B is similar and will not be presented here. This display of 20 individual graphs allows us to examine the kinematic patterns of each joint angle for

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multiple stance-swing step-cycles during 4 second sample. In all cases, kinematic patterns reflect active joint movements, differing in speed and amplitude. Each joint movement showed cyclical changes. However, the kinematic patterns were different across the limbs based on the differences in joint type. As can be seen by looking from left to right in the figure, stability in waveforms increased across the study period. For the most part, patterns for all joint trajectories were stable by day 432 and can be described in the context of the stance and swing phases. For example, on day 432, the waveform trajectory of the hip joint during the initiation of the stance phase was associated with a small downward deflection or trough (flexion). This was followed by a steady upward increase (extension) in the joint angle that peaked at the later part of the stance phase. Just before the termination of the stance phase, the hip joint angle decreased. Initiation of the swing phase was associated with a steady decrease in the joint angle attaining a trough at the later part of the swing phase. The hip joint angle then increased slightly, as the step-cycle changed from swing to stance phase. For the knee joint (day 432), initiation of the stance phase was accompanied by a rapid decrease in the joint angle with a notch at the middle part of the stance phase. Just after the beginning of the swing phase, the joint angle approached the trough and then increased sharply until the completion of the swing phase.

In contrast to relatively simple kinematic patterns of hip and knee joint angles, the ankle joint showed two cyclic changes in a single locomotion cycle. During each of the stance and swing phases, the waveforms were composed of downward and upward deflections, exhibiting two peaks and two troughs. The peak and trough during the stance phase appeared just before the termination and at the middle of the stance phase, respectively. The peak and trough during the swing phase appeared before the termination and at the middle of the swing

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phase, respectively. The waveform associated with the mp joint was composed of positive and negative saw-tooth waves with a distinct positive notch before the beginning of the stance phase. The peak and the trough appeared at approximately the middle of the stance phase and first one-third of the swing phase, respectively.

Interestingly, as we look at the hip and knee kinematic patterns across the training period, we can see that their movement is cyclical and relatively stable even at day 29 followed by refinement over time. In contrast, the kinematic patterns of the ankle and mp joints are not stable during the early stages of training (days 19 and 29). Stable, cyclic kinematic patterns are not well established in these joints until later training sessions (days 268 and 432). The data in this figure provide evidence that individual joint movements become stable at different times during motor learning. By looking from the top graph to the bottom for a given training day, one can derive the nature of the time-motion relationship among joints during the 4-second cycle. However, the process is cumbersome and the joint-joint relationships are not easily characterized. We have therefore drawn cyclographs to better demonstrate the relationships among neighboring joints.

Motion-motion relationships among limb joints.

Cyclographs depicted in Fig.10 show the motion-motion relationships between the hip and knee, knee and ankle, and ankle and mp joints during a sample of bipedal locomotion assessed at selected points during training from 19 to 432 days. Once again, the data from monkey B is similar to monkey A and will not be presented here. The data in this figure show that the kinematic relationships are different for neighboring joint pairs and the relationships among all joint pairs change from early to later stages of locomotor learning.

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More specifically, the motion-motion tracings of three pairs of joints show some coupling but large variability, early in the training period. By day 102, the relational pattern between hip and knee joints became tight but the patterns between knee and ankle, and ankle and mp joints were highly variable. By day 268, the relational patterns between hip and knee, and knee and ankle joints became tight but the pattern between ankle and mp joints was still highly variable. By day 432, the relational pattern indicates tight and stable coupling between three pairs of the neighboring joints.

The cyclographs on the top row displays show the replication of cycle-to-cycle movement represented by a *crescent-moon* shaped cyclograph indicating a tight coupling of the hip and knee joints during both stance and swing phases of the step-cycle. During the stance phase, the hip joint moves towards extension whereas the knee moves towards flexion. During the swing phase, the hip moves towards flexion whereas the knee moves towards extension. The knee and ankle cyclographs on the second row displays indicate a variable relationship during the initial periods of training. The variable coupling between these two joints is reflected in both the stance and swing phases. The cyclographs for 19 and 29 days reflect multiple degrees of freedom for movement between these two joints. By day 102 however, one can begin to see replication of cycle-to-cycle movement represented by a *distorted figure eight* shaped cyclograph. However, the relationship at this point in time is slightly more variable than that found between the hip and knee. The cyclograph pattern indicates that during the stance phase, the knee joint moves from extension to flexion whereas the ankle joint moves from flexion towards extension. During the swing phase, the knee moves from flexion towards extension and the ankle moves from extension to flexion followed by a movement towards extension again. As can be seen on days 286 and 432, there is little variability in the

relationship between the knee and ankle, indicating a stronger coupling between these two joints.

The cyclographs for the ankle and mp joints also show a highly variable relationship during the initial periods of training. The variable coupling between these two joints is reflected in both stance and swing phases. The cyclographs for 19 and 29 days reflect multiple degrees of freedom for movement between these two joints like that found in the knee and ankle data. Much of the variability appears during the transition from the stance to swing phase. By day 102, however, one can begin to see replication of cycle-to-cycle movement represented by an *elliptical shape* (with inner loop) cyclograph. The relationship at this point in time also is more variable than that found between the knee and ankle. On days 286 and 432, relational patterns of ankle and mp joints became much more replicable with less variability. The cyclograph pattern indicates that during the stance phase, the ankle moves first towards flexion and then extension whereas the mp joints move towards extension. During the swing phase, the ankle moves towards flexion as does the mp joint, followed by a quick mp and ankle adjustment for stance phase preparation.

It is apparent that maximum extension angle of both hip and ankle joints increased considerably from day 19 to day 432 with a progressive increase of maximum flexion angle. Maximum extension angle of knee joint did not change, whereas maximum flexion angle increased over time (Table 5). Such changes in hip, knee and ankle joint angles reflect monkey's acquisition of a more upright posture over the examined period of time. In addition, maximum extension angle of mp joint increased, whereas maximum flexion angle decreased considerably over time (Table 5). Over the time period from day 19 to day 432, the area surrounded by ankle-mp motion lines (see bottom row in Fig. 10) increased gradually,

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representing an increase in the mobile range of both ankle and mp joints. Comparisons across cyclographs show that functional coupling between neighboring joints are established progressively from proximal to distal pair in chronological order. We think that the attainment of stable and replicable coupling between joints is related to both functional differences among joints as well as the degrees of freedom for movement within and between joints. With sufficient experience and practice, together with physical growth and CNS maturation, monkeys will acquire kinematic patterns required for the attainment of an efficient and highly coupled movement system for elaboration of Bp locomotion.

Discussion

The data derived from this study provide fundamental information related to monkey's Bp

locomotor learning. This particular non-human primate model and the study's longitudinal

design produced a detailed set of observations that describe the dynamics of the acquisition

and refinement of Bp locomotion. Interestingly, the process of acquiring independent Bp

locomotion by these monkeys closely paralleled that observed in the young human as they

learn to walk bipedally (Bril and Breniere. 1993; McGraw. 1945; Okamoto and Kumamoto.

1972; Sutherland et al., 1980). The data obtained seem to reveal the basic principles thought to

be essential for successful motor skill acquisition.

**Ontogeny of gait in the macaque monkeys and establishment of cortico-motoneuronal
connections.**

Hildebrand (1967) studied the ontogeny of gait in infant monkey (*M. mullata*), and found

that it developed coordination of head, neck, forelimb, trunk and hindlimb motor segments in

rostrocaudal direction. Lawrence and Hopkins (1976) also studied postnatal development of

infant monkey (*M. mullata*). They found monkey's alternate gait on extended limbs at

approximately 3 weeks of age. Thereafter development continued in gradual fashion so that by

3 to 4 months of age the performance of the monkeys was virtually the same as that of normal

adult. The macaque of 2 to 6 months of age exhibited diagonal-sequence, diagonal couplet gait

of the adult. Such stage-like progression of monkey's locomotor development has been

considered to reflect CNS and musculoskeletal 'maturation' or a 'biological' process

genetically preprogrammed (Hildebrand 1967).

The brain of the 2- to 3- month old macaque is almost as large as that of the adult

(Passingham. 1985). Among the motor pathways descending from the supraspinal structures, the reticulospinal (RS) tract is the earliest developing pathway followed by vestibulospinal (VS) tract (Brodal, 1981). In contrast to these descending tracts, corticospinal (CS) tract develops postnatally. With the use of transcranial magnetic stimulation (TMS), Flament et al (1992a, b) studied cortico-motoneuronal (CM) connections in infant and adult macaque monkeys (*M. fascicularis, M. mullata and M. nemestria*). They could record short-latency EMG responses from forelimb muscles in monkeys that were 3.7 to 5.2 months of age. They could also record adult type EMG responses from tail, leg and foot muscles in monkeys that were around 7.5 months of age. These results showed a sequential developmental progression in the macaque from upper to lower limbs to tail, reflecting progressive rostro-caudal maturation of the CM connections. These findings supported the previous proposition by Lawrence and Hopkins (1976) that CM connections are formed postnatally to reach an adult density at approximately 8 months of age.

CNS neural mechanisms; supraspinal locomotor regions and descending pathways.

Eidelberg et al (1981) studied whether or not 'locomotor evoking' regions such as subthalamic (SLR) and midbrain locomotor region (MLR), which were identified in cats (Grillner. 1981; Shik and Orlovsky. 1976), do exist in the macaques (*M. fascicularis*) whose ages were between 2 and 4 years. The monkey was decerebrated and limbs were placed on the surface of a moving treadmill belt as in decerebrate cats. When movement of the treadmill belt was combined with electrical stimulation of 'positive site' in the posterior subthalamic region (SLR), and those in the vicinity of the cuneiform nucleus (MLR), they could evoke rhythmic limb stepping, resembling a pattern of a slow walk. Stimulation of the positive sites in the

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vicinity of the superior cerebellar peduncle also evoked locomotor movements. The last finding suggests that cerebellar 'positive site' is functionally equivalent to the cat's cerebellar locomotor region (CLR) which was recently delineated (Mori et al., 1998, 1999). Taken together, the monkeys with the age of around 2 years seem to be provided with the SLR, MLR and CLR, and multiple descending motor pathways necessary for the elaboration of Qp locomotion as in the cat. In the decerebrate animals, major locomotor driving signals originating from the SLR and MLR are mediated to the spinal cord by the RS tract, while those originating from the CLR are mediated by both the RS and VS tracts (Mori et al. 2000 b).

Several studies in the macaque (*M. mullata*) (Lawrence and Kuypers. 1968a, b; Lawrence and Hopkins. 1976; Kuypers. 1981) already demonstrated that locomotor driving signals are mediated mainly by the RS and VS tracts. These two motor tracts are the major components of the ventromedial system (Kuypers. 1981). Selective interruption of the ventromedial system at the medullary level resulted in flexion bias of trunk and limbs and a severe impairment of axial and of proximal extremity movements. Animals with such a lesion could not orientate themselves for 40 days after the lesion. When they could finally sit and walk, they were unsteady and walked with a narrow based gait. They had grave difficulties in keeping on course and avoiding obstacles. Independent distal extremity movements were, however, relatively unaffected.

In contrast, interruption of the CS and rubrospinal tracts, which constitute Kuyper's dorsolateral system, produced an impairment of independent distal extremity, especially of hand and digit movements, resulting impaired capacity to flex the extended limb. Total limb movements and combined movements of the body and limbs, such as Qp locomotion, were

relatively unaffected. After recovery, such an animal could even maintain an upright standing posture (Lawrence and Kuypers. 1968 a). Recent studies suggest that locomotor driving signals mediated by the RS and VS tracts are necessary for producing basic locomotor automatism, and that those mediated by CS and cortico-reticulospinal tracts contribute to the refinement of the locomotor automatism. With this, animal is able to accommodate it's locomotor pattern to internal and external perturbations (Mori F et al. 2001). It is apparent that integration of locomotor driving signals mediated by both ventromedial and dorsolateral system is essential for safe execution of locomotion   (Mori et al. 2000 b).

We think that young Japanese monkeys at the ages between 2.5 and 3 years are well provided with fundamental CNS mechanisms including supraspinal locomotor evoking regions and descending motor pathways required for the elaboration of Bp locomotion.

Possible changes in musculosketal sytems associated with locomotor learning.

With regard to the musculoskeletal growth of monkeys, only a few studies have been performed in relation the acquisition of Bp locomoton.   Hayama (1965) was the first to notice the compensatory spinal curvature of Bp walking monkeys (*M. fuscata*) trained according to the old Japanese tradition. Hayama (1986) and Preuschoft et al. (1988) further studied the extent of spinal curvature in 7 male monkeys between 3 and 11 years of age, and with the training periods between 13 weeks and 8 years. In all these monkeys, Bp locomotor training was started when they were 2 to 3 years of age. They found a gradual acquisition of a pronounced lordosis of the lumbar spine, resembling the development of lordosis in human children between 1 and 5 years. Lordosis of the monkey persisted even in the 'normal' pronograde posture of these animals. They suggested that such morphological change is an

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adaptation of the monkeys to the mechanical necessities of the upright body posture. In post-mortem examination of such a monkey, Gotoh (personal communication) found a pronounced hypertrophy of girdle muscles, which contribute to the stabilization of the lower spinal column with the pelvis and femur.

We have also performed X-ray examination of the spinal column in monkey C at days 13 and 468. Although preliminary, we found little curvature of spinal column at day 13 when the monkey just started to maintain an upright posture. At day 468 when the monkey C fully acquired a capability to walk bipedally as the monkeys A and B, we found a pronounced lordosis of lumbar spine (unpublished observation) as in the studies by Hayama (1986) and Preuschoft et al (1988). In addition, we found a pronounced development of girdle and hindlimb muscles in all 4 monkeys. Our findings suggest exercise (use)-dependent hypertrophy of girdle and limb muscles, and even the changes in the composition of muscle fibers related to those in the spinal and supraspinal neural mechanisms. The rostrocaudal progression of coordination in the hip-knee, knee-ankle, and ankle-mp joints may reflect rostrocaudal development of motor pathways descending from the supraspinal structures. The increase in the mobile range of mp joints may reflect a stronger contribution of CM connections.

Acquisition of Bp locomotion and upright posture by locomotor learning.

The acquisition of Bp locomotion by young Japanese monkeys can be interpreted in the context of motor learning. Schmidt (1988) suggested that motor learning involved a process consisting of both practice and experience resulting in an enduring ability to produce skilled action. According to Schmidt (1988), motor learning principles include: (a) the actual process of acquiring a skilled action, (b) that acquiring a skill requires practice and experience, (c) that

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learning can be assessed indirectly through changes in behavior, and (d) that motor learning results in long-lasting changes or production of the acquired skill. More recently, the definitions of motor learning have expanded beyond changes in the individual to include task solutions or outcomes based on the interactions among the individuals, the specific task, and the environment (Newell, 1991).

In our monkeys, the acqisition process included: (a) refinement of variables associated with each monkey's physical growth and functional CNS maturation (endogenous features of the individual), (b) operant conditioning of upright standing and locomotion (exogenous tasks and objectives), and (c) changes in environmental features (i.e., treadmill belt speed, position of food reward, visual and sound cues, among others). The patterns associated with the process of acquiring Bp locomotion indicate that task solutions were variable and changed as a function of growth, maturation, experience and practice. The results obtained from this study demonstrate that each monkey had to establish elementary skills for the maintenance of upright posture with adaptive changes in the musculoskeletal system. Next each monkey acquired elementary control of spatial and timing parameters involved in the movement of multiple motor segments associated with bipedal locomotion. All four monkeys gradually acquired body and hindlimb coordination as well as coordination of neighboring hindlimb joints and in addition, L-R hindlimb coordination through the process of refinement.

Postural control allows for positional stability as well as orientation. Shumway-Cook and Woollacott (1995) define postural coordination as the "ability to maintain an appropriate relationship between the body segments, and between the body and environment for a task". They define postural stability as the "ability to maintain the position of the center of body mass within specific boundaries of space". Stability requires efficient use of balance and

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equilibrium. · The acquisition and refinement of postural orientation and stability involves the integration of a complex set of components including musculoskeletal and neural systems. The musculoskeletal system is comprised of; (a) joint range of motion, (b) spine and trunk flexibility, (c) muscle function and properties, and (d) biomechanical relationship among body segments. Specific neural systems associated with postural stability and orientation can include; (a) neuromuscular response synergies, (b) visual, vestibular, and somatosensory systems, (c) sensory integration strategies, (d) internal representations of sensation to movement relationships, and (e) higher CNS level processes related to anticipatory and adaptive postural and locomotor control.

At this stage of our studies, we do not know yet what kinds of possible changes have occurred in the CNS with the monkey's acquisition of novel capability to walk bipedally. Non-invasive studies such as using positron emission tomography (PET) and TMS may give us a cue to understand plastic changes occurring in the CNS.

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Figure Legends

<u>Figure 1</u>. Physical growth patterns in monkeys A and B.

Top and bottom graphs represent the physical growth patterns across the study period for monkeys A and B, respectively. Weight is shown as a solid black line and height is shown as a dashed blue line. In both graphs, the left vertical axis reflects weight (in kg), whereas the right vertical axis reflects height (in cm). The horizontal axis in both graphs represents the length of the study period (in days on a logarithmic scale). Measurement probes included obtaining kinematic and digital recordings during the locomotor training session. Data were analyzed from these measurement probes and are reported in subsequent figures.

<u>Figure 2</u>. Fluctuation of body axis in relation to a fixed background reference line.

These serial photographs were taken with 1 of 2 single lens reflex cameras used during the measurement sessions. Three rows of 7 photographs represent from top to bottom, the same monkey on training days 31, 102, and 334, at treadmill belt speeds of 0.7, 1.0, and 1.3 m/s, respectively. Treadmill belt speeds reflect the fastest speed at which the monkey could successfully execute continuous Bp locomotion at that specific time in the learning period. The photographs shown in each row are consecutive, starting from the right, frame 1 and moving leftward frame-by-frame to 7. The frame interval is 100 ms in duration. The treadmill moving direction is from left to right as shown at the bottom of the figure. A *stick figure* (yellow line drawing) is superimposed on each photograph to illustrate the changes in trajectories of the head, body and lower limbs. Antero-posterior movement and changes in the body axis position can be viewed relative to a vertical reference line placed at the center of each picture. The body weight and height of the monkey on the training days 31, 102 and 334 days were 3.8kg and 65 cm, 3.9 kg and 68 cm, and 4.5kg and 74 cm, respectively. See text for the details.

<u>Figure 3</u>. Fluctuations in the trajectories of body and lower limbs in relation to a fixed reference line.

Stick figure drawings are depicted in 6 individual graphs representing monkeys A and B in the top and bottom rows, respectively. Drawings were created from movements sampled at 160 ms for a total of 5 consecutive locomotion cycles. Antero-posterior movements can be viewed relative to a vertical reference line running through the center of each graph. Vertical movements can be viewed relative to the vertical height reference line (in cm),

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located near the center of each row. The 6 drawings, from the left to right on the top and bottom rows represent data collected during training sessions on days 19, 41, 79, 164, 286 and 592, for monkey A, and on days 25, 37, 101, 194, 276, and 534, for monkey B, respectively. Stride lengths for the 5 consecutive steps for the left (red line) and right (black line) hindlimbs are represented with horizontal lines under each stick figure. These lines were aligned in relation to the vertical reference line.

Figure 4. Vertical fluctuation of head, hip, and knee position across locomotion periods.

This figure shows the longitudinal data for vertical fluctuations of head, hip and knee positions exhibited by monkeys A and B in left and right graphs, respectively. The horizontal axis in each graph represents training session days on which measurement probes were taken. The vertical axis in each graph represents vertical height (in cm). Head, hip and knee positions were derived from 5 locomotion cycles at a treadmill belt speed of 0.7 m/s. The sampling interval was 160 ms in duration. Body axis angle was defined as the angle between the body axis (ear-hip coordinates) and horizontal lines passing through the hip joint. Vertical positions of ear, hip and knee are represented by filled red, green, and blue circles, respectively. The arrow depicted to the right of the data for each session represents the mean with upper and lower bars depicting ± 1 standard deviation. The physical height of each monkey is represented by a solid black line.

Figure 5. Left and right fluctuation of pelvic position.

This figure shows leftward (L) and rightward (R) movement of the body during bipedal locomotion. The treadmill belt speed was 0.7 m/s. Lateral movements to the L and to the R can be viewed relative to a red-dashed vertical reference line drawn through the center of each photograph. The horizontal scale (in cm) placed at the bottom of each photograph represents lateral deflections to the L and to the R from the center point (0). All photographs were selected to show an example of body posture associated with the same point during the swing phase of the L hindlimb. The graphs were drawn from 10 to 12 consecutive steps with sampling interval of 40 ms in duration. In each graph, black and red vertical thick lines on the right show the duration of consecutive stance phases of the L and R hindlimbs, respectively, in an ascending order. Two black horizontal lines (one with a broken line) and two red horizontal lines (one with a broken line) were drawn to compare the timing of side to side deflections of the pelvic position with the beginning and termination of the stance phase of the L and R hindlimbs, respectively. Maximum deflection of the pelvic position to the L

and R appeared at early and late double support phase.

Figure 6. Chronological changes in left and right fluctuation of pelvic position.

The solid line in each graph shows fluctuation of pelvic position in relation to the midline reference line for consecutive steps (4 sec) from bottom to top. The width of red bar shows ± 1SD. The records on the left and right were obtained from monkey A and B, respectively.

Figure 7. Changes in body axis during locomotion at different treadmill speeds.

Data for body axis angles are depicted for monkeys A and B in left and right graphs, respectively. Body axis angle was calculated using the same coordinates as those described in Figure 4. The horizontal axis in each graph represents training session days on which measurements were taken. Body axis angles were derived from 20 locomotion cycles at each treadmill belt speed. Treadmill belt speeds were set at 0.7, 1.0 and 1.3 m/s. The sampling interval was 40 ms in duration. Means for each body axis angle are depicted by filled circles with associated vertical lines, representing ± 1 SD. Black, red, and green filled circles and connecting lines represent body axis data obtained from 0.7, 1.0, and 1.3 m/s, respectively. A dashed-blue line depicts the body weight of each monkey and serves as reference for tracking physical change across the study period.

Figure 8. Chronological changes in stance, swing, and frequency in relation to treadmill speed.

The top row graphs represent data from monkey A on training days 79, 215, and 432. The bottom row graphs represent data from monkey B on training days 101, 194 and 374. The left vertical axis represents phase durations (in sec). The right vertical axis represents step-cycle frequency (in cycle/sec). The horizontal axis in each graph represents three different treadmill speeds. Notice that for monkey A on day 79 and B on day 101, the treadmill belt speeds were set at 0.4, 0.7 and 1.0 m/s. For the second and third measurement probes, treadmill belt speeds were set at 0.7, 1.0 and 1.3 m/s (monkeys A and B, days 215 and 194, respectively), and 0.7, 1.0, 1.3 and 1.5 m/s (monkeys A and B, days 432 and 374, respectively). These speed differences reflect the fact that early in training, young monkeys were not able to execute continuous bipedal locomotion at higher treadmill belt speeds. Each measure of stance, swing, and frequency was calculated on 20 step cycles. Means for stance phase, swing phase, and step-cycle frequency, are represented by filled circles, open circles, and triangles, respectively. Associated vertical lines indicate ± 1 SD.

Figure 9. Angular changes in hip, knee, ankle, and metatarsophalangeal (mp) joints.

This figure shows four rows of for individual graphs depicting, from top to bottom, individual angular changes in the hip, knee, ankle, and metatarsophalangeal (mp) joints, for monkey A. Data are presented from measurements taken on days 19, 29, 102, 268 and 432. Changes in angle for each joint are depicted on the vertical axis of each joint graph. Upward deflections represent joint extension and downward deflections represent joint flexion. The horizontal axis in each graph represents the 4 second sample duration. Stance-swing cycles are indicated on each waveform. The stance period is represented by the black portion of the waveform, and swing period is represented by the red portion of the waveform. Top and bottom drawings to the left of the graphs depicts the features of stance and swing phases, respectively.

Figure 10. Cyclographs of hip-knee, knee-ankle and ankle-mp joints.

This figure comprised of 12 individual graphs, shows the motion-motion relationships between the hip and knee (top row), knee and ankle (middle row), and ankle and mp joints (bottom row) for monkey A on days 19, 29, 102 and 432. On each graph, joint angular changes are superimposed for 5 locomotion cycles. The stance phase and swing phase tracings are depicted in black and red, respectively, for each joint pair. Arrows indicate the direction of the movement pattern during locomotion. The vertical axis for each graph depicts the degree of extension and flexion for each joint, moving upward and downward. The horizontal axis for each graph depicts the degree of extension and flexion moving rightward and leftward, for the neighboring joint.

Table 1. Means, standard deviations (SDs) and coefficient of variations (CVs) of L and R stride lengths at 10 different days selected.

Numerical values obtained from monkeys A and B are shown on upper and lower set of tables.

Table 2. Means, SD and CV of vertical fluctuation of head, hip and knee positions at 10 different days selected.

Numerical values obtained from monkeys A and B are shown on upper and lower set of tables.

Table 3. Means, SD and CV of lateral fluctuation of pelvic positions at 10 different days selected.

Numerical values obtained from monkeys A and B are shown on upper and lower set of tables.

Table 4. Means, SD and CV of body axis at 10 different days selected.

Numerical values obtained from monkeys A and B are shown on upper and lower set of tables.

Table 5. Means, SD and CV of maximum extension and flexion angles in hip, knee, ankle and mp joints at 5 different days selected.

Numerical values of the maximum extension and flexion angles obtained from monkey A are shown on upper and lower set of tables, respectively.

Ackowledgements

Figure 1.

Figure 2.

31 days

102 days

334 days

Figure 3.

A

19 days   41 days   cm 80   79 days   164 days   286 days   592 days

60

40

20

0

B

25 days   37 days   cm 80   101 days   194 days   276 days   534 days
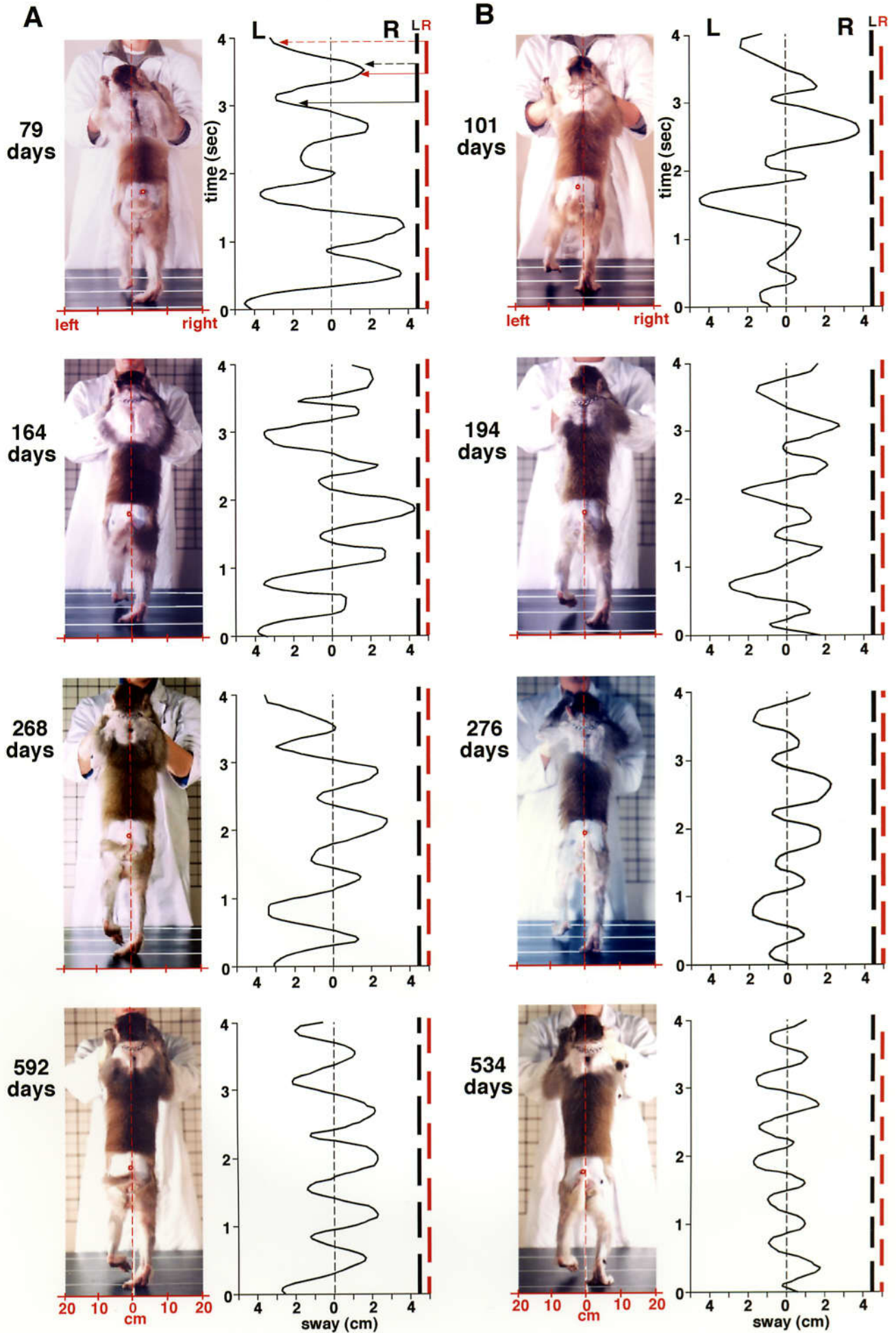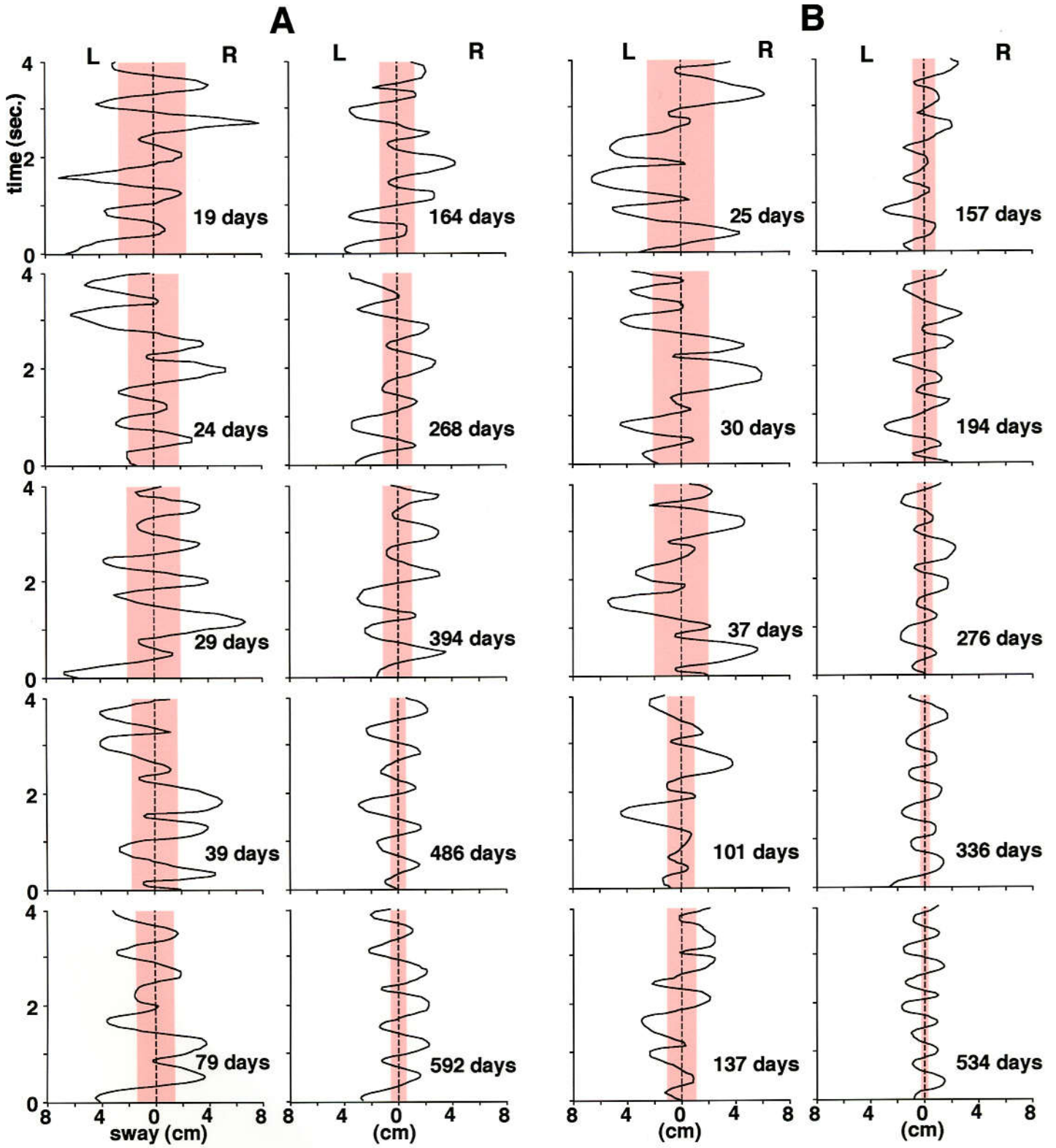
60

40

20

0

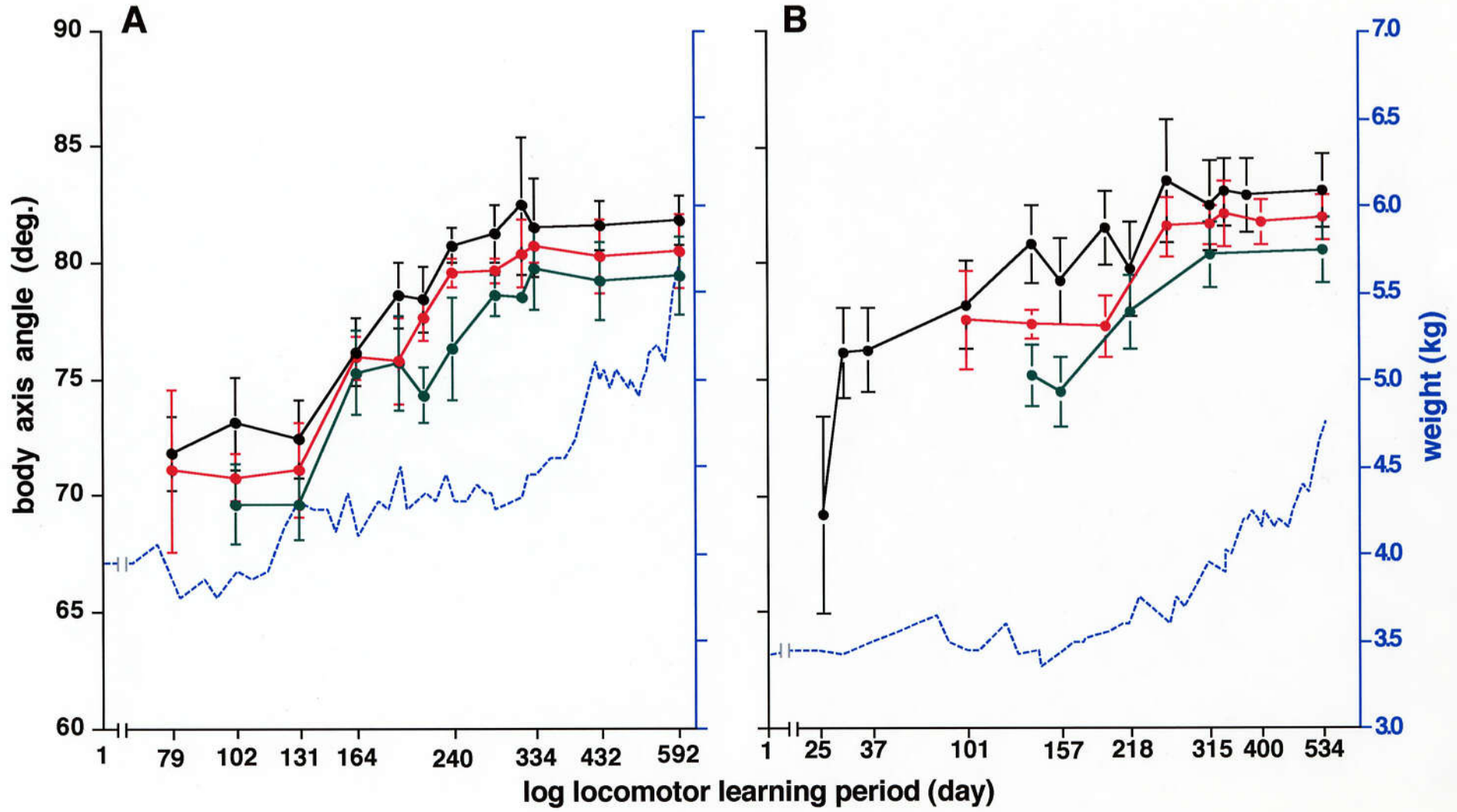40 cm
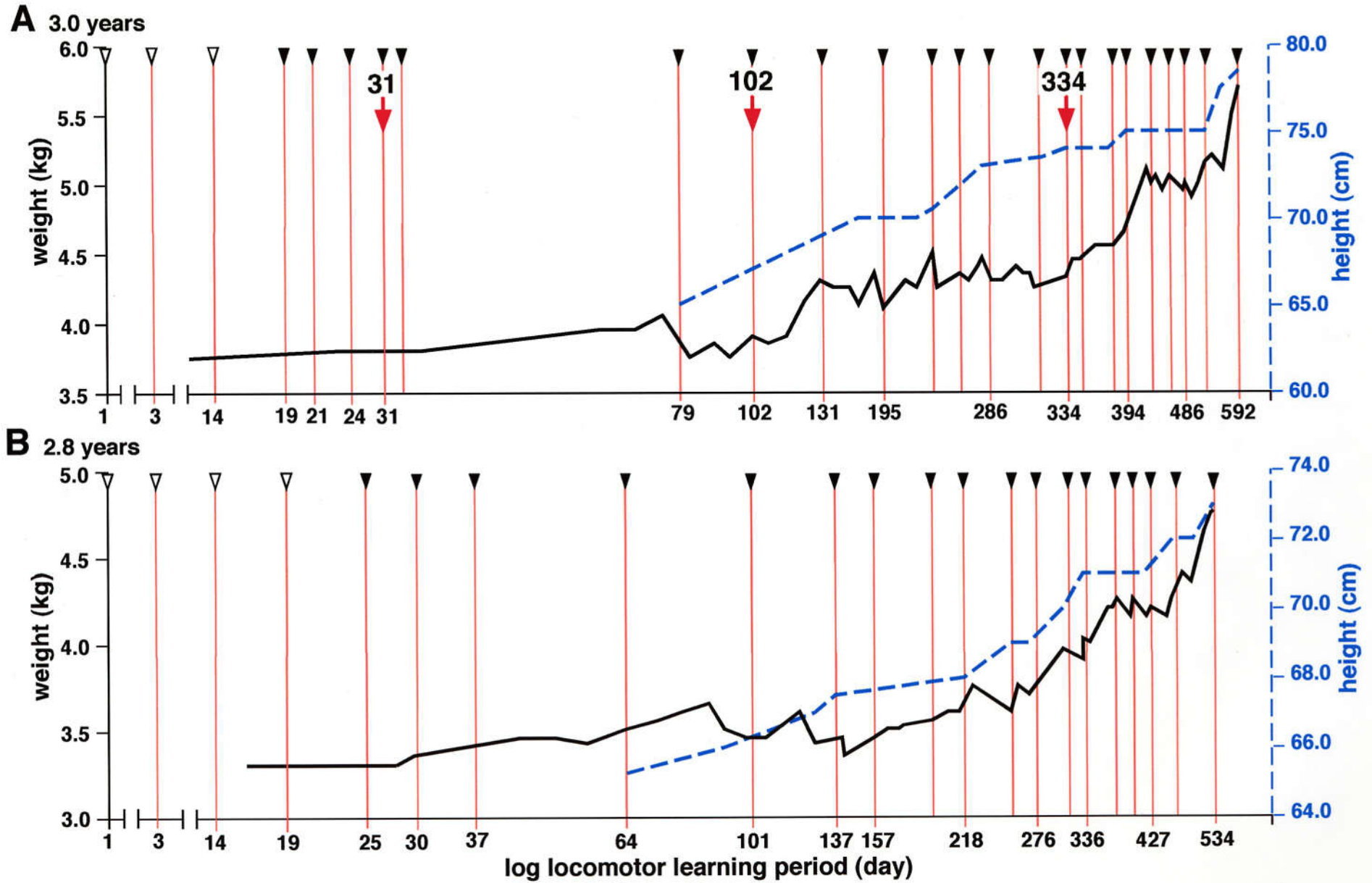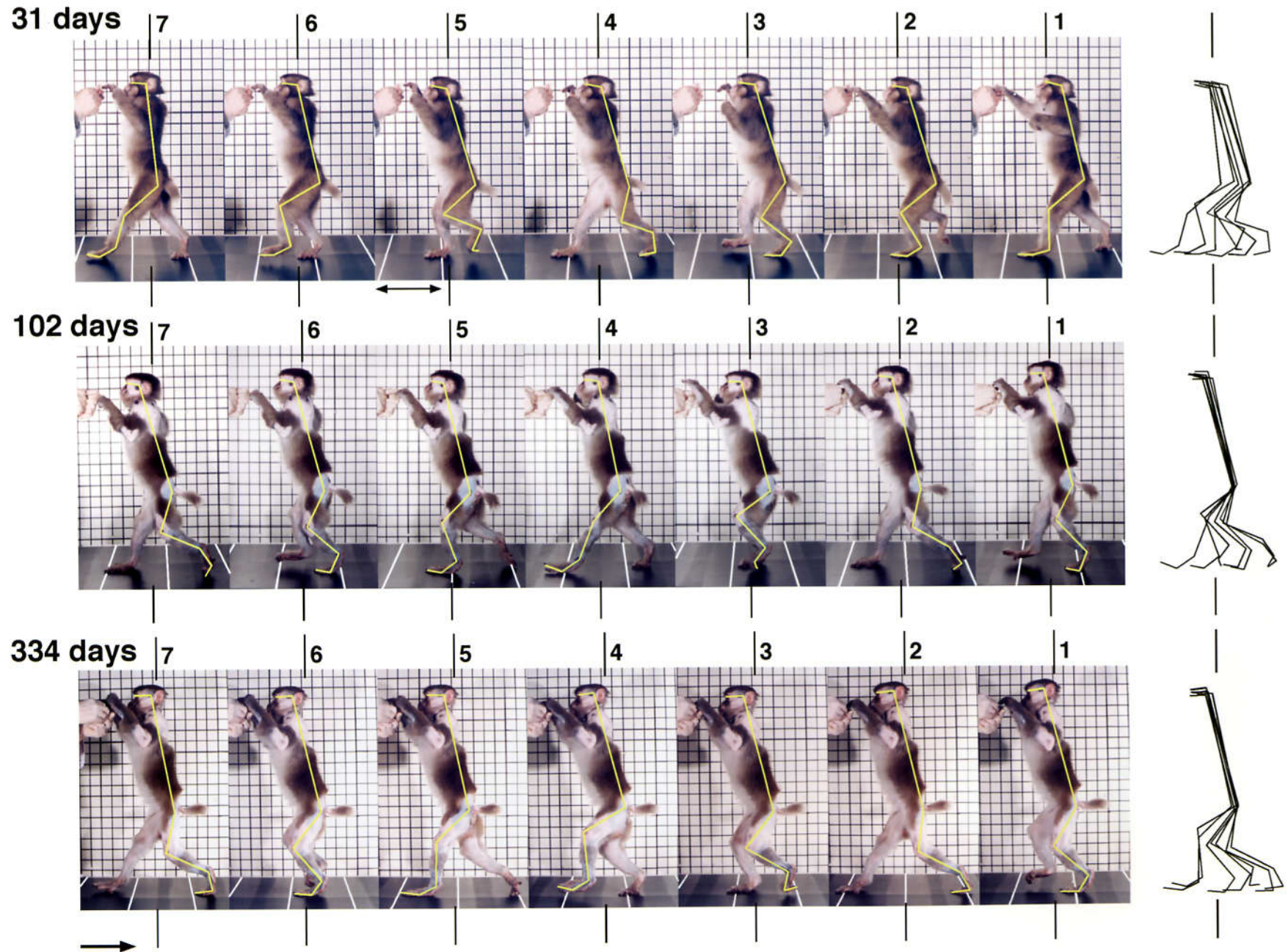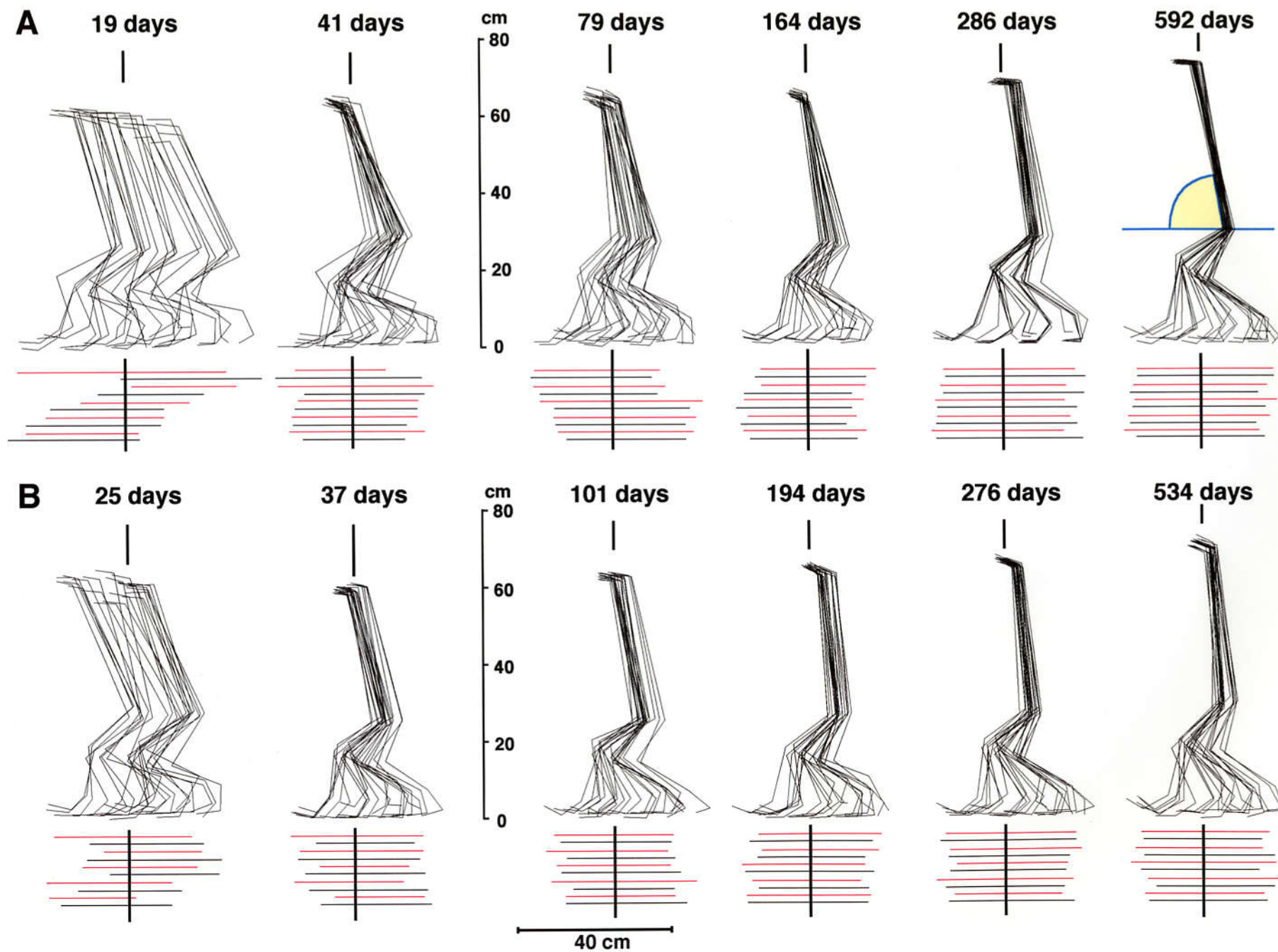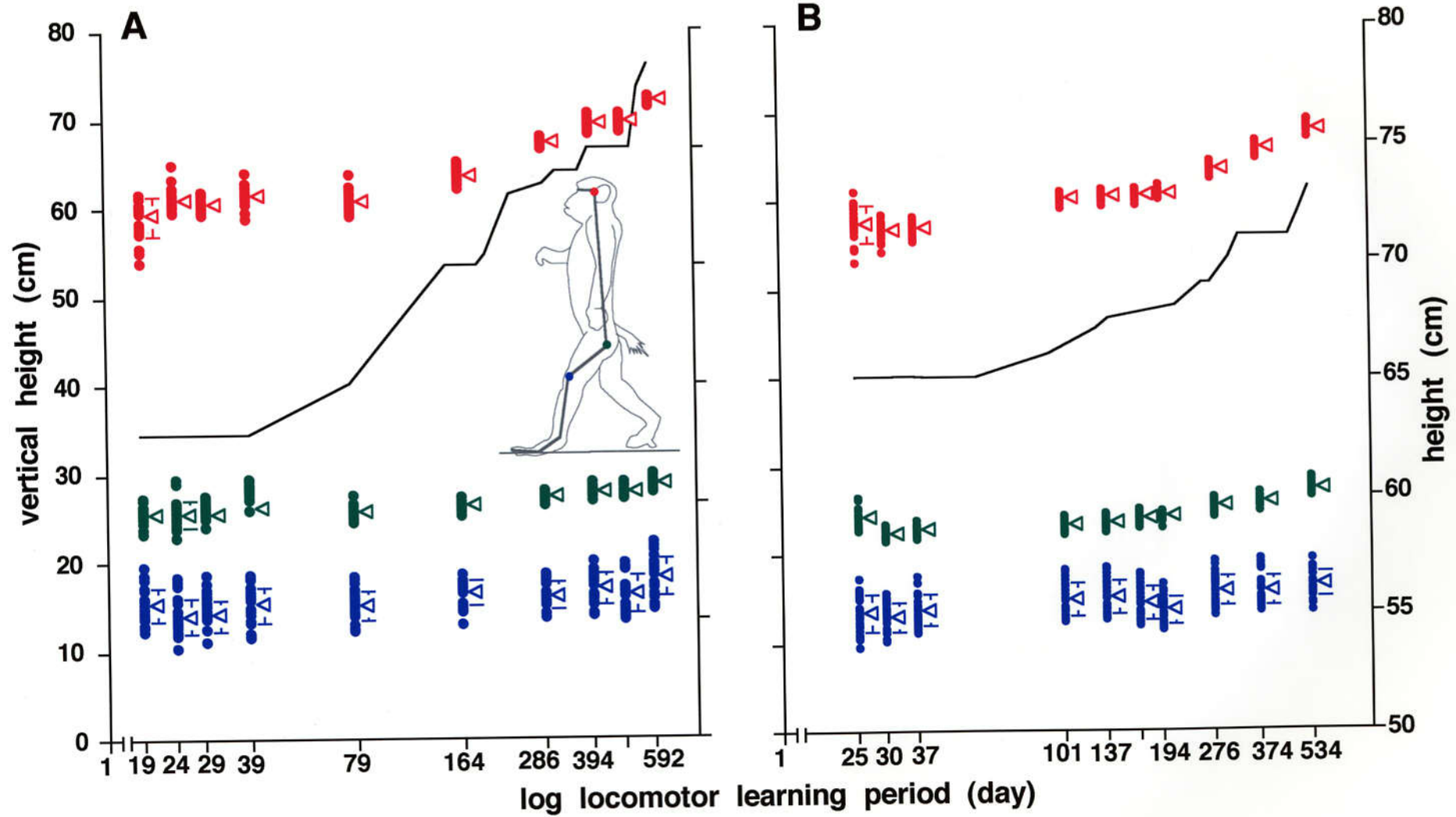
Figure 4.

Figure 5.

Figure 6.

Figure 7.

Figure 8.
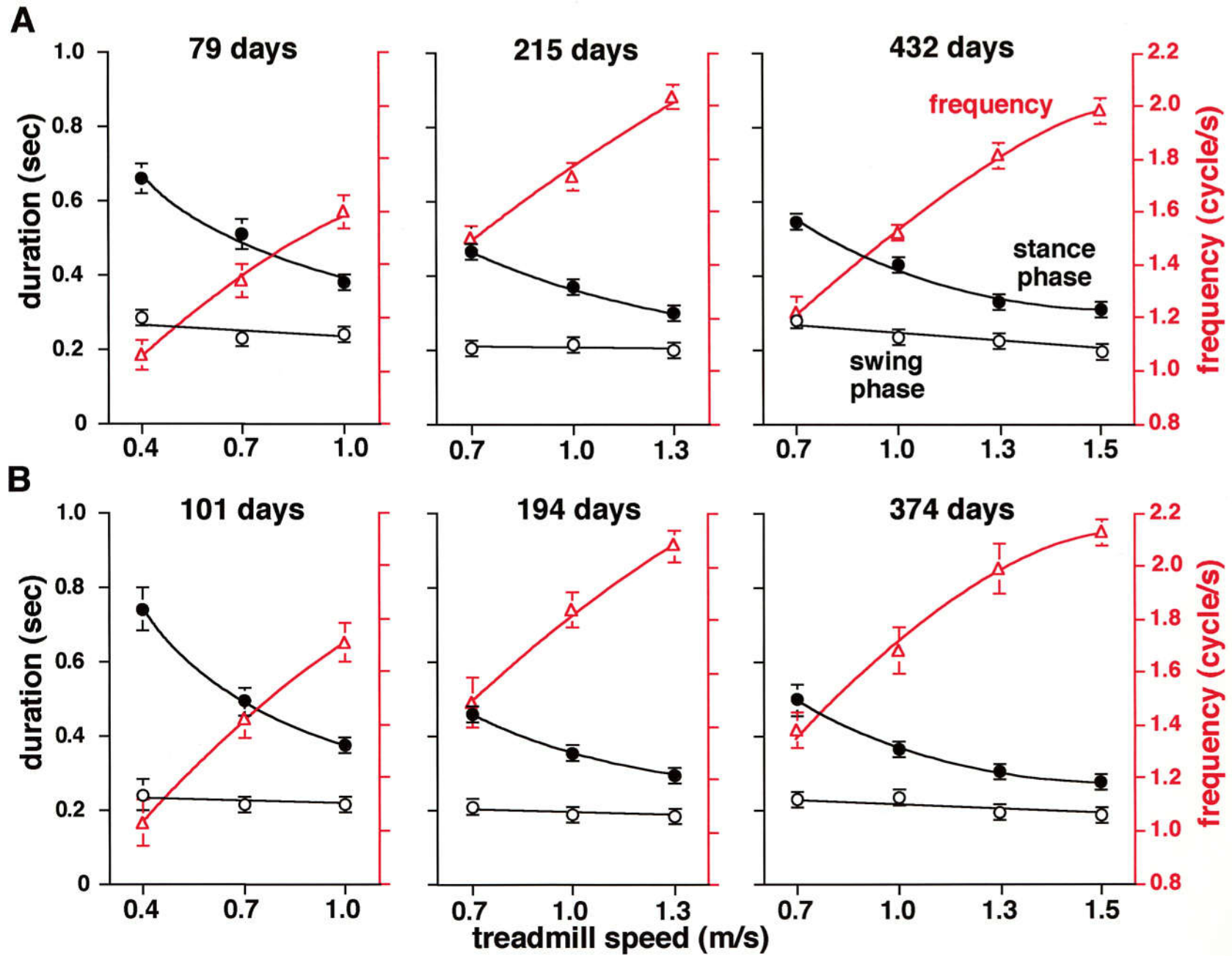
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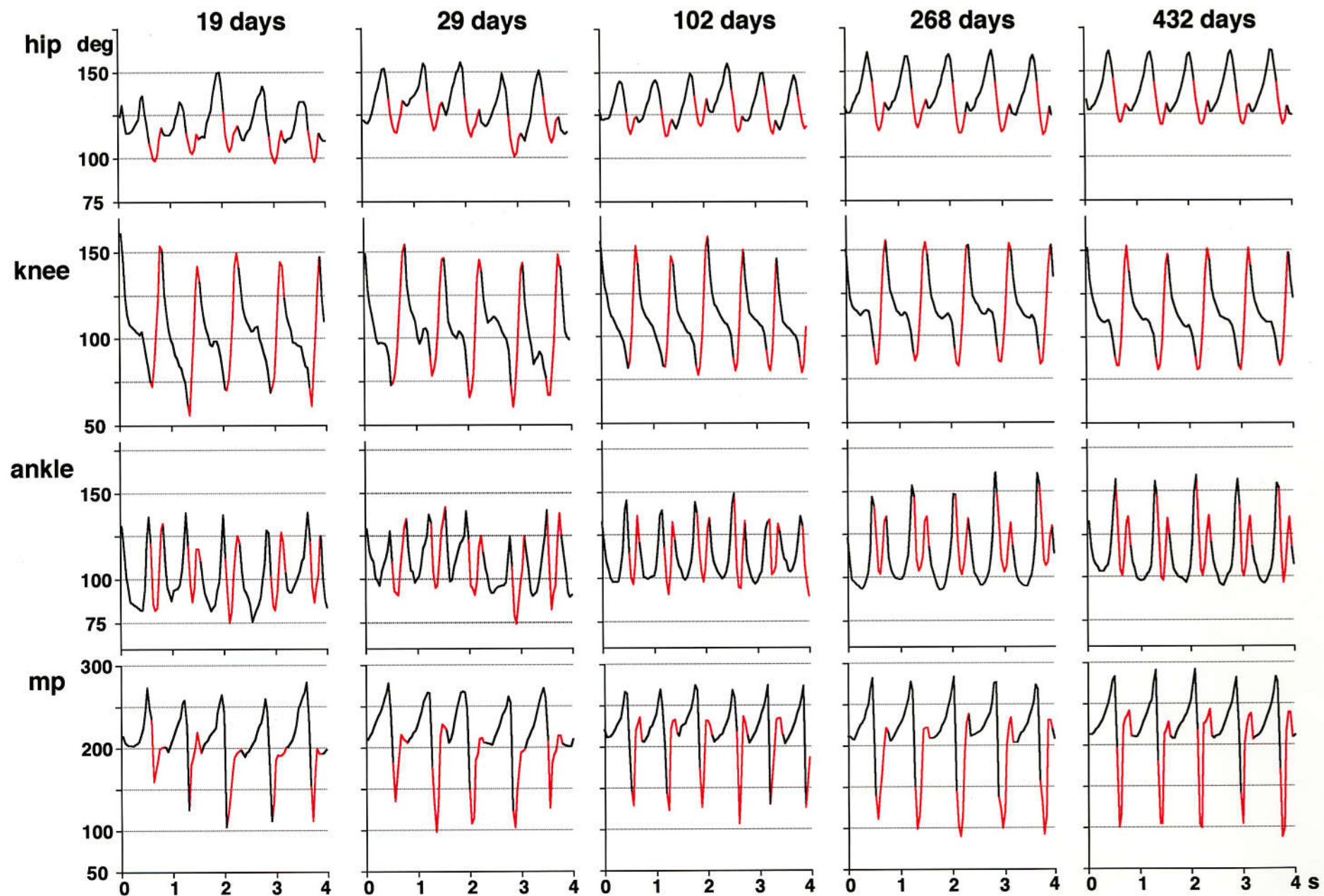
Figure 10.
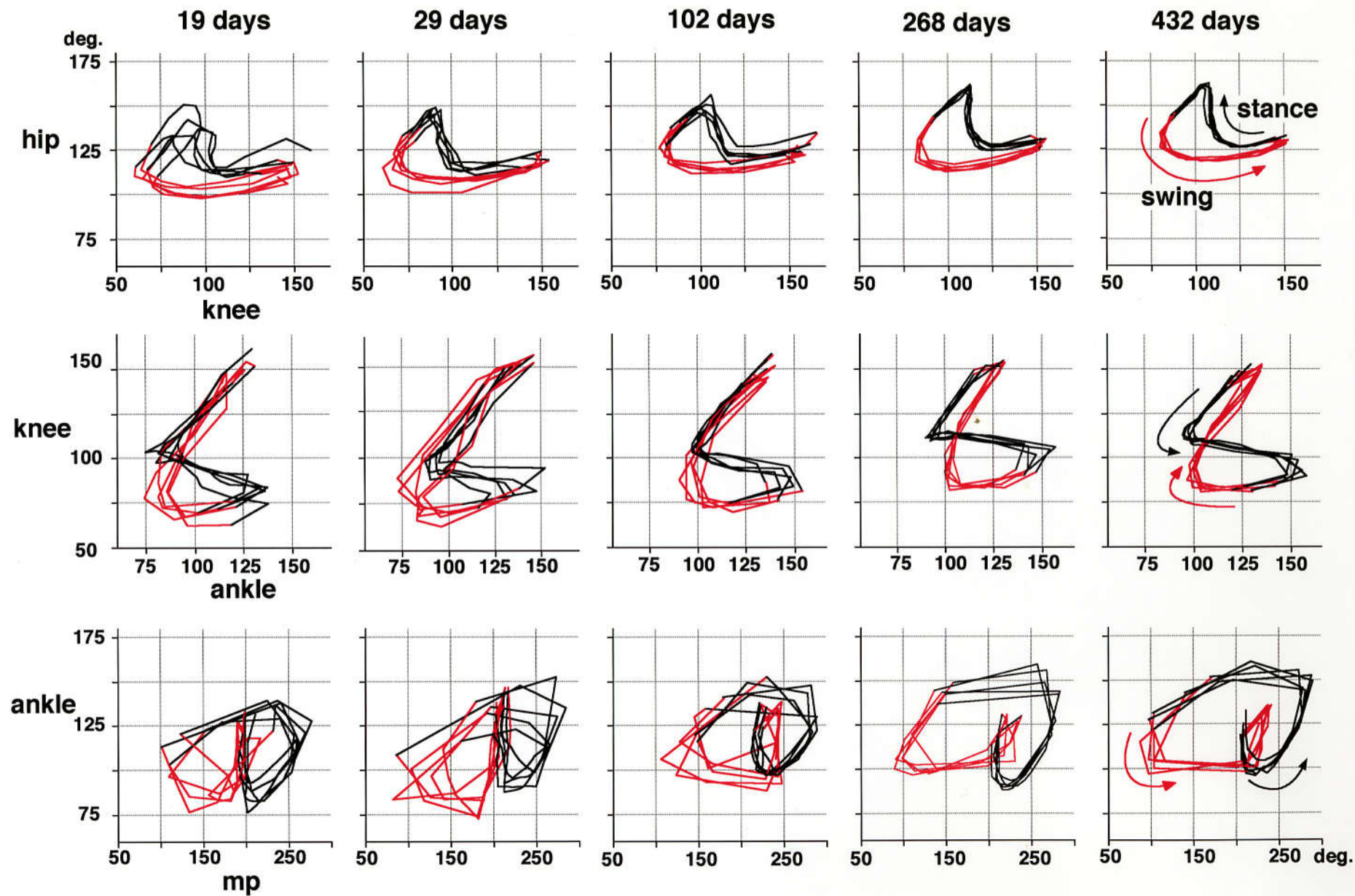
Table 1.

monkey-A

day	19	24	29	39	79	164	268	394	486	592
left foot	33.6±3.9	32.0±3.1	33.1±2.0	31.3±2.2	33.0±1.2	31.0±1.0	34.6±0.9	36.4±1.2	35.8±1.3	35.5±1.1
	11.6	9.8	6.1	7.2	3.7	3.3	2.5	3.3	3.7	3.0
right foot	32.6±3.9	32.3±2.6	32.8±1.8	31.3±4.2	32.3±1.9	31.6±1.4	35.4±1.1	35.7±1.6	35.1±0.8	34.9±1.2
	12	8.0	5.5	13.4	5.9	4.4	3.1	4.5	2.3	3.4

monkey-B

day	25	30	37	101	137	157	194	276	336	534
left foot	30.5±3.5	31.2±2.4	31.0±2.5	30.1±2.3	30.3±2.3	29.1±2.0	30.7±2.2	30.8±1.9	32.6±1.7	34.2±1.5
	11.5	7.6	8.1	7.5	7.8	6.9	7.2	6.1	5.3	4.4
right foot	30.5±3.1	31.2±4.3	30.5±2.5	30.0±2.1	29.9±1.7	28.8±1.3	30.1±2.3	31.3±2.8	32.7±2.8	33.2±1.3
	10.2	13.8	8.2	7.0	5.7	4.5	7.6	8.9	8.6	3.9

mean±SD (cm)

C.V. (%)

Table 2.

monkey-A

day	19	24	29	39	79	164	268	394	486	592
ear	59.2±2.2	61.1±1.2	61.2±1.2	61.3±1.2	60.8±1.2	63.6±0.8	67.2±0.4	69.4±0.7	69.7±0.6	71.9±0.4
	3.7	2.0	2.0	1.2	1.9	1.3	0.7	1.0	0.8	0.5
hip	25.3±1.0	25.5±1.5	26.0±1.0	26.2±0.8	25.6±0.8	26.3±0.5	27.4±0.4	27.9±0.5	27.7±0.5	28.6±0.6
	4.0	5.8	3.8	3.2	3.1	2.0	1.5	1.8	1.9	2.0
knee	15.3±1.9	13.9±2.0	15.0±2.1	15.2±2.0	15.1±1.7	16.5±1.4	16.1±1.6	16.9±1.8	16.3±2.0	18.1±2.1
	12.5	14.5	14.0	13.3	11.2	8.7	9.7	10.8	12.4	11.8

monkey-B

day	25	30	37	101	137	157	194	276	336	534
ear	57.4±2.0	56.7±0.9	57.0±0.8	60.2±0.5	60.3±0.4	60.5±0.4	60.8±0.4	63.7±0.6	65.8±0.6	68.1±0.8
	3.6	1.6	1.4	0.9	0.9	0.9	0.7	0.9	0.9	1.2
hip	24.3±1.0	22.3±0.6	22.8±0.7	23.3±0.6	23.7±0.8	24.0±0.7	24.3±0.5	25.3±0.8	25.9±0.7	27.4±0.7
	4.0	2.5	2.9	2.4	2.4	2.4	2.2	3.1	2.9	2.5
knee	13.4±2.0	13.0±1.6	13.8±1.7	14.9±1.9	14.5±1.8	14.2±1.7	13.6±1.5	15.9±1.6	15.8±1.7	16.6±1.6
	15.3	12.5	12.5	13.0	12.6	12.2	11.1	10.3	10.8	9.6

mean±SD (cm)

C.V. (%)

Table 3.

monkey-A

day	19	24	29	39	79	164	268	394	486	592
lateral	3.9±2.5	2.9±1.9	3.3±2.0	2.6±1.7	2.5±1.4	2.3±1.3	1.9±1.1	2.2±1.1	1.8±0.6	1.8±0.6
fluctuation	64.2	66.2	62.5	63.5	55.8	55.9	57.5	49.8	31.9	32.0

monkey-B

day	25	30	37	101	137	157	194	276	336	534
lateral	3.1±2.5	2.5±2.1	2.4±2.0	1.4±1.0	1.5±1.1	1.3±0.8	1.6±0.9	1.2±0.6	1.3±0.3	1.2±0.3
fluctuation	82.3	85.5	81.7	72.9	69.3	63.4	54.4	48.3	24.4	26.5

mean±SD (cm)

C.V. (%)

Table 4.

monkey-A

day	19	24	29	39	79	164	268	394	486	592
body axis angle: 0.7m/s	71.7±4.1 5.7	72.4±3.5 4.6	72.9±4.8 3.9	72.9±2.9 7.9	72.8±1.5 2.1	76.1±1.4 1.9	80.7±0.8 1	82.3±2.6 3.2	81.6±1.0 1.3	81.8±1.1 1.3
body axis angle: 1.0m/s					70.1±3.4 4.9	74.9±0.9 1.2	79.6±0.6 0.7	79.7±1.7 2.1	80.5±1.1 1.4	81.2±0.7 0.8
body axis angle: 1.3m/s						74.7±2.0 2.6	77.9±1.1 1.4	79.2±1.3 1.6	78.8±0.9 1.1	79.8±1.1 1.4

monkey-B

day	25	30	37	101	137	157	194	276	336	534
body axis angle: 0.7m/s	69.2±2.6 5.2	76.2±1.8 2.3	76.3±1.6 2.1	78.2±1.7 2.2	79.9±1.4 1.7	79.2±1.6 2.1	80.6±1.4 1.8	82.5±1.6 2	83.1±1.4 1.7	83.5±1.9 2.3
body axis angle: 1.0m/s				76.6±2.0 2.6	76.4±0.5 0.7	76.8±0.9 1.2	77.3±1.2 1.6	81.7±0.8 1	82.1±1.3 1.6	82.6±1.5 1.8
body axis angle: 1.3m/s					73.2±1.3 1.8	73.5±1.4 1.9	77.0±1.2 1.6	80.8±0.6 0.7	80.4±1.4 1.7	81.5±1.7 2.1

mean±SD (°)

C.V. (%)

Table 5.

maximum extension

day	19	29	102	268	432
hip	138.6±7.5 5.4	145.2±3.3 2.3	142.6±3.8 2.7	157.6±4.0 2.6	161±0.7 0.4
knee	151.2±5.2 3.5	151.2±1.8 1.2	152.4±4.3 2.8	153.0±1.9 1.2	150.6±1.5 1.0
ankle	135.4±4.2 3.1	145.8±5.0 3.4	141.8±5.9 4.2	149.0±2.8 1.9	154.2±4.2 2.7
mp	266.4±9.0 3.4	273.2±8.1 3.0	269.4±4.5 1.7	287±4.9 1.7	284.2±5.6 2.0

maximum flexion

day	19	29	102	268	432
hip	99.6±2.7 2.7	105.6±3.4 3.2	110.8±1.9 1.7	114.8±1.5 1.3	119.2±0.4 0.4
knee	66.4±4.0 6.1	68.2±3.4 4.9	74.0±2.1 2.8	83.4±1.1 1.4	81.4±1.5 1.9
ankle	81.0±5.8 7.1	79.8±6.4 8.0	95.1±10 10.5	85.2±4.4 5.2	97.2±1.9 2.0
mp	120.6±20.3 16.8	107.6±25.3 23.6	125.8±14.1 11.2	86.4±8.9 10.2	97.8±7.2 7.3

maen±SD (°)

C.V. (%)