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Higher Nervous Control System in Bipedally Walking Japanese Monkey, *Macaca fuscata*

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Abstract

With a long term operant locomotor learning, young Japanese monkeys (*M. fuscata*) acquire a novel strategy for controlling their lower limb joints that allows them to walk bipedally on a moving treadmill belt with generation of sufficient force to propel the center of gravity forward smoothly and swiftly. The current study was designed to evaluate how these monkeys are capable of controlling their locomotor patterns to the changes in treadmill grade and to the postural and gait perturbation. Our results suggest that the monkeys recruited both reactive and anticipatory control mechanisms to achieve the required walking task.

1. Introduction

Although simple in appearance, locomotion is a complex motor activity that requires the integrated control of multiple body segments such as the head, neck, trunk and limbs. Adequate control of each body segment is necessary for the stable execution of bipedal (Bp) and quadrupedal (Qp) locomotion and to accommodate its posture and gait to various external environments. Bp locomotion in human and non-human primates must meet simultaneously several highly inter-related internal and external requirements: 1) antigravity supports of the body, 2) stepping movements, 3) an appropriate degree of equilibrium, and 4) generation of propulsive force [1, 2]. To better understand the critical components of Bp locomotion, it is indispensable to have an animal model that can provide multi-system-level studies; i.e., behavioral, physical, biomechanical, neuroanatomical, and neurophysiological. In recent studies, we have tried to establish a non-human primate model that successfully elaborates Bp locomotion on a moving treadmill belt. The current study focused on the evaluation how these Bp walking monkeys can control their locomotor pattern to the changes in treadmill grade, and to the postural and gait perturbation.

2. Materials and Methods

Two adult monkeys that already acquired the skill of stable Bp locomotion were the subjects of this study. Our methods for analyzing kinematic features of Qp [3, 4, 5] and Bp [5, 6, 7, 8, 9] locomotion were described in detail. For operant conditioning, the experimenter stood in front of the treadmill. The rewards were presented intermittently and given to the monkey while they were walking on the moving treadmill belt. Behavioral characteristics of the monkey's locomotion were routinely analyzed by use of high-speed camera (250 frames/s) against a background on which was ruled a grid of 5 cm squares. Pivot points of selected forelimb and hindlimb joints were marked on the shaved skin with India ink. Postural and kinematic features of the walking monkeys were then analyzed by drawing stick pictures with reference to these pivot points.

2.1 Slanted treadmill locomotion

In uphill vs. downhill walking, the legs of the bipedally walking monkeys and human subjects need to generate a larger acceleration force to transfer the center of gravity forward and in parallel, postural adjustments are also required to maintain body equilibrium and to help generation of forward propulsive force [10, 11, 12]. In downhill walking, the legs must generate a larger deceleration force to prevent excessive forward transfer of the center of gravity, otherwise execution of bipedal walking becomes difficult. We examined body and limb kinematics during the skilled Bp locomotion of *M. fuscata* with a focus on the extent to which its movements resemble those of the human.

To study uphill vs. downhill locomotion, the treadmill (length x width: 150 x 60 cm) grade was set to 7, 15 degrees both up and down relative to the horizontal (0 degree) surface. During a constant treadmill speed, and at a fixed treadmill grade, the monkey could be motivated to walk continuously for 3~5 min, this comprising a single trial sequence. After sufficient rest for the monkey to recover its motivation to re-engage in Bp locomotion, there were additional trial sequences, using new combinations of treadmill speed and its grade. Each overall session concluded when the monkey was no longer motivated to seek the reward.

2.2 Perturbed locomotion

In the ordinary locomotion, the feet often collide with unexpected obstacles, thereby requiring compensatory postural and gait adjustments to prevent stumbling and falling, and reestablish smooth and stable locomotion. Such adjustments have been studied experimentally in the human by having a subject walk on an obstacle-obstructed pathway [13] or a moving treadmill belt [14, 15]. These studies demonstrated that humans use both reactive and anticipatory postural adjustments to perturbations encountered while walking [16]. Such adjustments occur in a proactive way during all phases of the step cycle, with visuomotor coordination a critical factor for both reactive and anticipatory control of posture and gait [17, 18, 19]. We have examined the extent to which *M. fuscata* can recruit such control mechanisms during its Bp locomotion.

To study obstacle clearance vs. stumbling, a small adjustable-height (2.4, 5.0, 7.0 cm) rectangular block (width, 2.0 cm; length, 25 cm) was placed on the left side of the treadmill belt. The left and right sides of the treadmill belt corresponded to the walking path of the left (trailing) and right (leading) hindlimb, respectively. The obstacle appeared in front of the trailing left hindlimb on each 4th to 6th step, as dependent on treadmill speed and stepping frequency.

3. Results

The kinematic features of Bp locomotion were essentially the same for the two monkeys studied. For this reason, we will describe the results obtained from a single monkey.

3.1 Slanted treadmill locomotion: kinematics

Figure 1 shows the exemplary walking patterns of *M. fuscata* on uphill (+15^o, A), level (0^o, B) and downhill (-15^o, C) treadmill at a fixed treadmill speed (1.3 m/s). Several lines were drawn on the animal sketches to depict relevant kinematic and joint angles: ear-hip angle and the angles at the hip, knee, and ankle joints. The line between ear and hip represents the body axis. We defined a body axis angle as the one that was intercepted by the body axis line and a reference line passing through the hip joint (Fig. 1). The latter line was drawn vertical to the treadmill surface.

Figure 1A-C show the instantaneous postural shift when the monkey placed the foot of its left, forward limb on the moving treadmill belt (i.e., touchdown; onset of the stance phase of the left limb). Subsequently, the monkey lifted the right foot, rearward limb up from the surface of the treadmill belt (i.e., take-off; onset of the swing phase of the right limb). In uphill walking (Fig. 1A), the monkey inclined its body axis maximally during the stance phase of both limbs (double support phase). The extent of forward body axis inclination was much larger than that observed during level walking. Throughout a single uphill vs. level step cycle, the monkey exhibited: (a) a larger flexion of the hip joint, lesser extension of the knee joint, and a larger ankle dorsi-flexion during the mid-swing and early-stance phase; and (b) a larger knee joint extension in the late stance phase. In downhill walking (Fig.1C), the monkey also inclined its body axis maximally during the stance phase of both limbs. The extent of body axis inclination was much smaller than that observed during level walking. Throughout a single downhill vs. level step cycle, the monkey exhibited: (a) a larger extension of the knee joint and lesser flexion of the hip joint during the late swing and early stance phase, and (b) a lesser extension of the hip joint and larger flexion of the knee joint during the late stance and early swing phase.

At a fixed treadmill speed (1.3m/s), we found that the body axis angle increased proportionately with an increase in treadmill grade (from –15^o to 15^o). An uphill increase in treadmill grade from 0^o to 7^o to 15^o resulted in an increase in the maximum body axis angle from 15^o to 24^o to 37^o, respectively. Similarly, a downhill increase in treadmill grade from 0^o to –7^o to –15^o resulted in a decrease in the maximum body axis angle from 15 ^{o} to 8 ^{o} to 2 ^{o}, respectively. This relationship between changes in treadmill grade and the body axis angle was near linear across all three of the tested treadmill speeds (0.7, 1.0 and 1.3m/s).

During level treadmill walking at a fixed treadmill speed (0.7m/s), the duration of the stance and swing phase of the step was ~0.60 and ~0.25 s, respectively.

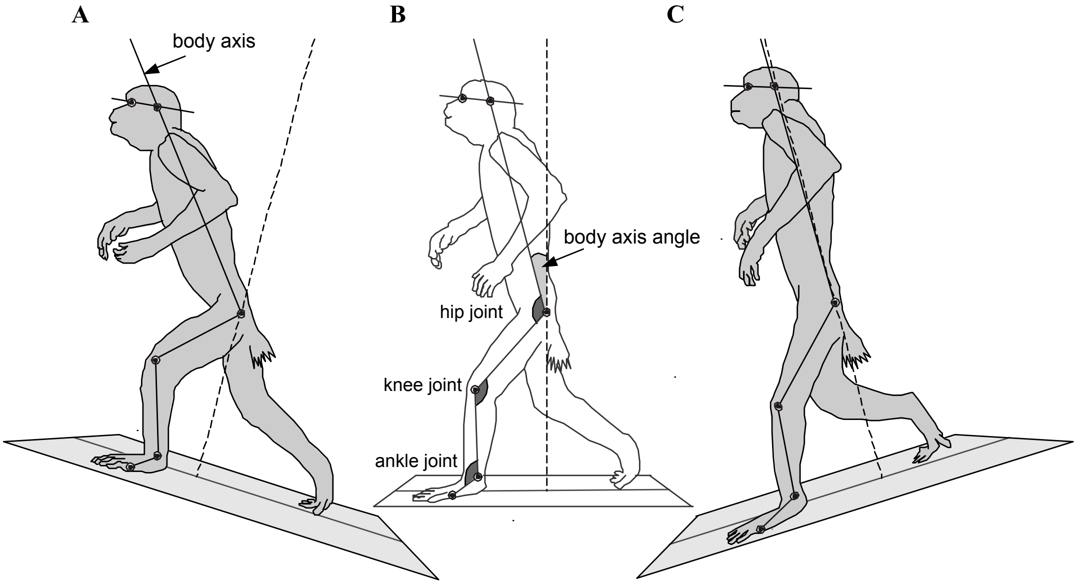

Fig. 1. Sketches of bipedally walking monkey on the uphill (15°, A), level (0°, B) and downhill (–15°, C) treadmill belt. Treadmill speed is 1.3m/s. In this and Fig. 2, the treadmill belt moved from the left to the right, and the monkey walked from the right to the left. Dotted line in each sketch represents the reference vertical line to the treadmill belt (see the text). Body axis, body axis angle, lower limb joints (hip. knee and ankle) and each joint angles were defined as shown in sketches A and B. Note the body axis angle is much larger during uphill walking than during downhill walking. Modified from reference [8].

Uphill and downhill walking at the same speed involved more prolonged and shortened stance-phase duration, respectively. This relationship was maintained across the treadmill speeds of 1.0 and 1.3m/s. The duration of the swing phase of the step cycle did not change significantly, however. We also found a linear relationship between treadmill grade and stride length: i.e., a progressively longer stride for an increase in treadmill grade from –15° to +15°. We found associations between stride length, treadmill grade and its speed. During uphill walking, step-cycle frequency decreased as stride length and treadmill speed increased, the reverse occurring during downhill walking. Healthy humans make quite similar adjustments to those described above for slanted walking [10, 11, 12]. Taken together, these results suggest that the operant-trained Bp locomotion of *M. fuscata* is smooth and versatile under varying external conditions, and its functional coupling between the lower limbs and body axis is quite similar to that of humans. The results demonstrate that bipedally walking monkeys have utilized reactively optimal kinematic parameters for the coordination of multiple motor segments during slanted walking (reactive control).

3.2 Perturbed locomotion: kinematics

During initial trials, the monkey often stumbled when the toe of the trailing left foot stepped on the obstacle's top (horizontal) surface, or slipped up on the initially-encountered (vertical) surface. After several sequential trials, the number of stumbles in a single trial decreased: i.e., the monkey gradually learned how to clear the obstacle, by use of what in humans has been termed a "hip-knee flexion strategy [20]". This involved the monkey increasing the extent of flexion of the left hip and knee joints simultaneously, and the leading right limb alone supporting the center of body mass and maintaining equilibrium. It was easier for the monkey to clear the obstacle when it meets the obstacle during the early to mid-swing phase of the trailing limb. During the late swing phase, the monkey could even change the foot trajectory to clear the obstacle with the aid of visual information. When the obstacle's height was raised, there was a corresponding increase in hip/knee joint flexion of the trailing limb so as to produce sufficient clearance space above the obstacle.

The sketches in Fig. 2 show an instantaneous posture of the monkey at various walking conditions. All four sketches were depicted at mid-swing phase

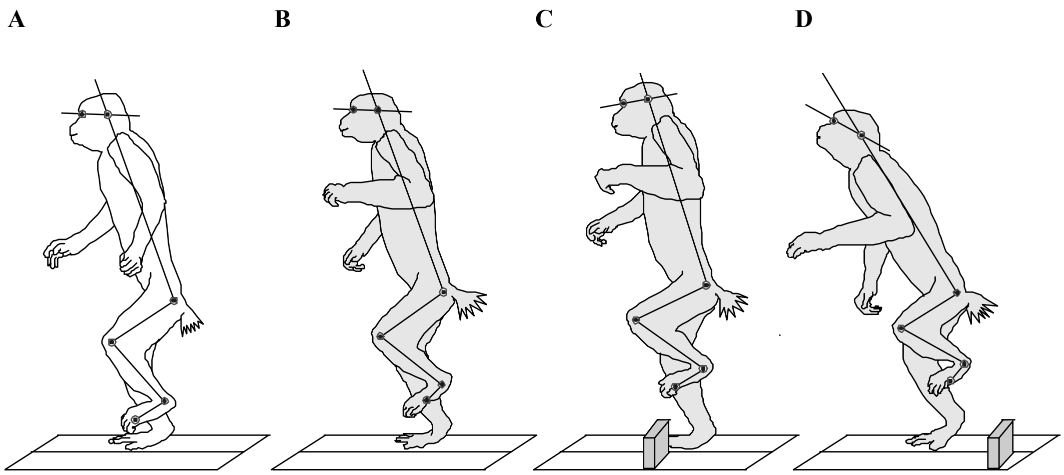

Fig. 2. Sketches of monkey's instantaneous posture. A; control (no obstacle) walking, B; obstacle is 3-4 steps ahead of walking monkey and out-of-site, C; successful clearance of the obstacle; D; defensive posture after stumbling over the obstacle. Treadmill speed is 1.0m/s. Modified from reference [8].

of the left trailing limb. In the control walking condition without an obstacle, the center of body mass was supported by the right limb alone with moderate flexion of the left limb at the hip and knee joints (Fig. 2A). During walking on the obstacle fixed treadmill belt, the monkey flexed its trailing limb's hip and knee joints larger than that at control condition even when the obstacle was out-of-sight (Fig. 2B). This finding indicates that the monkey took a preparatory posture anticipating the in-coming obstacle (anticipatory control), probably the learned memory of an obstacle contributing to this control. During successful clearance of the obstacle (Fig. 2C), hip-knee flexion was further pronounced with additional dorsi-flexion of the ankle joint. This finding suggests that the monkey learned a strategy of visuomotor integration to produce sufficient clearance space above the obstacles.

When the trailing foot failed to clear the obstacle with less careful attention of the monkey to the obstacles, stumbling occurred routinely (Fig. 2D). Such stumbling usually occurred when the toe of trailing limb stepped on or slipped up the obstacle during its late swing phase. Figure 2D shows monkey's pronounced postural perturbation (defensive posture) associated with slipping up the obstacle. Immediately after foot-obstacle contact, the monkey slightly moved its body axis backward followed by a rapid and pronounced (~40 ^{o}) forward movement of the body axis. Subsequently, the animal, 1) shortened the swing period of the leading limb, 2) lowered the center of gravity to the treadmill belt with the flexion of lower limb joints on the obstacle or the belt, and 3) extended its left (and/or right) forelimb forward and/or downward, then 4) extended its lower limb joints to raise the lowered body mass upward. The first 3 defensive compensatory reactions of multiple motor segments stabilized the perturbed posture, and extension of the lower limb joints, especially that of hip and knee joints, helped restoration of the animal's head and body position to the pre-perturbed position in the space. All these defensive reactions of the multiple body segments finally made the animal possible to restore its perturbed posture and walk safely and smoothly.

Recovery of walking required the restoration of (a) the center of gravity, (b) the head position, and (c) the body axis to its pre-disturbed position in space. Interestingly, the correction of the head position always occurred first followed by body axis and limb correction. Perhaps head position in space is the one of the most critical determinant of the nature and extent of reactive responses to perturbations encountered during walking.

When the animal stepped on the obstacle, the trailing limb instantly initiated a new swing phase from the top surface of the obstacle after landing of the leading right foot on the treadmill belt. Alternatively, if the trailing limb's foot slipped up the obstacle, the animal initiated the new swing phase from the belt surface.

From the above, it can be seen that *M. fuscata* recruited both reactive and anticipatory control mechanisms and accommodated its posture and gait to the incoming obstacle, even when it was still out-of-sight. We think that recruitment of dual control mechanisms in an interactive manner allows the monkey to restore the perturbed posture even after stumbling over the obstacle.

4. Discussions

Our analyses of *M. fuscata's* Bp locomotion indicate that this new animal model and human share common body-limb kinematics for the integration of posture and locomotion, particularly the hip joint kinematics.

When monkeys walked on the slanted treadmill belt, they utilized the most optimal kinematic parameters for the integration of multiple motor segments. Further, when the monkey encountered the obstacle, it changed its foot trajectory in advance (anticipatory control) and produced successfully a larger-than-usual clearance space above the obstacle. Moreover when the monkey stumbled over the obstacle, it quickly recovered from its perturbed posture, and continued smooth and well-coordinated Bp locomotion. These findings suggest that the central nervous system (CNS) of the Bp walking monkey received and transformed salient visual, vestibular, proprioceptive, and exteroceptive sensory information into output (command) motor signals appropriate for the integration of multiple body segments which is essential for successful accommodation to the external demands. Such an accommodation mechanism [17, 18, 19] would allow the monkey and human subjects to adjust incessantly their ongoing locomotor patterns and accompanying posture, and thus to respond to the slanted walking path, and even to the unexpected postural and gait perturbations.

The results of the present studies demonstrate clearly that the new non-human primate model we have developed will be the one appropriate for the studies of the CNS mechanisms not only related to the control of Bp locomotion and accompanying posture, but also compensatory processes to stumbling and falling, and eventually several other types of pathological locomotor disturbances. Our animal model will also contribute to substantiation of *integration center, execution center, central program* and *learned memory* [21]. These terms are currently vague, but they are nonetheless useful in the quest to understand how the CNS can achieve a seamless integration of multiple motor segments for the execution of Bp locomotion.

References

[1] Martin, J. P., 1967, *The Basal Ganglia and Posture*, Pitman Medical Publishing, London.

[2] Mori, S., 1997, Neurophysiology of locomotion: Recent advances in the study of locomotion. In: *Gait Disorders of Aging* (eds. J. C. Masdeu, L. Sundarsky, L. Wolfson), Lippincott-Raven, Philadelphia, pp. 55-78.

[3] Mori, S., Miyashita, E., Nakajima, K., et al., 1996, "Quadrupedal locomotor movements in monkeys (*M. fuscata*) on a treadmill: kinematic analyses," *Neuroreport*, Vol. 7, pp. 2277-2285.

[4] Nakajima, K., Mori, F., Takasu, C., et al., 2001, Integration of upright posture and bipedal locomotion in non-human primates. In: *Sensorimotor Control* (eds. R. Dengler and A. R. Kossev), IOS Press, Amsterdam, pp. 95-102.

[5] Nakajima, K., Mori, F., Takasu, C., et al., Biomechanical constraints in hindlimb joints during the quadrupedal vs. bipedal locomotion of *M. fuscata*. In: *Higher Nervous Control of Posture and Locomotion* (eds. S. Mori, M. Wiesendanger, D. G. Stuart), Elsevier, Amsterdam, in press.

[6] Mori, F., Nakajima, K., Gantchev, N., et al., 1999, A new model for the study of the neurobiology of bipedal locomotion: The Japanese monkey, *M. fuscata*. In: *From basic motor control to functional recovery* (eds. N. Gantchev and G. N. Gantchev), Academic Publishing House, Sofia, pp. 47-51.

[7] Mori, F., Tachibana, A., Takasu, C., et al., 2001, "Bipedal locomotion by the normally quadrupedal Japanese monkey, *M. fuscata*: Strategies for obstacle clearance and recovery from stumbling," *Acta Physiol. Pharmacol. Bulg.*, vol. 26, pp. 147-150.

[8] Mori, F., Nakajima, K., Tachibana, A., et al., Reactive and anticipatory control of posture and bipedal locomotion in a non-human primate. In: *Higher Nervous Control of Posture and Locomotion* (eds. S. Mori, M. Wiesendanger, D. G. Stuart), Elsevier, Amsterdam, in press.

[9] Tachibana, A., Mori, F., Boliek, C. A., et al., "Acquisition of operant-trained locomotion in juvenile Japanese monkeys (*Macaca fuscata*): a longitudinal study," *Motor Control*, in press.

[10] Wall, J. Z. C., Nottrodt, J. W., Charteris, J., 1981, "The effect of uphill and downhill walking on pelvic oscillations in the transverse plane," *Ergonomics*, Vol. 24, pp. 807-81.

[11] Kawamura, K., Tokuhiro, A., Takachi, H., 1991, "Gait analysis of slope walking: a study on step length, stride width, time factors and deviation in the center of pressure," *Acta Med. Okayama*, Vol. 45, pp. 179-184.

[12] Leroux, A., Fung, J., Barbeau, H., 1999, "Adaptation

of the walking pattern to uphill walking in normal and spinal-cord injured subjects," *Exp. Brain Res.*, Vol. 126, pp. 359-368.

[13] Eng, J. J., Winter, D. A., Patla, A. E., 1994, "Strategies for recovery from a trip in early and late swing during human walking," *Exp. Brain Res.*, Vol. 102, pp. 339-349.

[14] Dietz, V., Quitern, J. Q., Sillem, M., 1987, "Stumbling reactions in man: significance of proprioceptive and pre-programmed mechanisms," *J. Physiol.*, Vol. 386, pp. 149-163.

[15] Schillings, A. M., Van Wezel, B. M. H., Duysens, J., 1996, "Mechanically induced stumbling during human treadmill walking," *J. Neurosci. Methods*, Vol. 67, pp. 11-17.

[16] McFadyen, B. J., Bélanger, M., 1997, Neuromechanical concepts for the assessment of the control of human gait. In: *Three-dimensional analysis of bipedal locomotion* (eds. P. Allard, A. Cappozzo, A. Lundberg and C. L. Vaughan), John Wiley & Sons, Chichester, pp. 49-66.

[17] Georgopoulos, A. P., Grillner, S., 1986, "Visuomotor coordination in reaching and locomotion," *Science*, Vol. 245, pp. 1209-1210

[18] Drew, T., 1991, "Visuomotor coordination in locomotion," *Curr. Opin. Neurobiol.*, Vol. 1, pp. 652-657.

[19] Patla, A. E., Pretice, S. D., Robinson, C., et al., 1991, "Visual control of locomotion: strategies for changing direction and for going over obstacle," *J. Exp. Psycol. Hum. Percep. Perform.*, Vol. 17, pp. 603-634.

[20] McFadyen, B. J., Winter, D. A., 1991, "Anticipatory locomotor adjustments during obstructed human walking," *Neurosci. Res. Commun.*, Vol. 9, pp. 37-44.

[21] Mori S, Nakajima K & Mori F, Fastigial nucleus as a center for control and integration of posture and locomotion: Parallel control of multiple motor segments. In: *Higher Nervous Control of Posture and Locomotion* (eds. S. Mori, M. Wiesendanger, D. G. Stuart), Elsevier, Amsterdam, in press.

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