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Higher Nervous Control of Quadrupedal vs Bipedal Locomotion in Non-Human Primates; Common and Specific Properties

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Introduction

We acquire a novel capability of walking bipedally according to a genetically designed program. Based on such a program, we postnatally develop our musculoskeletal system and its control system so as to elaborate bipedal (Bp) standing and Bp locomotion. The musculoskeletal system comprises multiple motor or movement segments such as head, neck, trunk, fore- and hind-limbs, each segment having a number of degree of freedom [1]. The control system is the central nervous system (CNS) comprised of the cerebrum, basal ganglia, cerebellum, brainstem and spinal cord [2]. Neural circuitries functionally uniting each of them also develop postnatally with maturation of individual CNS component. Motor segments are innervated by spinal motoneurons (MNs) which are called “final common path” because most command motor signals descending from the supraspinal structures and ascending signals arising from the motor segments converge on them [3]. Thus, the MNs integrate all the descending and ascending signals and send final motor outputs to the skeletal muscles of motor segments.

Previous studies have already shown that the brainstem is equipped with neuronal structures that can subserve a variety of postural reflexes and fundamental movements [3]. From a phylogenetical point of view, the motor pathways descending from the brainstem to the spinal cord are the earliest developing ones [4]. In contrast, the motor cortices establish functional connections postnatally first with the cervical MNs innervating the fore-limbs and then the lumbar MNs innervating the hind-limbs. In the macaque monkey, Olivier et al. [5] showed that full myelination (maturation) of corticospinal axons in the spinal cord would occur at around 36 months of age. Such a rostrocaudal development of cortico-motoneuronal (CM) connection is well reflected in the postnatal developmental pattern of posture and movements in both the human [6] and non-human primates [7]. In parallel with the growth of musculoskeletal system and the CNS, locomotor learning due to daily practice and experience is necessary for the acquisition of a skill of Bp locomotion. Locomotor practice and experience helps the development of CM connections to distally located muscles of the foot, and built up and storage of ‘locomotor memory’ [8].

To advance understanding of CNS control of Bp standing and Bp walking, we have been analyzing the unrestrained normal quadrupedal (Qp) and operant-trained Bp locomotor behavior of a non-human primate, the Japanese monkey, *M fuscata* [9, 10, 11, 12, 13, 14]. Japanese monkeys are originally Qp, but with long-term locomotor training, they acquire a novel strategy of walking bipedally on the surface of a moving treadmill belt. To explain the functional significance of our findings, the present report addresses four major aspects relating to the elaboration of Bp locomotion: (a) our concept of locomotor control CNS mechanisms including anticipatory and reactive control mechanisms, (b) emergence, acquisition and refinement of Bp locomotion in juvenile Japanese monkeys, (c) common and different control properties of Qp and Bp locomotion, and (d) similarity and difference in the kinematics of lower limbs during Bp walking in our monkey model and the human.

Locomotor control CNS mechanisms including anticipatory and reactive control mechanisms

We have recently proposed a new concept of CNS mechanisms related to locomotor control [15]. As shown conceptually in Figure 1, we hypothesize that descending commands from the cognitive and emotive portions of the higher CNS, and activity of both locomotion evoking centers and posture control centers are constantly compared with that of the reference centers, with their collective output sent to the integration centers. Such a system incorporates both anticipatory and reactive control processes. Critical components of the reference centers are the postural and locomotor memory which are built up by daily walking practice and experience. It’s other component includes postural body scheme or the reference frame of body configuration for Bp locomotion [16]. The integration centers participate in a comparator function: comparing top down locomotor command feedforward signals with bottom up feedback signals revealing the current state of locomotion, and minimizing impairments of posture and locomotion. The integration center's efferent output is distributed by way of executing centers. The latter's concern is that motor signals must be sent to a number of different muscle-control systems such that multiple motor segments they control are activated in a coordinated manner. Major elements of motor control units are 'interneuronal circuitries including central pattern generator (CPG)', spinal MN columns and motor segments. Output signals arising from the execution centers are mediated to the spinal cord by the phylogenetically old reticulospinal (RS) and vestibulospinal (VS) pathways, and ensure that appropriate and timely forces are applied to relevant limb joints, the results being a smooth execution of locomotion, with correctly phased limb movements and adequate degrees of postural muscle tone [2]. Output signals arising from the higher CNS, such as the sensorimotor cortex and supplementary motor cortex (SMA), are also mediated to the MNs of motor control units by ways of phylogenetically recent corticospinal and cortico-reticulospinal pathways, and contribute to the refinement of limb movements.

During Bp standing and Bp walking, changes in body configuration are first registered by both the labyrinthine and proprioceptive receptors embedded in the motor segments. Changes in the external world are received by distant receptors, such as eyes and ears [3]. By continuous reception and processing of multi-modal interoceptive and exteroceptive afferent inputs, the integration centers can compare the body's moment-to-moment configuration relative to the immediate and distant environment. When both quadrupeds and bipeds encounter unexpected obstacles, they adopt preparatory or anticipatory posture to avoid them. When they fail to clear the obstacles, they take reactive posture to minimize and compensate for the impairments of ongoing locomotion. The central feedback from the integration center combined with peripheral feedback at the cerebral cortical level enables the animal conscious perception of its kinesthetic aspects of volitional (anticipatory) and automatic (reactive) adjustments of locomotion. Anticipatory control mechanisms are probably stored at a high CNS level and interconnecting network, whereas reactive control mechanisms are probably stored at a low CNS level and interconnecting network [10].

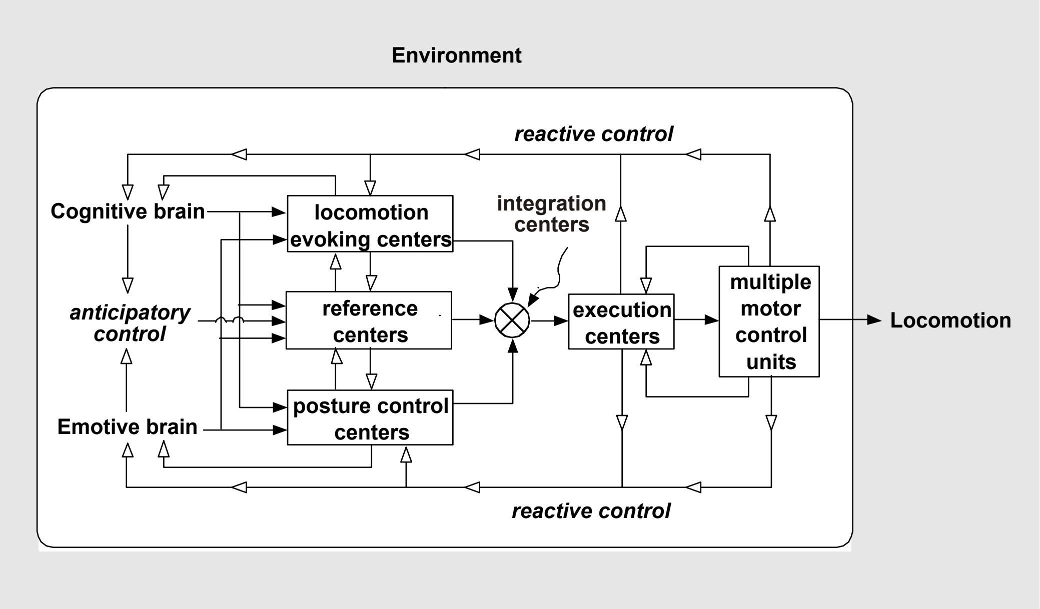

Fig. 1. A conceptualization of the overall integrated control of posture and locomotion including anticipatory and reactive control. From the left to right, the CNS structures and their proposed processes include: cognitive processing, emotive processing, locomotion evoking centers, posture control centers, reference centers, integration centers, execution centers, and multiple motor control units. Open and closed arrowheads represent the ascending and descending flow of signals. Modified from reference [15]

Emergence, acquisition and refinement of Bp locomotion in juvenile Japanese monkeys

With a long-term locomotor training, we have recently found that generically Qp young Japanese monkey, *M. fuscata*, can acquire a novel capability of Bp walking on the surface of a moving treadmill belt [14]. The operant-conditioning methods with which monkey learned to walk quadrupedally and/or bipedally are described in detail elsewhere [11, 13]. After sufficient physical growth and locomotor learning (12 to 24 months), young monkeys (estimated age: 1.6 to 2.4 years) gradually acquired a more upright and a more stable posture, a more stable (less variable) cyclic patterns of joint angles in the lower limbs and coupling among the neighboring joints, and also faster speeds of Bp walking. It was also found that stability of kinematic patterns developed in the rostro-caudal direction, i.e. in the same direction as observed in developing human infants. Our findings demonstrated for the first time the basic principles of the developing monkey to integrate the neural and musculoskeletal mechanisms required for sufficient coordination of upper (head, neck, trunk) and lower (hind-limbs) motor segments so that Bp standing could be maintained and Bp locomotion elaborated.

Once the monkeys acquired Bp walking capability, they still could walk bipedally even after a few weeks of interruption in the locomotor training. This suggests that the monkeys stored postural body scheme or the reference frame of body configuration necessary for Bp walking. We also found that the Qp walking monkey on the moving treadmill belt can right its posture and continue with Bp locomotion [13]. The transition from Qp to Bp locomotion always begins when the left (L) or right (R) hind-limb initiates a stance (ST) phase of the step. For example, at the time when the imaginary position of the monkey's center of body mass projects to the supporting L hind-limb, the monkey begins an upward excursion of the angle of the weight-bearing hip joint. The L forelimb is then freed from the constraints of weight bearing. With further upward excursion of the hip joint angle, the monkey starts to right its posture and initiates reaching and grasping movements, extending the freed fore-limb forward to attain the reward and to eat it ad libitum. This suggests that the monkey's CNS can rapidly select and combine integrated subsets of posture- and locomotor-related neural control mechanisms appropriate for the elaboration of a required task.

During the transitional period from Qp to Bp locomotion, the monkey coordinates sequentially independent movements of multiple motor segments such as eyes, head, neck, trunk, fore and hind-limbs, in order to satisfy the dual purpose of freeing the forelimbs from the constraints of weight-bearing and adopting Bp locomotion. The locomotion conversion process involves the rapid and smooth succession of targeting, orienting, and righting. Targeting requires the coordinated activity of head, neck, trunk and fore-limbs, and righting that of head, neck, trunk and hind-limb. Kinematics of eye-head positions, body axis, and major joint angles of the hind-limbs have revealed the significance of a hip maneuver strategy for the monkey's conversion from stable Qp to similarly stable Bp locomotion [17]. Each of these processes includes visuo-motor coordination and requires that multiple command signals descend in parallel from the higher CNS to the spinal cord and vice versa. Our model animal has given us unique opportunity to compare kinematics of Qp and Bp locomotion in a single animal.

Common and different control properties of Qp and Bp locomotion

During monkey's Qp walking, there were periods in which the body mass was supported by either three or two diagonal limbs. At treadmill speeds of 0.4 and 0.7 m/s, for example, the body mass was supported by the L fore-limb, R hind-limb and R fore-limb when the monkey lifted the L hind-limb from the treadmill belt initiating 'swing (SW) phase'. At treadmill speeds of 1.0 and 1.3m/s, the body mass was supported mainly by the fore- and hindlimbs along a diagonal axis. During this period, two other diagonal limbs were often lifted from the treadmill surface and were in 'SW phase'. With an increase in the treadmill speed, the period of double support phase (ST phase) by the diagonal limbs was shortened so that these two limbs promptly initiate next SW phase. In addition, the monkey considerably increased 'stride length' of the fore- and hind-limbs by increasing 'mobile ranges' of hip joint angle [11]. Such changes in the stride length were accompanied by marked dorsi- and plantar flexion of fore- and hind-limb's toes during SW and ST phases, respectively [11].

As during the human Bp walking, *M. fuscata* showed Bp walking characterized by double and/or single support phases of the L and R hind-limbs. During the SW phase of the L hind-limb, for example, the weight of the body mass was fully supported by the R hind-limb alone (single support phase). The stance R hind-limb soon became the swing limb. However, 'stride length' of the Bp hind-limbs was considerably shorter than that of Qp hind-limbs due to kinematic reconfigurations of the hind-limbs, presumably related to biomechanical constraints of Bp standing. These included smaller mobile ranges of the hip and ankle joints. Interestingly, the profile of angular changes of the knee joint was similar for Qp and Bp locomotion, except for a slight change at the ST phase. At faster speed of Bp walking, the monkey inclined its body axis together with the shortening of the period of double support phase. Marked dorsi- and plantar flexion of hind-limb's toes were also observed during SW and ST phases, respectively [11]. The SW and ST phases and step cycle frequency are interactive parameters during Qp and Bp locomotion [18]. In two adult monkeys, we have compared the changes in these interactive parameters during Qp and Bp walking with the treadmill speeds being increased from 0.4 to 1.5 m/s [17]. As forward speed increased from 0.4 to 1.5 m/s, the average duration of the ST phase for the two animals during Qp locomotion reduced from ~0.9 to ~0.4s, whereas the SW phase remained at ~0.3 s. The associated increase in step cycle frequency was ~0.9 to 1.5 Hz. During Bp locomotion, the corresponding changes were: ST phase, 0.7 to 0.3; SW phase, constant at ~0.2 s; and step cycle frequency, ~1.1 to ~2.0 Hz. These results show that *M. fuscata* increased the speed of its trained Bp locomotion by an increase in the stepping frequency of the hind-limbs whereas it increased the speed of its Qp locomotion by an increase in the total excursion distance of the fore- and hind-limbs. Similar changes in these interactive parameters suggest that our monkeys used the same overall CNS strategy for both Qp and Bp locomotion.

Similarity and difference in the kinematics of lower limbs during Bp walking between our monkey model and the human

The bipedal striding gait is uniquely human, and is a most efficient way of moving over the ground. With bipedal walking over the ground, there is the heel-strike at start of the ST phase and push-off by big toe at the end. In the human, the hip joint extends steadily from approximately 160 ^{o} at initial foot contact to approximately 180^{o} at the end of ST phase, whereas the knee joint shows initial flexion (~20 ^{o}) and extension (~15 ^{o}) at mid-ST phase followed by major flexion (~45 ^{o}) at the latter half of this phase. The mobile ranges of the hip and knee joints were estimated to be approximately 50 ^{o} and 70 ^{o}, respectively [19]. In five species of non-human primates (chimpanzee, gibbon. baboon, Japanese macaques and spider monkey) walking over the ground, Okada (1985) found that, at a foot contact, the joint angles of hip and knee operate in mobile ranges far from a completely stretched position (i.e., 180^{o}). Hip extension is delayed until the latter half of the ST phase, and the knee joint flexes steadily from the beginning to the end of this phase. All the non-human primates excepting the spider monkeys walked with a bent-hip, bent-knee posture.

From above findings, Okada (1985) suggested that the propulsive force which carries the body mass forward is contributed largely by the movement of hip joint during human Bp walking, whereas the knee joint has this function in the non-trained, non-human primates. In our trained adult monkey, the Bp walking pattern was quite different from the "bent-hip, bent-knee" walking pattern [20]. We have not found, however, the heel-strike at the start of ST phase but we found push-off by toes, probably including big toe, at the end of this phase. During Bp walking, the mobile ranges of hip and knee joints were approximately 50^{o} (~120^{o} - ~170^{o}) and 60^{o} (~95^{o} - ~155 ^{o}), respectively. The general pattern of hip extension and flexion was comparable to the pattern in Bp walking humans. It was also noteworthy that at mid-ST phase, knee joint angle changed from a decrease (flexion) to an increase (extension). This flexion and extension pattern was also comparable to that in humans. Our results suggest that Bp walking *M. fuscata* has acquired a new hip and ankle joint motion appropriate for the generation of propulsive force in a fashion quite similar to that of the human.

Our suggestion has been reinforced with the results related to anticipatory and reactive control of Bp locomotion [9,10]. To study anticipatory and reactive control capabilities of Bp walking monkey, it was required to walk on the treadmill belt on which a rectangular block was attached as an obstacle (block height: 3, 5 or 7 cm) (see details, F Mori and S Mori in this volume). We have found that the monkey cleared the obstacle with larger than usual flexion of hip and knee joints so that the trailing hind-limb produces an enough clearance space over the obstacles while the leading limb alone supporting the weight of the body mass. Even before encountering the obstacles, the monkey adopted this "hip and knee flexion strategy" indicating monkey's recruitment of "anticipatory control mechanisms". When failed to clear the obstacles, the monkey adopted a defensive posture to compensate for the perturbed posture indicating monkey's recruitment of "reactive control mechanisms". The observed "hip and knee flexion strategy" of the monkey was essentially the same as that in human's [21].

Summary and Discussion

For the Qp and Bp locomotion of non-human primates, most previous studies are those of anthropologists and biologists seeking to elucidate their kinematics, and the relationships between morphology and species-specific locomotor behavior [22]. For example, Okada (1985) compared our form of bipedalism to similar habits in our closest relatives, the non-human primates [19]. Recently, D'Août et al. (2002) studied kinesiological features of bonobo (*Pan panicus*) walking, the extant great apes, because of its phylogenetical and morphological affinities with early hominids. They compared spatio-temporal characteristics of natural Bp and Qp walking over the ground, especially of hind-limb joint movements, and found that they differ strongly from the human patterns as characterized by "bent-hip, bent-knee" walking. In relation to the heel, they found it is being lifted relative to the toe tips throughout ST phase.

The control mechanisms of Bp human locomotion have been the subject of studies since Marey's first study in 1894 [23]. A series of photograph was taken of human Bp walking by Muybridge [24]. Bernstein depicted stick figures of body movements from such photographs [1]. Herman et al. measured angular displacement of the hip, knee and ankle joints during human Bp walking and revealed a precise spatio-temporal ordering between them [18]. Nilsson and Thorstensson recorded three orthogonal ground reaction force components in the weight bearing limbs during Bp walking and running, and found complex interaction between the vertical and horizontal forces needed for propulsion and equilibrium [25]. For six species of anthropoid primates including a human, Yamazaki (1985) calculated muscular forces acting at the joints during Bp walking by computer simulation [26]. Using SPECT (Single Photon Emission Computed Tomography), Fukuyama et al. identified several brain regions whose activity increased during Bp walking [27].

The change from Qp walking to Bp walking must have required a redesign of the CNS along with reconfiguration of the musculoskeletal system. In Eccles's 1989 monograph he mentioned that much of the evolution from the simpler mammalian brains had already been accomplished in the higher primates [28]. From an evolutional point of view, he also summarized several anatomical changes specific to humans. These included elongation of hind-limb relative to fore-limb; shortening and broadening of the pelvis; reshaping of the foot; a forward curvature of the vertebral column in the lumbar region (lordosis) with a forward rotation of the iliac portion of the pelvis. The movements of human Bp walking based on such anatomical changes clearly demonstrate that there had been a transformation in the operation of the neural machinery of the brain, but far fewer studies have been undertaken from a movement neuroscience perspective, and our knowledge of the neuronal machinery involved in Bp standing and/or Bp walking, and causal relationships between CNS activity and the control mode of the multiple motor segments is still inadequate.

Our group's long-term goal is to elucidate CNS mechanisms controlling Bp locomotion in the non-human primate, wherein non-invasive studies of the CNS and functional inactivation are feasible. Our preliminary study using PET (Positron Emission Tomography) has already revealed that the activity of the primary motor cortex (M1), SMA, visual cortex and cerebellum increased in parallel, with some intriguing differences noted between Bp and Qp walking [29]. Inactivation of the M1 and SMA also resulted, respectively, in focal and general impairments of the Bp standing and Bp walking [29]. With a newly developed Bp walking monkey model, we are now at the beginning of a long-term goal to compare and extrapolate such discovered-mechanisms to those that might operate in the human.

We plan to continue such investigations on *M. fuscata*, in the hope that our multi-disciplinary approach will provide definitive information about the role and operation of higher CNS structure in the integrated control of Bp standing and Bp walking.

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