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Towards emulating adaptive locomotion of a quadrupedal primate by a neuro-musculo-skeletal model

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Abstract

To emulate the adaptive nature of primate quadrupedal locomotion, a neuro-musculo-skeletal model is constructed. The model is designed so as to naturally induce locomotion adaptive to both environment and body structure, due to the dynamic interaction between the convergent dynamics of a recurrent neural network and the passive dynamics of a body system. The simulation results show that the proposed model can adapt to maintain its posture against an external perturbation. Moreover, the model can generate stepping motions, exhibiting its potential adaptability implemented inherently in the system. The proposed framework for the integrated adaptive control of posture and locomotion may be extended for elucidating the adaptive mechanism of primate locomotion.

1. Introduction

Morphologies of locomotor organs in primates are well correlated with their primary locomotor behaviors [1]. Biomechanical studies also suggest that primary locomotory pattern, bipedal locomotion in human and brachiation in gibbon, is induced as the natural oscillation pattern of the body linkage determined by its body proportion [2,3,4]. These findings imply that locomotion is basically generated so as to adapt and depend upon the structures of body system formed rationally through the evolutional process.

Locomotion of animals, including that of primates, is often regarded adaptive in terms of robustness against environmental changes and unknown perturbations. However, there are actually two sides in adaptive mechanism of animal locomotion; to the environment, and as implied above, to the body structure.

Such two-fold adaptivity of primate locomotion can be hypothesized to be emerged by dynamic interaction between the nervous system and the musculo-skeletal system. A network of neurons recurrently connecting to the others can be viewed as a dynamical system which autonomously behaves based on a minimization principle; it behaves convergently to decrease an energy function defined in it [5]. Moreover, a body is also a dynamical system which has a passive properties due to its physical characteristics such as segment inertial parameters and joint mobility [6]. If these dynamical systems are mutually connected, as they are in biological systems, appropriate constraints may be self-organized because of the convergent characteristics of the both systems, and the adaptive nature of the primate locomotion could be spontaneously emulated.

In the present study, a neuro-musculo-skeletal model of a quadrupedal primate is constructed based on the above mentioned idea. Such model may emulate adaptive nature of primate locomotion and comprehensive analysis of the mechanism may become possible.

2. Model

2.1 Mechanical model

A quadrupedal primate is modeled as a 16-segment, three-dimensional rigid body kinematic chain as shown in Figure 1. The equation of motion of the model is derived as

$$\mathbf{M}\ddot{\mathbf{q}} + \mathbf{h}(\dot{\mathbf{q}},\mathbf{q}) + \mathbf{g} - \alpha(\mathbf{q}) + \beta(\dot{\mathbf{q}}) = \mathbf{T} + \Phi \quad (1)$$

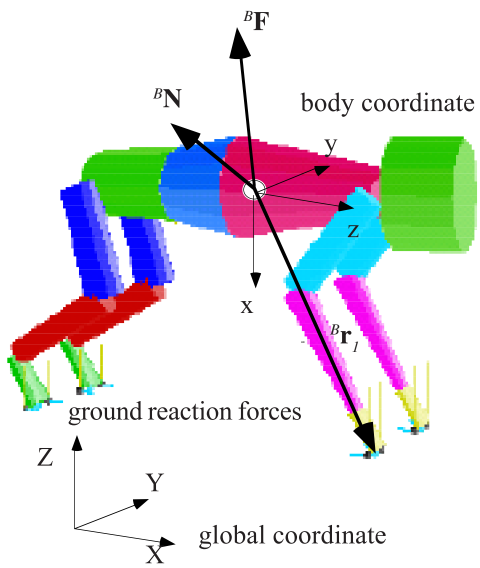

Figure 1. Mechanical model

where **q** is a (51 x 1) vector of translational and angular displacement of the middle trunk segment and 45 joint angles, **T** is a vector of joint torques, **M** is an inertia matrix, **h** is a vector of torque component depending on Coriolis and centrifugal force, **g** is a vector of torque component depending on gravity, α and β are vectors of elastic and viscous elements due to joint capsules and ligaments (passive joint structure) which restrict ranges of joint motions, $\mathbf{\Phi}$ is a vector of torque component depending of the ground reaction forces acting on the limbs, respectively. The primate model is constructed after a female Japanese macaque cadaver. Each segment is approximated by a truncated elliptical cone to calculate its inertial parameters.

All joints are modeled as three degree-of-freedom joints in this model. However, abduction-adduction and medial-lateral rotation of elbow, wrist, knee and ankle joints are restricted by a rigid spring (10Nm/rad) and a damper (0.2Nms/rad). In addition, joints connecting the trunk segments (including the head) are also fixed by rigid springs (100Nm/rad) and dampers (0.5Nms/rad), so that the head and the trunk segments can be treated as one rigid segment. The other joint elastic elements are represented by the following double-exponential function [7]:

$$\begin{aligned} \alpha_j &= k_{j1}\exp(-k_{j2}(q_j - k_{j3})) - k_{j4}\exp(-k_{j5}(k_{j6} - q_j)) \\ \beta_j &= c_j \dot{q}_j \end{aligned} \tag{2}$$

where α_j and β_j the torque exerted by elastic and viscous element around the j th joint, q_j is the j th joint angle, and $k_{j1\sim6}$ and c_j are coefficients defining the passive joint properties, respectively. In this study, the coefficients $k_{j1\sim6}$ are arbitrarily determined so as to roughly imitate actual joint properties, although we are now trying to measure passive joint properties of Japanese macaque for more precise modeling. c_j is 0.2Nms/rad for all joints.

The ground is modelled by springs and dampers. The elasticity and viscosity coefficients of the ground are 4000N/m and 100Ns/m for vertical direction. Horizontal ground reaction force is applied according to the Coulomb friction where $\mu = 0.5$. The hand and the foot are modeled with four points that can contact the ground. The actual center of pressure (COP) is calculated using the points. The global coordinate system and the body (trunk) coordinate system are defined as illustrated in Figure 1.

2.2 Nervous model

2.2.1 Integrated control of posture and locomotion

It is generally accepted that locomotion is generated by alternating the activities of the extensor and flexor muscles under the control of rhythm-generating neural circuits in the spinal cord known as the central pattern generator (CPG) [8,9]. However, previous research on decerebellated cats shows that coordination of limbs is greatly disturbed and balance of the trunk is lost in these animals [10]; whereas decerebrate cats, whose cerebellums are left intact, can balance themselves and walk in more coordinated ways [11]. The cerebellum is a region where various sensory information, such as the vestibular organ and afferent signals from proprioceptors and exteroceptors, is all integrated. Thus, the integration of multimodal afferent information in the cerebello-spinal systems is suggested indispensable for integrated control of posture and locomotion [12].

Meanwhile, from the biomechanical and kinesiological viewpoint, both posture and locomotion can be seen as being controlled by adjusting ground reaction forces acting on the limbs. To sustain the trunk segment at a certain position and orientation in three-dimensional space, an appropriate force and a moment have to be applied to the center of the mass (COM) of the trunk. Correspondingly, in locomotion, such force must be applied in a travelling direction to displace the body. Such force and moment can only be applied by generating the reaction forces acting on the limbs from the ground and the nervous system somehow needs to control them.

Therefore, it is assumed that activities of neurons in the nervous system represents ground reaction forces necessary to maintain the posture and locomotion, and appropriate forces are spontaneously computed based on the multi-modal sensory inputs.

2.2.2 Recurrent neural network model

In this study, an array of 12 neurons is expressed as $\mathbf{u} = [\mathbf{u}_1\ \mathbf{u}_2\ \mathbf{u}_3\ \mathbf{u}_4]^T$, where $\mathbf{u}_L$ is the (3 x 1) vector of the state variables corresponding to three components of the ground reaction force vector of the Lth limb (L=1,2,3,4; 1=right fore, 2=left fore, 3=right hind, 4=left hind). In order to sustain the trunk posture, the nervous system consisting of the neurons is assumed to behave so as to spontaneously fulfill the following equations of equilibrium:

$$\begin{aligned} {}^B\mathbf{F} &= \sum_{L=1}^{4} \gamma_L \mathbf{u}_L \\ {}^B\mathbf{N} &= \sum_{L=1}^{4} ({}^B\mathbf{r}_L) \times (\gamma_L \mathbf{u}_L) = \sum_{L=1}^{4} \mathbf{S}({}^B\mathbf{r}_L) \cdot \gamma_L \mathbf{u}_L \\ \mathbf{S}(\mathbf{r}) &= \begin{bmatrix} 0 & -r_z & r_y \\ r_z & 0 & -r_x \\ -r_y & r_x & 0 \end{bmatrix} \end{aligned} \tag{3}$$

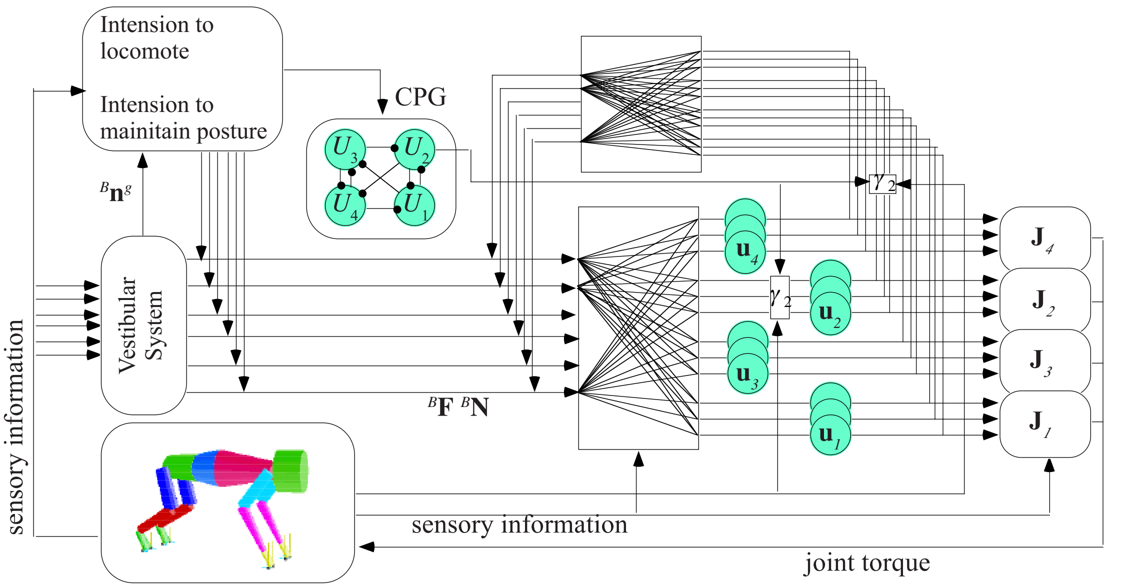

Figure 2. Neural network model. The output from the CPG is only drawn for L=2.

where ${}^B\mathbf{F}$ and ${}^B\mathbf{N}$ are the (3 x 1) vectors corresponding to the neuronal representation of force and moment ought to be applied at the COM of the trunk segment, ${}^B\mathbf{r}_L$ is the position vector from the COM to the COP of the Lth limb, γ_L is the signal from the cutaneous receptor of the palm/sole of the Lth limb (=1 when the limb touches the ground, and 0 otherwise), $\mathbf{S}(\mathbf{r})$ is a matrix representing skew operation on the vector $\mathbf{r}$, respectively. The left superscript B indicates that the vectors are represented in the body (trunk) coordinate frame.

Such nervous system can be modelled by a recurrent neural network [5] as

$$\frac{d\mathbf{u}_L}{dt} = -\gamma_L \mathbf{A}\cdot\mathbf{Q}_L^T\cdot\mathbf{W}\cdot\Big(\sum_L \mathbf{Q}_L\gamma_L\mathbf{u}_L - \begin{bmatrix}{}^B\mathbf{F}\\ {}^B\mathbf{N}\end{bmatrix}\Big) - (1-\gamma_L)\mathbf{B}\mathbf{u}_L - \lambda[\max(u_{L,x},0),0,0]^T \quad (4)$$

$$\mathbf{Q}_L = \begin{bmatrix}\mathbf{I}\\ \mathbf{S}({}^B\mathbf{r}_L)\end{bmatrix}$$

where $\mathbf{Q}$ is the (6 x 3) matrix, $\mathbf{I}$ is the (3 x 3) unit matrix, $\mathbf{W}$ is the (6 x 6) diagonal weight matrix, $\mathbf{A}$ is the (3 x 3) diagonal matrix of reciprocals of time constants of the neurons, $\mathbf{B}$ is the (3 x 3) diagonal matrix, λ is a coefficient, respectively. According to the first term in the right side in Equation (4), the following potential function is autonomously decreased during the change in the neural states $\mathbf{u}$:

$$E = \frac{1}{2}\Big(\sum_L \mathbf{Q}_L\gamma_L\mathbf{u}_L - \begin{bmatrix}{}^B\mathbf{F}\\ {}^B\mathbf{N}\end{bmatrix}\Big)^T\cdot\mathbf{W}\cdot\Big(\sum_L \mathbf{Q}_L\gamma_L\mathbf{u}_L - \begin{bmatrix}{}^B\mathbf{F}\\ {}^B\mathbf{N}\end{bmatrix}\Big) \quad (5)$$

where E is the potential function representing the weighted summation of square errors of Equation (3).

Therefore, the proposed neural network, given the input ${}^B\mathbf{F}$ and ${}^B\mathbf{N}$, can autonomously estimate the ground reaction forces necessary to sustain the balance of the posture. The second term in Equation (4) implies that $\mathbf{u}_L$ approaches to zero when the Lth limb is not in contact with the ground. The third term represents that $u_{L,x}$ is always positive since the model can only generate reactive force by pushing the ground, but not by pulling, since grasping is not modelled here.

The joint torques are then assumed to be generated according to the following equation derived by the principle of virtual work:

$$\mathbf{n}_L = -\mathbf{J}_L^T\mathbf{u}_L \quad (6)$$

where $\mathbf{n}_L$ is the (9 x 1) vector of the joint torques of the Lth limb, $\mathbf{J}_L$ is the (9 x 3) Jacobian matrix. Another recurrent neural network can be added which produces the joint torques from $\mathbf{u}_L$ based on the anatomical constraints of the musculo-skeletal systems [13]. However, here the torques are generated as in Equation (6) for simplicity.

The inputs to this recurrent neural network, ${}^B\mathbf{F}$ and ${}^B\mathbf{N}$, are assumed to be determined by the intension of motion, that is to keep the trunk stable at an appropriate position and orientation, and the input from the vestibular organ, which works as the sensor of the translational and rotational velocities of the head (trunk) segment, as

$${}^B\mathbf{F} = \mathbf{K_F}({}^B\mathbf{p}^d) - \kappa(\delta-\zeta)\,{}^B\mathbf{n}_g - \mathbf{C_F}\,{}^B\dot{\mathbf{p}} \quad (7)$$

$${}^B\mathbf{N} = \mathbf{K_N}\,{}^B\Theta^d - \mathbf{C_N}\,{}^B\omega \quad (8)$$

$${}^B\mathbf{p}^d = \sum_L \gamma_L\,{}^B\mathbf{r}_L \Big/ \sum_L \gamma_L$$

where ${}^{B}\mathbf{p}^{d}$ is the position vector from the COM to the centroid of the polygon formed by the COP's of the limbs, ${}^{B}\mathbf{n}^{g}$ is the unit vector showing the direction of the gravitational force, ${}^{B}\mathbf{v}$ is the velocity of the COM of the trunk segment, δ is the distance between the COM and the ground along the vector ${}^{B}\mathbf{n}^{g}$, ${}^{B}\Theta^{d}$ is the Eulerian angles between the present and the desired orientation of the body, ${}^{B}\omega$ is the angular velocity vector of the trunk segment, κ and ζ are coefficients, $\mathbf{K}_{\mathbf{F}}$, $\mathbf{K}_{\mathbf{N}}$, $\mathbf{C}_{\mathbf{F}}$, $\mathbf{C}_{\mathbf{N}}$ are (3 x 3) diagonal matrices of coefficients, respectively. The third term in the right side in Equation (7) and the second term in Equation (8) show the input from the vestibular organ, while others show the intension of motion, that is to keep the body's position at a stable location and orientation, at some distance apart from the ground.

Since ${}^{B}\mathbf{r}^{d}$, ${}^{B}\mathbf{n}^{g}$, ${}^{B}\mathbf{v}$, ${}^{B}\omega$ are all represented in the body's reference frame, the nervous system is assumed to be able to sense these quantities; ${}^{B}\mathbf{r}^{d}$ by the cutaneous receptors on the palm/sole and the muscle spindles (joint angle sensors); ${}^{B}\mathbf{n}^{g}$, ${}^{B}\mathbf{v}$, and ${}^{B}\omega$ by the vestibular system. $\mathbf{Q}$ and $\mathbf{J}$ are sensory-motor maps which are the functions of the sensory inputs ${}^{B}\mathbf{r}^{d}$ and $\mathbf{q}$.

2.2.3 Rhythm pattern generator

The rhythm pattern generator, which coordinate sequential limb movement in a quadrupedal animal, exists in primates as well [14]. Here it is modeled by the following equations proposed by Matsuoka [15,16]:

$$\begin{aligned} \tau \dot{U}_L &= -U_L + \sum_i z_{Li} y_i + s_0 - h_L V_L \\ \tau' \dot{V}_L &= -V_L + y_L \\ y_L &= \max(U_L, 0) \end{aligned} \tag{9}$$

where U_L is the inner state of the Lth neuron whose activation corresponds to the stance-swing phase of the Lth limb, V_L is a variable representing self-inhibition of the U_L, τ and τ' are time constants, y_L is the output of the Lth neuron, z_{Li} is the weight of neural connections, h_L is the weight of self-inhibition, s_0 is the constant input, respectively.

If the model is in standstill with all limbs in contact with the ground, γ_L is 1 for all. However, when the model starts to locomote, according to the input from the higher center, γ_L is assumed to overridden by the rhythmic signal y_L as:

$$\gamma_L = \begin{cases} 1 & \text{if } y_L > 0 \\ 0 & \text{if } y_L = 0 \end{cases} \tag{10}$$

Therefore, vertical ground reaction forces of the four limbs become zero sequentially according to the output of the rhythm pattern generator. In this way, stand-swing phase of a limb is coordinated and locomotion may be generated.

2.3 Mutual interaction between neuro-mechanical systems

Figure 2 shows a schematic diagram of the interaction between neuro-mechanical systems. Given the intension to maintain the posture as well as the input from the vestibular organ, the nervous system can autonomously generate the signal $\mathbf{u}$, which corresponds to the ground reaction forces, such as to decrease the potential function defined in Equation (5). $\mathbf{u}$ is then transformed by the sensory-motor map $\mathbf{J}$ to produce the joint torques $\mathbf{n}$ and the posture is maintained. The sensory information of resultant motion by the vestibular systems, ${}^{B}\mathbf{n}^{g}$, ${}^{B}\mathbf{v}$, and ${}^{B}\omega$, the cutaneous receptor γ_L, the proprioceptor $\mathbf{q}$, are returned to the nervous system, so that the entire neuro-musculo-skeletal systems are mutually integrated.

When the model intends to locomote, the rhythmic signal is generated and the limbs start to move sequentially. This rhythmic signal can be regarded as a perturbation interfering the maintenance of the posture. But because of the inherent convergent properties of the nervous system and the body system, adaptive locomotion is assumed to be self-organized.

3. Calculation Method

The model is expressed as simultaneous differential

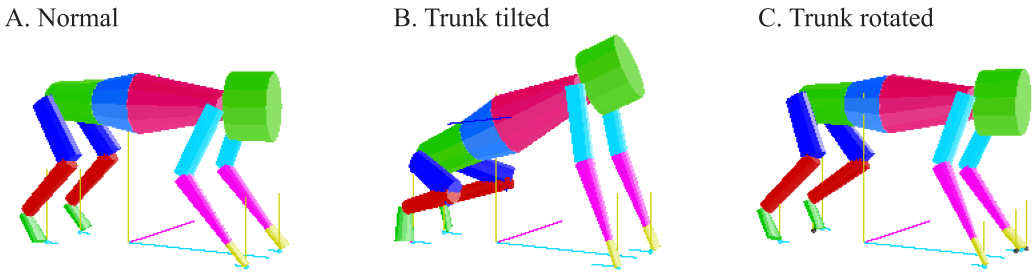

Figure 3. Generated Stationary Postures

equations. They are numerically integrated using the variable time-step Runge-Kutta method with Merson error estimator. It is difficult to estimate a steady states of the entire systems because the touches to the ground at many points. Therefore, the model is initially placed apart from the ground. The initial joint angle are determined according to a measured quadrupedal posture of a Japanese macaque. The initial angular velocities are set to zero. The initial values of **u** are also set to zero.

The neural parameters which define the behavior of the system are arbitrarily chosen as:

$$\mathbf{W} = diag[10,10,10,100,100,100]$$

$$\mathbf{A} = diag[40,40,40], \mathbf{B} = diag[4,4,4]$$

$$\lambda = 50, \kappa = 500, \zeta = 0.4$$

$$\mathbf{K_F} = diag[50,50,50], \mathbf{C_F} = diag[1,1,1]$$

$$\mathbf{K_N} = diag[10,10,10], \mathbf{C_N} = diag[3,3,3]$$

The sensory-motor maps, **J** and **Q**, are assumed to be correctly acquired prior to generation of locomotion by an appropriate learning algorithm. Such assumption is reasonable since both are forward maps and thus uniquely determined.

The neurons in the rhythm pattern generator are connected as in Figure 2, so that the limbs move in diagonal sequence. The parameters, τ, τ', z_{Li}, h_L, and s_0, are set to be 0.125, 1.5, -1.5, 2.5, and 1, respectively.

4. Results

4.1 Generation of stationary postures

When the nervous system is not incorporated, the model collapses on the ground. In order for a quadrupedal animal to sustain its posture, of course, appropriate joint torques has to be generated by the nervous system. Figure 3A shows that the primate model with the proposed neural network can autonomously generate appropriate joint torques and successfully sustain its body.

Furthermore, the model can alter inclination of the trunk segment and its axial rotation without falling down, as illustrated in Figure 3B and C. The model can change its intended posture autonomously by coordinating joint torques, just by altering one signal input from the cortex, ${}^{B}\Theta^{d}$.

It should be noted that the model can stand without any prior knowledge about the environment. Therefore, the same model should be able to stand on uneven terrain.

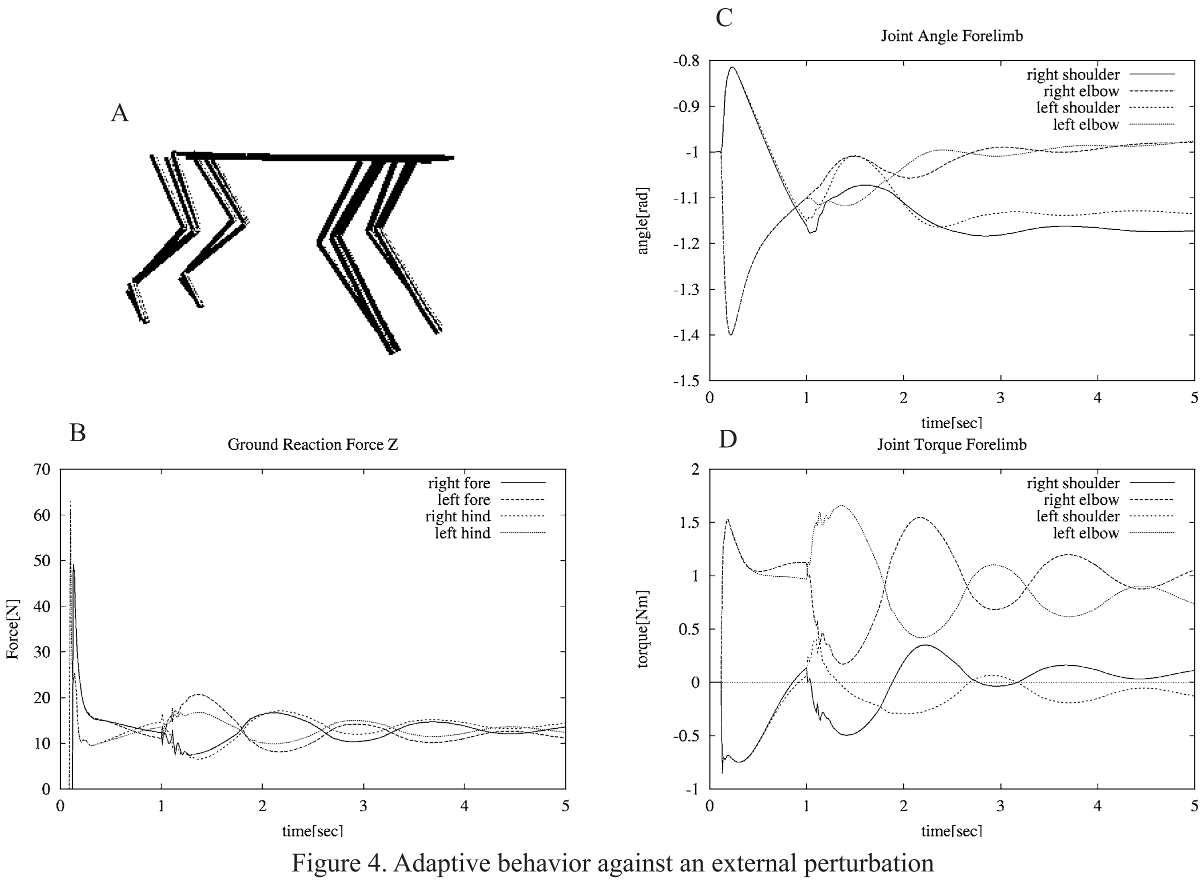

Figure 4. Adaptive behavior against an external perturbation

4.2 Adaptivity to perturbations

To examine the adaptivity of the generated posture, a perturbation is applied (10N in the forward direction plus 10N in the lateral direction for 0.1sec) to the trunk segment. Figure 4 illustrates the stick picture of the adaptive behavior of the model, as well as changes in vertical ground reaction forces, forelimb joint angles, and joint torques over time. The stick diagram is traced every 0.4sec after the perturbation is applied at t=1sec.

Soon after the calculation is started, the impulsive ground reaction forces are applied to the model because it touches to the ground. Then the body is swayed at t=1sec because of the perturbation, but it can spontaneously coordinate its joints motions to balance itself due to the dynamic interaction between the neural and the body systems. The graphs indicate the body oscillates after the perturbation is applied because of the adjustments of viscous coefficients; yet, the body approaches to another steady state autonomously.

4.3 Generation of stepping motion

The rhythm pattern generator starts to produce the rhythmic locomotory signal at t=1sec to generate a stepping motion here. The stick diagram is traced every 0.5sec from t=1 to 5.5sec.

As shown in Figure 5A, presently, it can only generate an awkward stepping motion. Figure 5B illustrates that the ground reaction forces are sequentially generated according to the rhythm pattern generator, but not all four limbs are lifted up from the ground as in usual locomotion. Moreover, the generated motion does not display bilateral symmetry (Figure 5B,C). The model has not succeeded in generating locomotion pattern that is comparable to that of actual Japanese macaque.

However, the model here autonomously reacts to keep its balance while continuously jiggling the body due to the rhythmic signal, indicating that the proposed model has a potential adaptability which the primates possess inherently. In this study, no mechanism is implemented for controlling the swing phase. If proper constraints are imposed for the swing phase in the nervous system as in human walking [17], proper locomotion could probably be generated.

5. Discussions

The calculated results show that the proposed model

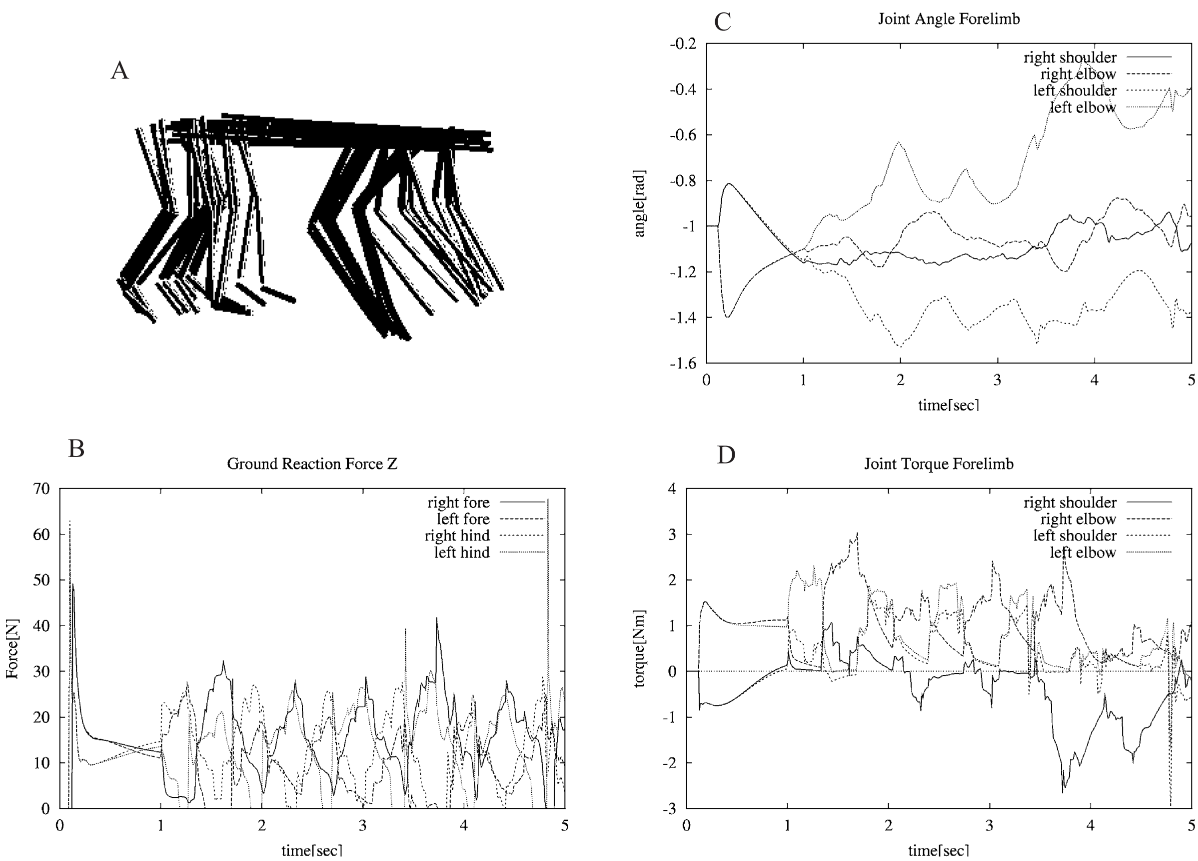

Figure 5. Generated stepping motion

possesses the adaptive feature and can generate infantile awkward locomotion. Here, the joint torques are not preplanned like a humanoid robot [18] at all, but they are spontaneously yielded by the natural behavior of the combined dynamics of the passive body and the neural circuit. The proposed recurrent neural network implicitly implements the adaptive, coordinative dynamics which behaves as if a virtual visco-elastic element is attached between the body and the space [19,20], and integrates postural and locomotory controls based on the ground reaction force. Therefore, the enormous number of joint degree of freedom is spontaneously coordinated to produce appropriate reaction forces, and motions are naturally generated in terms of the body structure.

This dynamical structure also shows robustness to changes in body parameters and noises on the neural activities. Even though the mass of a segment or a parameter defining a joint property is altered, the model can still maintain its posture. Moreover, local reflex mechanism, such as righting reflexes, could be added in this model coordinately, since the proposed neural system can adapt the resultant effect of the added reflex without any modifications.

Although there is no direct evidence showing such proposed neural network actually exists, however, recently, the fastigial nucleus in the cerebellum is found to be a new locomotion inducing site [21,22], indicating that the integration of multimodal sensory information and the rhythmic signals at this level is important for generation of coordinated limb movements. In addition, it is noted that load receptors take very important roles in generation of locomotion [23,24], suggesting that reaction forces may be computed by the activities of the neurons like in the proposed model, and the posture and locomotion is functionally integrated. The framework of the proposed model may thus be biologically feasible and similar representation and integration of the neural information is suggested to be implemented in the actual locomotory nervous system.

6. Concluding Remarks

In this study, we attempt to construct the neuro-musuclo-skeletal model capable of emulating adaptive locomotion of a quadrupedal primate based on the dynamic interaction between the convergent neuro-dynamics and the passive body dynamics. To reify such hypothesized mechanism, we introduce a series of neurons, activity of which represents the ground reaction forces acting on the limbs, and the recurrent neural network is constructed so as to self-organize adaptive nature of primate locomotions.

We believe this kind of synthetic approach is important for elucidating adaptive nature of primate locomotion. It is because physiological study by itself does not illuminate how the actual nervous system functions as a dynamical system. Certainly, advances in physiology and neuroscience have revealed to where each of neurons is connected and how it functions. Newly developed instrumentations also successfully visualize functional localization of activity in the brain in various tasks or functions including human walking [25]. These alone, however, does not indicate how the nervous system controls the timing and magnitude of activity of each of muscles to generate adaptive locomotion in various environments. Whereas, the proposed synthetic approach can qualitatively predict the interactive dynamics of the entire neuro-musculo-skeletal system, so that the underlying hypothesis can be tested. If it becomes possible to integrate experimental research and the computational approach like this study, the modeling of the nervous system becomes more pragmatic and thus comparable to the experimental findings. It may also be possible to establish experimental paradigms based on insights gained through the simulation, as insisted in the systems biology approach [26].

However, this is still not sufficient; what should also be investigated is the body system, its anatomy and the functional morphology, besides the nervous system. The dynamical system where the adaptive nature of locomotion emerges is formed due to the immanent intertwinement of the both nervous system and the body system; the body dynamics becomes a part of the neural dynamics and vise versa. Therefore, the physical characteristics of the body system determined by its anatomy and morphology greatly affects the integrated dynamics. Understanding of inherent reasonability embodied in the body system is thus essential, and should be investigated in future studies.

Acknowledgments

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References

[1] Gebo, D.L. (ed) , 1993, Postcranial Adaptation in Nonhuman Primates. Northern Illinois University Press, DeKalb.
[2] Mochon, S. & McMahon, T.A., 1980, "Ballistic walk-

ing" J Biomech, Vol.13, pp.49-57.
[3] Yamazaki, N., 1990, "The effect of gravity on the interrelationship between body proportions and brachiation in the gibbon" Human Evolution, Vol.5, pp.543-558.
[4] Yamazaki, N., 1992, "Biomechanical interrelationship among body proportions, posture, and bipedal walking" In: Matano, S., Tuttle, R.H., Ishida, H. & Goodman, M. (eds) Topics in Primatology Vol. 3. University of Tokyo Press, Tokyo pp.243-257.
[5] Hopfield, J.J. & Tank, D.W., 1986, "Computing with neural circuits: A model" Science, Vol.233, pp.625-633.
[6] McGeer, T., 1992, "Principles of walking and running" In: Alexander, M. (ed) Mechanics of Animal Locomotion (Advances in Comparative and Environmental Physiology Vol.11). Springer-Verlag, Berlin pp.113-139.
[7] Davy, D.T. & Audu, M.L., 1987, "A dynamic optimization technique for predicting muscle forces in the swing phase of gait" J Biomech, Vol.20, pp.187-201.
[8] Grillner, S., 1975, "Locomotion in vertebrates: central mechanisms and reflex interaction" Physiol Rev, Vol.55, pp.274-304.
[9] Shik, M.L. & Orlovsky, G.N., 1976, "Neurophysiology of locomotor automatism" Physiol Rev, Vol.56, pp.465-501.
[10] Orlovsky, G.N., 1970, "Influence of the cerebellum on the reticulo-spinal neurones during locomotion" Biophysics, Vol.15, pp.928-936.
[11] Mori, S., 1987, "Integration of posture and locomotion in acute decerebrate cats and in awake, freely moving cats" Progress in Neurobiology, Vol.28, pp.161-195.
[12] Armstrong, D.M., Apps, R. & Marple-Horvat, D.E., 1997, "Aspects of cerebellar function in relation to locomotor movements" In: de Zeeuw, C.I., Strata, P. & Voogd, J. (eds) Progress in Brain Research. The Cerebellum: From Structure to Control. Elsevier, Amsterdam pp.401-421.
[13] Ogihara, N. & Yamazaki, N., 2001, "Generation of spontaneous reaching movement based on human anatomical constraints" (in Japanese with English abstract) Transactions of the Japan Society of Mechanical Engineers, Vol.C-67, pp.2314-2320.
[14] Eidelberg, E., Walden, J.G. & Nguyen, L.H., 1981, "Locomotor control in macaque monkeys" Brain, Vol.104, pp.647-663.
[15] Matsuoka, K., 1985, "Sustained oscillations generated by mutually inhibiting neurons with adaptation" Biol Cybern, Vol.52, pp.367-376.
[16] Matsuoka, K., 1987, "Mechanisms of frequency and pattern control in the neural rhythm generators" Biol Cybern, Vol.56, pp.345-353.
[17] Ogihara, N. & Yamazaki, N., 2001, "Generation of human bipedal locomotion by a bio-mimetic neuro-musculo-skeletal model" Biol Cybern, Vol.84, pp.1-11.
[18] Hirai, K., Hirose, M., Haikawa, Y. & Takenaka, T., 1998, "The development of Honda humanoid robot" Proceedings of IEEE International Conference on Robotics and Automations, pp.1321-1326.
[19] Pratt, J., Chew, C.M., Torres, A., Dilworth, P. & Pratt, G., 2001, "Virtual model control: An intuitive approach for bipedal locomotion" Int J Robot Res, Vol.20, pp.129-143.
[20] Sari, K., Nelson, G. & Quinn, R., 2000, "Dynamics and control of a simulated 3-D humanoid biped" Proceedings of the International Symposium on Adaptive Motion of Animals and Machines, Vol.1, pp.ThP-I-2.
[21] Mori, S., Matsui, T., Kuze, B., Asanome, M., Nakajima, K. & Matsuyama, K., 1999, "Stimulation of a restricted region in the midline cerebellar white matter evokes coordinated quadrupedal locomotion in the decerebrate cat" J Neurophysiol, Vol.82, pp.290-300.
[22] Mori, S., Matsui, T., Mori, F., Nakajima, K. & Matsuyama, K., 2000, "Instigation and control of treadmill locomotion in high decerebrate cats by stimulation of the hook bundle of Russell in the cerebellum" Can J Physiol Pharmacol, Vol.78, pp.945-957.
[23] Dietz, V., Muller, R. & Colombo, G., 2002, "Locomotor activity in spinal man: significance of afferent input from joint and load receptors" Brain, Vol.125, pp.2626-2634.
[24] Duysens, J., Van de Crommert, H.W.A.A., Smits-Engelsman, B.C.M. & Van der Helm, F.C.T., 2002, "A walking robot called human: lessons to be learned from neural control of locomotion" J Biomech, Vol.35, pp.447-453.
[25] Miyai, I., Tanabe, C.T., Sase, I., Eda, H., Oda, I., Konishi, I., Tsunazawa, Y., Suzuki, T., Yanagida, T. & Kubota, K., 2001, "Cortical mapping of gait in humans: A Near-Infrared spectroscopic topography study" Neuroimage, Vol.14, pp.1186-1192.
[26] Kitano, H., 2002, "Computational systems biology" Nature, Vol.420, pp.206-210.