An analytical estimation of the energy cost for legged locomotion

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Abstract

Legged locomotion requires the determination of a number of parameters such as stride period, stride length, order of leg movements, leg trajectory, etc. How are these parameters determined? It has been reported that the locomotor patterns of many legged animals exhibit common characteristics, which suggests that there exists a basic strategy for legged locomotion. In this study we derive an equation to estimate the cost of transport for legged locomotion and examine a criterion of the minimization of the transport cost as a candidate of the strategy. The obtained optimal locomotor pattern that minimizes the cost suitably represents many characteristics of the pattern observed in legged animals. This suggests that the locomotor pattern of legged animals is well optimized with regard to the energetic cost. The result also suggests that the existence of specific gait patterns and the phase transition between them could be the result due to optimization; they are induced by the change in the distribution of ground reaction forces for each leg during locomotion.

Key words: legged locomotion, energetic cost of transport, gait transition, optimization

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1 Introduction

Gait transition is a phenomenon generally observed in cats and dogs; it has attracted the attention of many researchers in the biological and engineering fields. However, the reason for the transition has not been clearly explained. The first experimental result that suggested the reason was given by Hoyt and Taylor who measured the oxygen consumption during horse locomotion and reported that horses select a gait that suppresses the cost of locomotion, i.e., the metabolic cost to move a unit distance [1]. Their result is often considered to be an evidence for the hypothesis that gait patterns are optimized in order to suppress energetic cost. However, it does not directly support the hypothesis, instead, raises questions such as (1) Why does walk gait suppresses the metabolic cost at lower speeds and galloping at higher speeds? (2) Why do horses exhibit only a few gait patterns such as walking and trotting? In other words, why do they not exhibit intermediate gait patterns? (3) Is the observed gait really an optimum solution to minimize the metabolic cost?

It has been reported that many legged animals, such as horses, cats, cockroaches, and crabs, exhibit not only the gait transition but also many other common features of locomotor patterns. (1) Stride period, which is the duration of one leg-movement cycle, decreases with locomotion speed and reaches an almost constant value, and swing duration, which is the duration for which a leg is not in contact with the ground, is almost constant or decreases slightly with locomotion speed, thereby decreasing the duty ratio [2–14]. The duty ratio is defined as the ratio of a stance duration to a stride period, and stance duration is the duration for which a foot applies a force to the ground to support the body. The decrease in the duty ratio also implies a decrease in the average number of legs that contact the ground. (2) Stride length, which is the forward distance the body moves within the stride period, and stance length, the forward distance in a stance duration, increase slightly with locomotion speed or remain almost constant [4,8,9,12,15–17]. They begin to increase when the stride period become almost constant [2,12]. (3) The gait pattern tend to not only exhibit a nongraded change and but also be restricted to certain specific patterns such as walking and trotting [1,18]. However, graded transition has also been observed in sheep [19] and insects [20,21]. (4) The metabolic cost per unit time linearly increases with locomotion speed. Hence, the cost of transport, which is the metabolic cost for moving a unit mass by a unit distance, decreases with speed and becomes almost constant in a wide region of locomotion speed [1,3,6,15,22–29].

Despite of significant differences in body size, body structure, and the number of legs, the observation of the above-mentioned characteristics in many legged animals suggests the existence of a basic strategy for selecting the locomotor parameters in legged locomotion, as suggested by Full and Tu [3]. The criterion of the minimization of the transport cost would be one of cogent candidates for this strategy. In order to examine this hypothesis, we have to find the optimal locomotor pattern for minimizing the metabolic cost among all the possible patterns including those that cannot be realized in experimental studies. In this decade several theoretical studies were conducted in order to examine the optimality of the legged locomotor patterns. Minetti and Alexander [30] and Nishii [31,32] demonstrated that many characteristics of the optimal locomotor patterns for minimizing the transport cost which were estimated for the dynamical models of a biped and hexapod, respectively, appropriately predict the characteristics of the actual locomotor parameters such as stride period, stride length, and duty ratio. In these studies, the optimal locomotor patterns were determined by employing the inverse dynamics method, however, no explicit equation to estimate the energetic cost during locomotion was formulated. Therefore, it becomes difficult to explain in detail the cost during locomotion and the relation between cost and locomotor parameters.

In this study, we derive an equation to estimate the cost of transport including the mechanical internal work and heat energy loss due to torque generation and show that the criterion of the minimization of the cost explains many characteristics of legged locomotion.

2 Estimation of the energetic cost of transport

For moving a physical object, an actuator requires an energy cost due to mechanical work. Apart from the mechanical work, actuators also lose energy by generating heat and muscles are not the exception. Conventional studies on the optimal legged locomotor pattern for minimizing the transport cost have considered the mechanical work, however, the cost due to heat generation has rarely been considered [33–35]. In this section, we estimate the energy loss of a leg movement due to mechanical work and heat energy.

2.1 Locomotor parameters

In order to define the gait pattern, we consider the following locomotor parameters: duty ratio β, stride period T, and stance length S. We assume that these parameter have the same values for all legs, the stance length is much shorter than the leg length, and the body moves horizontally with an almost constant speed V. Hence, the parameters satisfy the relation:

$$V = S/\beta T. \tag{1}$$

Therefore, there exists two degrees of freedom for selecting the locomotor parameters, β, S, and T.

2.2 *Definition of foot trajectory*

The relative velocity $\dot{x}_i$ of i-th foot to the body during the stance phase is given by $\dot{x}_i = -V$, and the relative foot velocity during the swing phase is assumed to be sinusoidal, i.e.,

$$\dot{x}_i(t) = a - b\cos\frac{2\pi}{T^{sw}}t, \ (0 \leq t < T^{sw}) \tag{2}$$

$$a = \frac{\beta V}{1-\beta}, \quad b = \frac{V}{1-\beta}, \tag{3}$$

where $T^{sw} = (1-\beta)T$ represents the swing duration and $t = 0$ is the time at which the swing phase begins. The position and acceleration of a foot required for analysis in later sections are obtained by the integration and differentiation of the above equation. The subscript i is omitted in the following equations when there is no difference between each leg.

2.3 *Mechanical work for leg movement*

——————— Insert Figure 1 here ———————-

Although the legs of legged animals are composed of multiple links with multiple joints, we consider a leg as a simple one-link system with one joint in order to estimate the mechanical work required to move a leg (Fig. 1). We also ignore the effect of gravity on leg movement. The inertia moment of the body is considered to be sufficiently large such that pitching movements of the body can be ignored. Negative mechanical work is ignored in the estimation of the energy cost, because muscles consume positive energy even while performing negative work but the energy loss for negative work is considerably smaller than that for positive work with the same absolute value [36]. Therefore, the energy cost due to mechanical work W to move a leg within a stride period is given by

$$W = \int_T f(\tau\dot{\theta})dt, \tag{4}$$

where τ and $\dot{\theta} \simeq \dot{x}(t)/l$ represent the joint torque and angular velocity of a leg, respectively, l represents the length of a leg, and $f(x) = x$ for $x \geq 0$ and $f(x) = 0$ for $x < 0$.

By denoting the inertia moment of the leg around its joint by I, the required joint torque during the swing phase τ^{sw} can be expressed as

$$\tau^{sw}(t) = I\ddot{\theta}(t) \simeq I\ddot{x}(t)/l. \tag{5}$$

Equations (2) and (5) determine the mechanical work during the swing phase W^{sw} as follows (see appendix A for details):

$$W^{sw} = \int_{T^{sw}} f(\tau^{sw}\dot{\theta})dt \simeq I\left(\frac{V}{l}\right)^2 \frac{1+\beta^2}{(1-\beta)^2}. \tag{6}$$

This equation corresponds to work that supplies kinetic energies for the maximum angular velocities during the swing phase $(1+\beta)/(1-\beta) \cdot V/l$ and the stance phase V/l. The mechanical power, which is the work in a unit time, is obtained by dividing the above equation by the stride period, and takes the same form as that of power estimated by Minetti [37] except a constant coefficient.

During the stance phase, the angular velocity of a leg is $\dot{\theta} \simeq -V/l$, and the joint torque τ^{st} is given by

$$\tau^{st}(t) = -N(t)x(t), \tag{7}$$

where $N(t)$ is the vertical component of the ground reaction force for a leg, and the horizontal component is zero because we assume a constant locomotion speed. Therefore, the mechanical work during the stance phase W^{st} can be expressed as

$$W^{st} \simeq \int_{T^{st}} f(N(t)x(t)) \cdot \frac{V}{l} dt, \tag{8}$$

where $T^{st} = \beta T$ is the duration of the stance phase. From eq. (6) and (8), we obtain the total mechanical work in a stride period:

$$\begin{aligned} W &= W^{sw} + W^{st} \\ &\simeq I \left(\frac{V}{l}\right)^2 \frac{1+\beta^2}{(1-\beta)^2} + \int_{T^{st}} f(N(t)x(t)) \cdot \frac{V}{l} dt. \end{aligned} \tag{9}$$

2.4 Heat energy loss due to force generation

Muscles consume energy during force generation even if no mechanical work is being performed such as in isometric contractions, and the consumed energy is lost in the form of heat energy. The metabolic cost during muscle contraction has been studied by many researchers from the dates of Hill [38], however, data in these studies were obtained from the activities of a specific muscle fiber due to tetanic stimulation. During locomotion, different types and numbers of muscle fibers are activated depending on the force required at each moment. For example, it is reported that few fast muscle fibers that require high metabolic cost are activated for slow locomotion, however, the number of fast muscles recruited increases in fast locomotion [39]. Therefore, it is possible that the energy cost estimated by using data taken from the specific muscle fibers might be inappropriate to estimate the metabolic cost during locomotion. In order to estimate the total energy cost from the data on the specific muscle fibers, we require data that shows which muscle fibers are activated and their number at each moment during locomotion, However, it is a difficult task to obtain such data that can show the detailed muscle activities during locomotion. Based on these considerations, we estimate the cost for force generation by using a relatively simple equation and consider the essential property of energy cost to trigger a gait transition and the other common characteristics of legged locomotion.

Hatze and Buys (1977) analyzed the combined activity of different types of muscle fibers, i.e., slow muscles, fast muscles, and intermediate muscles, by using a mathematical model and suggested that the total heat energy loss H would increase nonlinearly with the total muscle force f during the isometric contractions. This result corresponds to the fact that the ratio of the activated fast muscle fibers that require high cost increases with the force required during locomotion, as stated above. Hence, we assume that the heat energy loss H is proportional to the k-th power ($k > 1$) of the generated joint torque τ, and assess the suitability of our assumption for explaining the characteristics of legged locomotor patterns.

The heat energy loss during the swing phase H^{sw} is caused by the torque required to swing a leg (eq. (5)) and given by

$$H^{sw} = \gamma \int_{T^{sw}} |\tau^{sw}(t)|^k dt \simeq \gamma \left(I/l\right)^k \int_{T^{sw}} |\ddot{x}_i(t)|^k dt, \tag{10}$$

where γ is a constant that indicates the ratio of heat energy loss to mechanical work. The heat energy loss during the stance phase H^{st} is estimated as

$$\begin{aligned} H^{st} =& \gamma \int_{T^{st}} (|\tau^{st}(t)|^k + |\alpha N(t)|^k) dt \\ =& \gamma \int_{T^{st}} |N(t)|^k (|x(t))|^k + \alpha^k) dt. \end{aligned} \tag{11}$$

The first term indicates the cost required for the generation of rotational torque to move a leg against the ground reaction force. Since the legs of most insects extend radially from their body, a steady joint torque is required to maintain a posture. Most mammals also require a steady joint torque to maintain a bent leg posture below their bodies. The second term represents the heat energy loss due to such steady joint torque, and $\alpha > 0$ is a constant value that represents the amplitude of the torque.

When a stationary body is supported by n legs and the body weight M is distributed equally on each leg, i.e., the ground reaction force for each supporting leg is given by $N = M/n$, the total heat energy loss for all the legs is proportional to $n(M/n)^k$. The assumption $k > 1$ implies that distributing body weight at many legs reduces the heat energy loss for supporting the body, because $n(M/n)^k < m(M/m)^k$ holds true for $n > m$. On the other hand, when $k < 1$, the heat energy loss is lower when the entire body weight is supported by a single leg.

From eq. (10) and (11) we obtain the total heat energy loss:

$$\begin{aligned} H &= H^{sw} + H^{st} \\ &= \gamma \left\{ \int_{T^{sw}} |\tau^{sw}(t)|^k dt + \int_{T^{st}} \left\{ |N(t)|^k (\alpha^k + |x(t)|^k) \right\} dt \right\}. \end{aligned} \tag{12}$$

2.5 Cost of transport

We further analyze the total energy loss given by eq. (9) and (12) with the assumption that the ground reaction force N is equal to the body weight W divided by the average number of stance legs $n\beta$, i.e., $N = M/n\beta$, where n is the number of legs. Under this assumption, the mechanical work during the stance phase W^{st}, which is given by eq. (8), is transformed into

$$W^{st} = \frac{M}{8nl}\frac{S^2}{\beta}, \tag{13}$$

which is equal to the mechanical work required to elevate the body accompanied by a leg movement.

When the heat energy loss is proportional to the square of the generated torque, i.e., $k = 2$, the heat energy losses, H^{sw} in eq. (10) and H^{st} in eq. (11), becomes

$$H^{sw} = \gamma \frac{2\pi^2 I^2}{l^2} \frac{\beta V^3}{(1-\beta)^3 S}, \tag{14}$$

$$H^{st} = \gamma \left(\frac{M}{n}\right)^2 \frac{T}{\beta} \left(\alpha^2 + \frac{S^2}{12}\right). \tag{15}$$

The cost of transport e, which is the energetic cost for moving a unit weight by a unit distance, is given by

$$e = \frac{\sum_{i=1}^{n} (W_i + H_i)}{MVT}. \tag{16}$$

From eq. (6), (13), (14), and (15) we obtain the transport cost as follows:

$$
\begin{aligned}
e(V,\beta,S) &= e_w^{sw} + e_w^{st} + e_h^{sw} + e_h^{st},\\
e_w^{sw} &\equiv \frac{\sum_{i=1}^{n} W_i^{sw}}{MVT} = \frac{nI}{l^2M}\frac{\beta V^2}{S}\frac{1+\beta^2}{(1-\beta)^2},\\
e_w^{st} &\equiv \frac{\sum_{i=1}^{n} W_i^{st}}{MVT} = \frac{1}{8l}S,\\
e_h^{sw} &\equiv \frac{\sum_{i=1}^{n} H_i^{sw}}{MVT} = \gamma\frac{2n\pi^2 I^2}{l^2M}\frac{V^3\beta^2}{(1-\beta)^3S^2},\\
e_h^{st} &\equiv \frac{\sum_{i=1}^{n} H_i^{st}}{MVT} = \gamma\frac{M}{n}\frac{1}{\beta V}(\alpha^2+\frac{S^2}{12}),
\end{aligned}
\tag{17}
$$

where e_w^{sw} and e_w^{st} are the transport costs due to mechanical work and e_h^{sw} and e_h^{st} are the costs due to heat energy loss during the swing and stance phases, respectively.

Equation (17) indicates that a larger duty ratio β suppress the heat energy loss during the stance phase e_h^{st} because the torque required to support the body weight is distributed on many legs. However, this leads to large values of the costs, e_h^{sw} and e_w^{sw}, to move a leg in a shorter duration of the swing phase. During the swing phase, the stance length S does not affect the mechanical work W^{sw} (eq. (6)), and a larger stance length results in lesser heat energy loss H^{sw} (eq. (14)) and a smaller step number to move a unit distance, which results in lower values of e_w^{sw} and e_h^{sw} for moving a unit distance during the swing phase. However, a larger stance length requires greater leaning of a leg during the stance phase, which requires a larger rotational torque against the body weight. This results in a larger energy loss during the stance phase, e_w^{st} and e_h^{st}. Therefore, the optimal stance length S and the optimal duty ratio β are determined by balancing the costs due to the torque against the body weight during the stance phase and the torque required to move a leg during the swing phase.

At lower speeds, the heat energy loss e_h^{st} during stance phase dominates in the total energy cost in order to support the body, therefore, a larger duty ratio β and smaller stance length S are required to suppress the cost. On the other hand, at higher speeds, the costs e_w^{sw} and e_h^{sw} during the swing phase become dominant in order to swing the legs, as suggested by Delcomyn and Usherwood [20]. Hence a smaller duty ratio β and larger stance length S are required to suppress the costs. Based on these considerations, it is expected that as the locomotion speed increases, the duty ratio decreases, i.e., the number of stance legs decreases, while the stance length increases, as observed in legged locomotion. However, at medium speeds, the increase in the stance length might be suppressed by mechanical work during the stance phase e_w^{st}.

When the heat energy loss is assumed to be in direct proportion to the generated force, i.e., $k = 1$, the transport cost due to heat emission becomes

$$\begin{aligned} e_h^{sw} &= \gamma \frac{4nI}{lM} \frac{\beta V}{S(1-\beta)}, \\ e_h^{st} &= \gamma \frac{1}{V} (\alpha + \frac{S}{4}). \end{aligned}$$

In this case, the total cost of transport given by the above equation, and e_w^{sw} and e_w^{st} in eq. (17) increase monotonously with the duty ratio β for all speeds. Therefore, the smallest duty ratio always yields the minimum cost, which fails to explain the observed gait transition in legged animals.

These results suggest that the gait transition occurs when a larger number of stance legs suppress the total cost to support the body. Hence, a nonlinear increase in the heat energy loss, i.e., $k > 1$ or $\frac{\partial H}{\partial \tau} > 1$, can explain the change in the duty ratio, as observed in legged animals. From these considerations, we assume $k = 2$ and obtain the optimal locomotor pattern for minimizing the cost eq. (17) in the next section.

3 Optimal locomotor pattern

3.1 Optimal locomotor pattern with identical legs

——————————— Insert Figure 2 here ——————————-

——————————— Insert Figure 3 here ——————————-

——————————— Insert Figure 4 here ——————————-

——————————— Insert Figure 5 here ——————————-

The optimal locomotor parameters for minimizing the cost of transport given by the eq. (17) were obtained for different locomotion speeds. The number of legs are set at $n = 6$, body parameters are described in appendix B, and duty ratio is assumed to be greater than 0.5 ($\beta \geq 0.5$), which is the minimum value to enable static locomotion in hexapods. These assumptions affect only the quantitative features in the results obtained in this section. This is because the characteristics of all legs are identical and the body structure does not affect the estimation of the transport cost given by eq. (17) except the quantitative characteristics resulting from body weight W and number of legs n. Therefore, the results would exhibit the essential characteristics of low-cost legged locomotor patterns.

Figure 2, 3, and 4 show the relation between the optimal parameters and the locomotion speed. Figure 2 shows that the optimal duty ratio β decreases with speed as predicted in section 2.5, i.e., the optimal number of stance legs decreases with speed. Figure 3 shows that the optimal stride length $VT(= S/\beta)$ increases gradually with locomotor speed, while the stance length S is almost constant at lower speeds ($v < 0.21$ [m/s]). These parameters increase when the duty ratio reaches its minimum value ($v > 0.21$ [m/s]). Figure 4 shows that the optimal stride period T decreases with speed and reaches an almost constant value when the duty ratio attains its minimum value, while no change is observed in the swing duration $T^{sw} = (1 - \beta)T$. Figure 5 shows the energetic cost per unit time calculated using the optimal parameters for each speed and indicates that the energetic cost increases linearly with speed.

——————— Insert Figure 6 here ———————-

——————— Insert Figure 7 here ———————-

——————— Insert Figure 8 here ———————-

Figure 6 shows the cost of transport and indicates that the heat energy loss that occurs while supporting the body is dominant at lower speeds, however, the mechanical work required to swing a leg becomes dominant as the locomotion speed increases. By balancing these two costs, we can obtain a speed range that yields a low value of the total cost of transport. If the available locomotor parameters are restricted, this region becomes narrower, as shown in Fig. 7 which shows the transport cost given by specific typical duty values. However, most legged animals widen this range by selecting the optimal parameters and utilize this speed range for normal locomotion (Fig. 8). This could be the reason behind the metabolic cost of transport of legged animals remaining almost constant for a wide range of locomotion speeds and that gait transition is observed at usual locomotion speeds.

These characteristics of the optimal locomotor parameters that minimize the transport cost are in good agreement with those of observed legged patterns mentioned in the introduction.

3.2 From graded to non-graded gait transition

For the optimal locomotor pattern calculations in the previous section, the ground reaction force $N = M/n\beta$ for each stance leg was set as a time-independent constant value. However, in practice, this force changes depending on the changes in the number of stance legs and posture due to leg movement. We again calculated the optimal locomotor parameters from eq. (9), (12), and (16) by considering a more practical distribution of the ground reaction forces.

In this case, the number of legs is set at $n = 6$ again, and the order of leg movement is determined according to the rule observed in insects [13]: (1) antiphase movement of contralateral legs, and (2) forward propagation of leg movements in ipsilateral legs by the same time delay given by the swing duration T^{sw}. Based on this rule, the gait pattern is defined for an arbitrary duty ratio and stride period. The ground reaction force for each stance leg is determined as follows: (1) the body weight divided by the number of stance legs, i.e., $N_i = M/n^{st}(t)$, where $n^{st}(t)$ is the number of stance legs, and (2) computed by using pseudoinverse matrix by considering the balance of forces around a body at each moment by assuming that vertical movement of the base of a leg due to leg movement is sufficiently small and the body is a rigid plate, which results in a minimum variance of the ground reaction forces. The body parameters are shown in appendix B. In the first case no lower limit of the duty ratio is assumed, however, in the second case, the duty ratio is assumed to be greater than 0.5 ($\beta \geq 0.5$) so as to prevent the negative ground reaction forces.

——————— Insert Figure 9 here ———————-

In Fig. 9, the pluses and circles indicate the optimal duty ratios when the ground reaction forces are given by $N_i = M/n^{st}(t)$ and computed by using the pseudoinverse matrix, respectively. In both cases, the optimal duty ratio decreases with overall speed but does not change monotonously and assumes some specific values, e.g., $\beta = 10/12, 8/12, 6/12, 4/12$ in pluses and $\beta = 9/12, 8/12$ in circles. Among these values, all except $\beta = 4/12$ correspond to the typical gait patterns observed in insects, as reported by Wilson (1966), e.g., wave gait ($\beta \sim 10/12$), quadruped gait ($\beta \sim 8/12$), and tripod gait ($\beta \sim 6/12$). The transitions between gaits indicate not only a graded transition but also a discrete transition around $v = 0.03$ [m/s] in circles and around $v = 0.28$ [m/s] in pluses. These characteristics were not observed in Fig. 2 in which the ground reaction forces are set equally as time-independent value $N_i = M/n\beta$.

These results suggest that the emergence of specific gait patterns and discrete gait transition is due to the optimization of the transport cost. The change in the number of stance legs at each moment, which affects the body balance and the distribution of ground reaction forces on stance legs, might be a crucial to trigger cause such nongraded gait transition, as suggested by Nishii (2000).

The emergence of a different set of stable duty ratios for a different distribution of the ground reaction forces suggests that the body structure for determining the body balance would yield a different optimal set of gait patterns. This might explain the observations that different species and different birth stages of some insects exhibit different sets of gait patterns [13,41].

4 Discussion

We derived an equation to estimate the cost of transport in legged locomotion and obtained the optimal locomotor pattern for minimizing this cost. The heat energy loss due to force produced was considered to take a simple form, however, the characteristics of the optimal values of the duty ratio, stance and stride lengths, stride period, swing duration, and transport cost were in good agreement with those of observed locomotor patterns. Although we treated a leg as a simple one-link system to estimate the mechanical work, the characteristics of the obtained locomotor pattern for minimizing the estimated cost are also in good agreement with those obtained by computations using inverse dynamics method on a six legged dynamical model with two-link legs [31,32]. These results suggest that eq. (17) might not be accurate, however, it would effectively account for energetic costs to qualitatively explain the gait transition during locomotion. Moreover, the locomotor pattern of legged animals would be optimized suitably with regard to the cost of transport.

In the analysis of the optimal locomotor pattern in section 3, the heat energy loss H is assumed to be the square of the generated torque τ. It has also been reported that other types of nonlinear increases, such as $H = \tau^{\alpha}$, $\alpha = 1.5$ and 3.0, also predict the characteristics of the legged locomotor pattern [32]. These results suggest that a nonlinear increase in the heat energy loss against the generated force, $\dfrac{\partial H}{\partial \tau} > 1$, would play a critical role in many characteristics of legged locomotion. This is because such property of heat loss shows the characteristics opposite to that of the work required to move a leg at slow locomotion speeds as shown in section 2.5. In other words, if we obtain the Taylor expansion of the heat energy loss in muscles using the term of generated force, the second and higher order terms would be essential terms to explain many characteristics of legged locomotion. Such nonlinear property of heat energy loss in muscles is supported by the fact that the number of recruited fast muscle fibers increases in faster locomotion, as discussed in section 2.4.

In our analysis, the effects of elastic components in the musculo-skeletal system and the pendulum effect of the leg were neglected. These factors would contribute to a decrease in the transport cost by saving the kinetic energy required to move a leg as elastic energy or potential energy. We also ignored some other factors that could affect the cost, such as the energy loss due to friction, and the acceleration and deceleration of the center of body mass in a stride period. Even by considering these factors, energy required for the actuators to swing a leg and to support the body is inevitable. Therefore, the scenario that gait transition occurs due to the change in the balance of costs for swinging the leg and supporting the body would also hold true.

Our result of this paper indicates that the existence of specific gait patterns and phase transition could be a result of the optimization of the energetic cost. In order to realize the optimum locomotor pattern, a neural system must be well organized for determining and producing the optimal motor command. How does a neural circuit compute the motor command? What triggers the neural system to produce a gait transition? Are the observed gait patterns that are realized by a neural system strictly optimized based on the energetic cost for all locomotor speeds?

A famous experiment using a mescencephalic cat by Shik et al. [42] and the other several studies [43,44] reported that the central pattern generator (CPG) in the spinal cord has the ability to generate a periodic signal to produce the basic locomotor pattern and the gait transition is induced by an increase in a burst signal from a higher center such as the brainstem and the midbrain to the CPG and sensory feedback signals to the CPG. These results suggest that the basic locomotor patterns are programmed in the CPG, and the trigger for the gait transition might be induced by a simple signal such as a burst signal from a higher center or a signal from proprioceptors in the musculo-skeletal system.

Farley and Taylor (1997) reported that the gait transition observed in horses occurs at a speed that is not energetically optimal, and it appears to be induced by a critical value of muscle forces. There could be two possible reasons behind this result. The first possibility is that the gait transition might be triggered by a critical force to avoid overloading of the musculo-skeletal system, as suggested by Farley and Taylor. In other words, horses might choose a gait pattern under two constraints: minimization of cost of transport and avoiding any risk to the physical-system. The second possibility is that the gait transition is simply programmed as the function of a stimulus from the force sensor in the musculo-skeletal system, which would require a simpler neural mechanism than to compute the optimal locomotor pattern for minimizing the energetic cost as a function of several input signals at all times. This implies that horses might choose a strategy to simplify the neural circuit rather than to minimize the transport cost around gait transition speeds. During usual locomotion, horses select energetically optimal locomotion speeds for each gait and do not exhibit a steady locomotion around the gait transition speed [1]. This indicates that the optimization of the gait pattern around these speeds might not be important for horses.

In summary, the criterion of the minimization of the cost of transport appears to determine the characteristics of overall locomotor pattern for many legged animals. However, as mentioned in the case of horses, other criteria should also be considered to explain the detailed features of a gait transition for some classes of animals. Further investigation is required for this criterion to understand not only the strategy of animal locomotion but also the design of neural systems for legged locomotion.

A Estimation of mechanical work during the swing phase

The mechanical work during the swing phase W^{sw} is obtained by using eq.(2) and (5) , i.e.,

$$\begin{aligned} W^{sw} &= \int_0^{T^{sw}} f(\tau\dot{\theta})dt \\ &= -\int_0^{t_0} \tau\dot{\theta}dt + \int_{t_0}^{\frac{T^{sw}}{2}} \tau\dot{\theta}dt \\ &= Ib\omega\left\{\frac{b}{2\omega} - 2\left(-\frac{a}{\omega}\cos\omega t_0 + \frac{b}{4\omega}\cos 2\omega t_0\right)\right\}, \end{aligned} \tag{A.1}$$

where t_0 is the time when $\dot{\theta} = 0$, i.e., $a - b\cos\omega t_0 = 0$. Thus, we obtain

$$W^{sw} = I(a^2 + b^2).$$

By substituting eq.(3) into the above equation, we get

$$W^{sw} = I\left(\frac{V}{l}\right)^2 \frac{1+\beta^2}{(1-\beta)^2}. \tag{A.2}$$

B Body parameters

In the computations in this study, we used the following parameters: the total body mass $m_b = 3$ [g], the length of the body $L = 5$ [cm], the leg mass $m_l = 0.2$ [g], the leg length $l = 1$ [cm], and constants $a = 1$ and $\gamma = 10$. The legs are situated in the front, the middle, and the back of the body.

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List of Figures

8 Schematic representation of cost of transport. The heat energy loss to support the body is dominant at lower speeds and mechanical work is dominant at higher speeds. The balance of these costs results in low total cost of transport in a speed range. The selection of the optimal parameters would contribute to widen this low-cost region. 31

9 Optimal duty ratio. The pluses and circles show the optimal duty ratios when the ground reaction forces are calculated from body weight divided by the number of stance legs and computed by considering the balance of forces around the body, respectively. 32

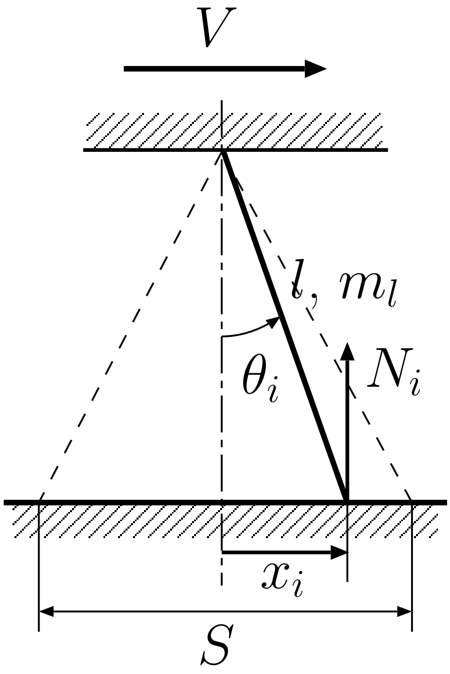


Fig. 1. A simple leg model. Although the leg of most legged animals is a multiple link system with multiple joints, we consider it as a simple one-link system to estimate the mechanical work.

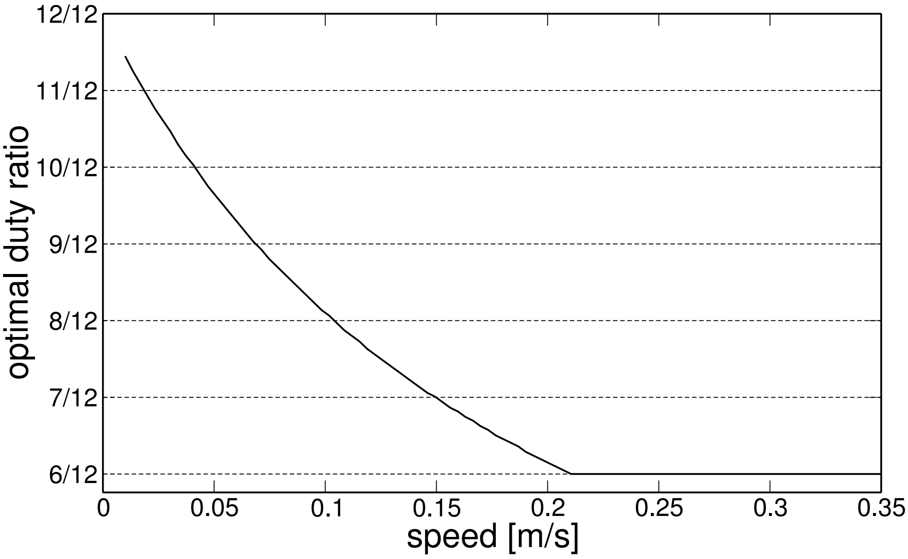


Fig. 2. Optimal duty ratio that yields minimum cost of transport.

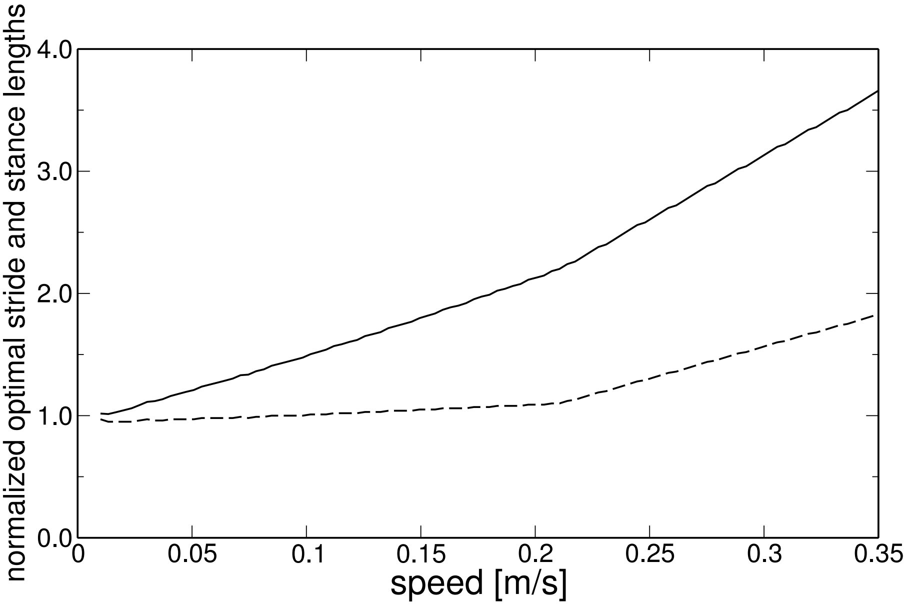


Fig. 3. Optimal values for a stride length (solid line) and stance length (dashed line). These values are normalized by the leg length.

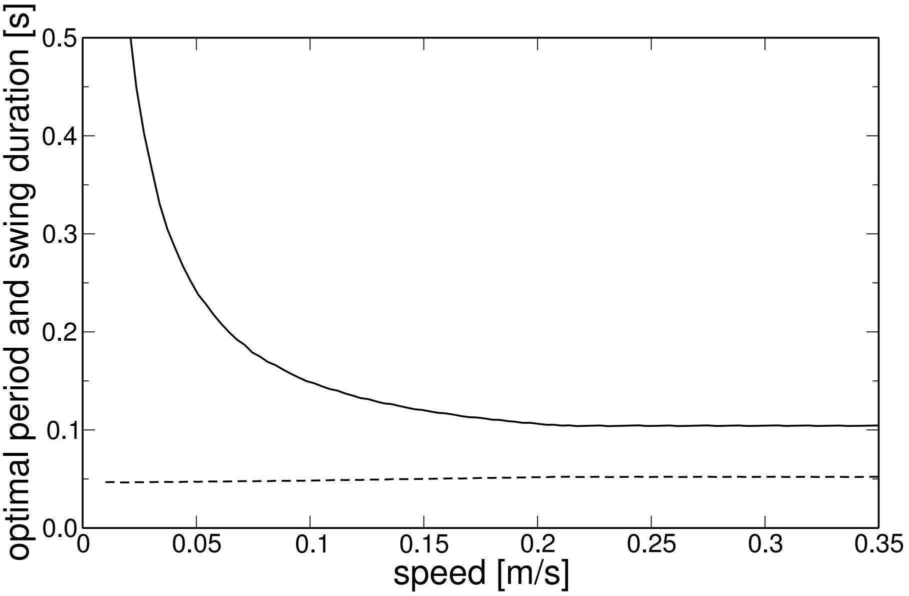


Fig. 4. Optimal stride period (solid line) and duration of swing phase (dashed line).

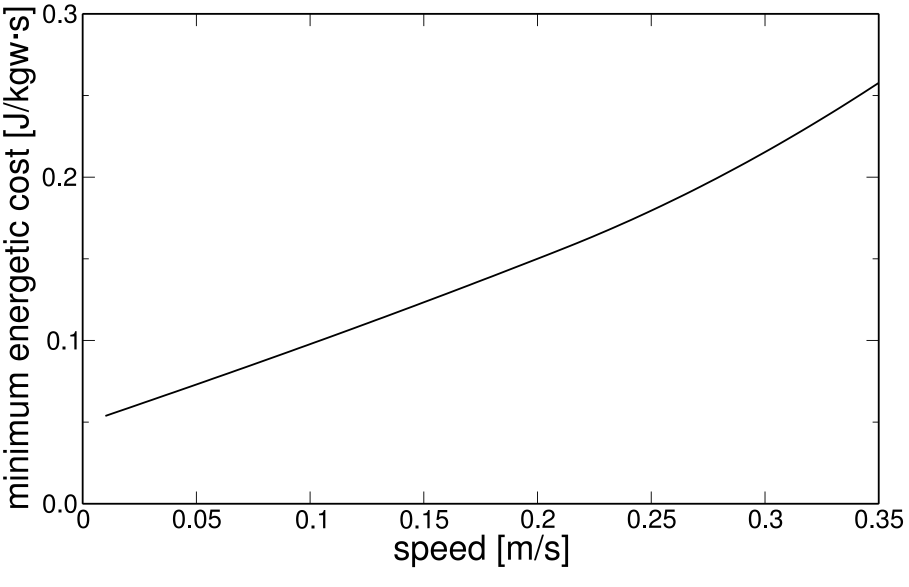


Fig. 5. Minimum energetic cost per unit time obtained from the optimal parameters.

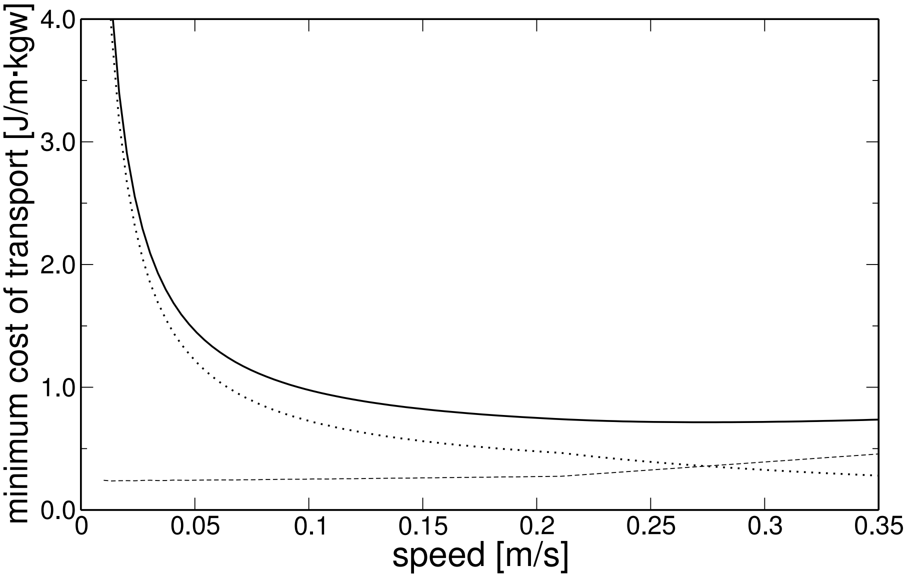


Fig. 6. Minimum cost of transport obtained from the optimal parameters at each locomotion speed. The solid line represents the total cost of transport, dotted line represents the cost due to heat energy loss, and dashed line represents the cost due to mechanical work.

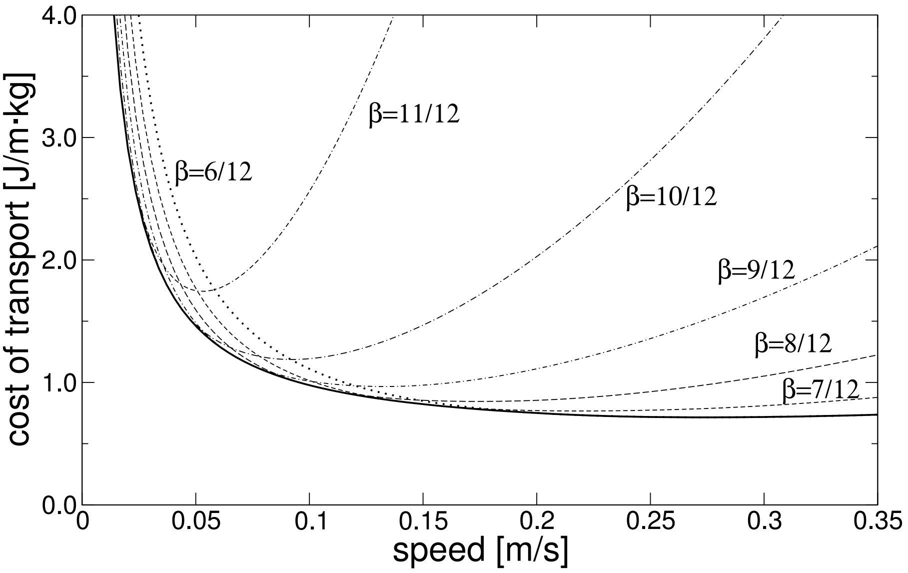


Fig. 7. The cost of transport obtained from typical duty values. The stance length is selected so as to minimize the cost of transport for each duty value and each locomotion speed. The thick solid line that shows the convex line given by the optimal parameters at each locomotion speeds is the same as the solid one in Fig. 6.

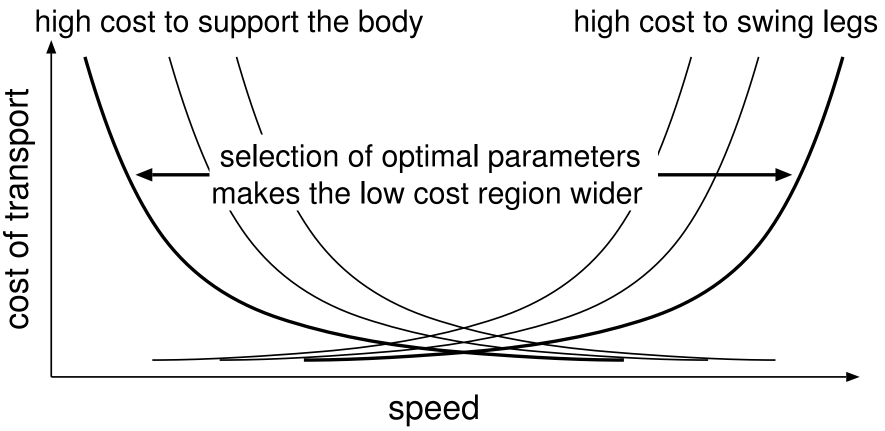
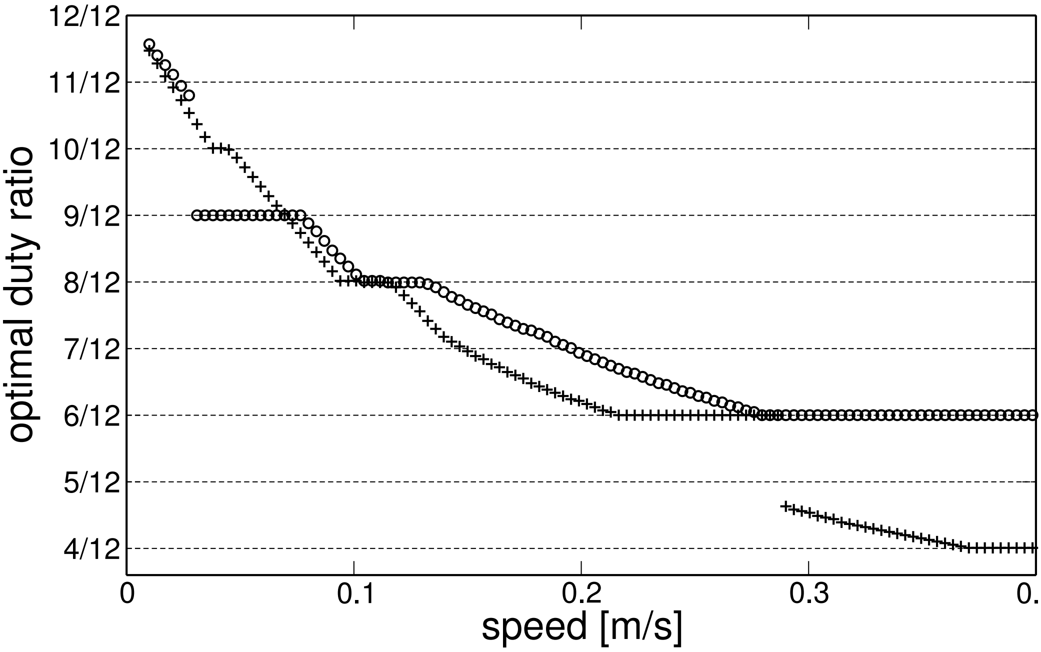


Fig. 8. Schematic representation of cost of transport. The heat energy loss to support the body is dominant at lower speeds and mechanical work is dominant at higher speeds. The balance of these costs results in low total cost of transport in a speed range. The selection of the optimal parameters would contribute to widen this low-cost region.



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