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PHYSIOLOGY

Mathematical Model of the Evolution of Locomotion in Tetrapods

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During the locomotion of Monotremata and lower tetrapods, their limbs are spread apart, so that the stylopodias (femur and shoulder) move in an almost horizontal plane. Retraction of the stylopodias in the phase of support is observed in all species of these tetrapods [1–4, 6, 7, 9]. Only representatives of the family Tachyglossidae of the order Monotremata are characterized by an absence of limb retraction [5, 8]. Therefore, we divided the locomotion patterns into two groups: retraction (the shoulder moves backward about the vertical axis) and pronation (the shoulder turns around the horizontal axis). These groups were given their names based on the main locomotor movement of the shoulder during the stage of support. The main features of morphological and kinematic difference between these locomotion patterns are summarized in Table 1.

The locomotion efficiency depends on minimization of energy expenditures for increasing the step length and for preventing the animal body from falling down. However, the characteristic features of the locomotor apparatus in evolutionary ancestors of modern animals may also have a significant effect on the locomotion pattern in the latter. For example, the shoulder bone of primitive tetrapods was very short. Therefore, both shoulder retraction and shoulder joint protraction were equally suitable for locomotion of these animals. It was also reported [4–6, 8] that, in animals adapted to the two locomotion patterns, the angle of the shoulder joint pronation in the support stage was about 60°. To perform pronation in the support stage, the shoulder joint at the stage of transfer should supinate. The main shoulder joint supinators in Monotremata are m. supraspinatus and m. infraspinatus. The two muscles prevent the stylopodias from being retracted or protracted. The other tetrapods are devoid of such mechanism.

Let us construct a model intended to determine which structural and kinematic features of the locomotor apparatus determine the step length. For the sake of simplicity, let the stylopodia move in a horizontal plane and step kinematics be symmetrical about the middle point of the phase of support. In this case, the step length (body displacement relative to the point of support) is uniquely determined by the following factors: the stylopodia and zeigopodia lengths, size of body bends (undulation), retraction of the stylopodia, shoulder joint pronation, flexion and extension, as well as adduction and abduction in the elbow joint. In the case of extension, it is suggested that, if the palm is under the elbow joint or abducted outwards or inwards, it assumes zero, positive, or negative value, respectively.[1]

Parameters known from the literature for each locomotion pattern were used for primary analysis. Substitution of the parameters of one of the locomotion patterns into parameters of another locomotion pattern (Table 2) enabled us to analyze the appearance of specific kinematic and morphological features of each locomotion pattern.

To determine the effects of changes in elbow joint extension and body undulation on the step length, four different variants of relationships between these factors were analyzed (Table 2). The following cases were considered: a normal ratio between all factors corresponding to each locomotion pattern (Table 2, rows 2, 4, 5, 7) and hypothetical ratios between limb segments adapted to the pronation locomotion pattern (as in animals with retraction locomotion) or to the retraction locomotion pattern (as in animals with pronation locomotion) (Table 2, rows 1, 3, 6, 8). An increase in the elbow joint extension is accompanied by an increase in the step length (Fig. 1a). The increase in the elbow joint extension causes a particularly large increase in the step length in the case of retraction locomotion (compare curves *2* and *4* in Fig. 1). Although extension is advantageous in terms of step length increase, it is insignificant or negative in the case of retraction [4, 6] or prona-

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[1] Let us introduce the following notation: *St*, stylopodia; *Ze*, zeigopodia; *u*, angle of body undulation; *r*, angle of shoulder retraction; *p*, angle of shoulder pronation; *a*, angle of forearm abduction; and *e*, angle of elbow extension. Then, the step length (*L*) can be calculated by the following equation:

$$L = 2\sqrt{(St + Ze\ \sin e)^2 + (Ze\ \cos e\ \sin(p+a))^2} \times \sin\left(u + r + \arctan\left(\frac{Ze\ \cos e\ \sin(p+a)}{St + Ze\ \sin e}\right)\right).$$

Table 1. Specific features of the morphology and movement mechanisms typical of the two locomotion patterns

Object and spatial position	Percentage ratio of length to the sum of lengths	
	retraction	pronation
Stylopodia	60	40
Zeigopodia	40	60
Effect of body undulation increase	Negative	Positive
Long stage of lateral support in cycle	Absent	Necessary
Stylopodia retraction	60°–100°	Less than 7°
Elbow joint extension	Positive	Negative
Back hunching at the stage of support	Absent	Necessary
Obstacles to shoulder retraction	No	Yes

Table 2. Different combinations of factors affecting the step length and shown in Fig. 1: (A) stylopodia and (B) zeigopodia at the sum of their lengths equal to one

Curve no.	A	B	Angle, degrees			
			retraction	pronation	undulation	extension
1	0.4	0.6	80	60	60	–20, –10, 0, 10, 20
*2***	0.6	0.4	80	60	60	–20, –10, 0, 10, 20
3	0.6	0.4	0	100*	60	–20, –10, 0, 10, 20
*4***	0.4	0.6	0	100*	60	–20, –10, 0, 10, 20
*5***	0.6	0.4	80	60	0, 20, 40, 60, 80	0
6	0.4	0.6	80	60	0, 20, 40, 60, 80	0
*7***	0.4	0.6	0	100*	0, 20, 40, 60, 80	0
8	0.6	0.4	0	100*	0, 20, 40, 60, 80	0

* Pronation in the shoulder joint + abduction in the elbow joint.

** Normal ratio between segment sizes and angles for each locomotion pattern.

tion [5, 8] locomotion, respectively. This can be explained by the fact that the step-length increase caused by elbow-joint extension increase is in conflict with other conditions of locomotion efficiency. The longer the distance from the point of palm support to the center of gravity, the larger the load on adductor muscles preventing the animal body from falling down.

In the case of pronation locomotion, an increase in the undulation angle is connected with an increase in the step length (Fig. 1, curve *7*). On the other hand, in the case of retraction locomotion, the effect exerted by an increase in the undulation angle on the step length is more likely to be negative than positive (Fig. 1, curve *6*). An increase in the undulation angle causes a particularly large increase in the step length if the ratio between limb segments in the case of pronation locomotion coincides with that in animals with retraction locomotion (Fig. 1, curve *8*). However, the absolute step length, rather than the rate of its increase, is advantageous for locomotion. It should be noted the absolute step length in this case is shorter than in the case of the ratio between limb segments typical of animals with pronation locomotion (compare curves *7* and *8* in Fig. 1).

Back hunching and shortening of step length in Tachyglossidae also reduce energy expenditure. However, this may cause palm-to-foot interference during the cycle. To avoid this interference, the palm should touch the ground after the foot. In other words, the cycle should contain a lateral support stage. So far, this stage has been regarded as impossible because of its instability in tetrapods with limbs spread apart [2, 4, 7]. However, a normal gait with a locomotion-rhythm shift toward amble and a prolonged stage of lateral support

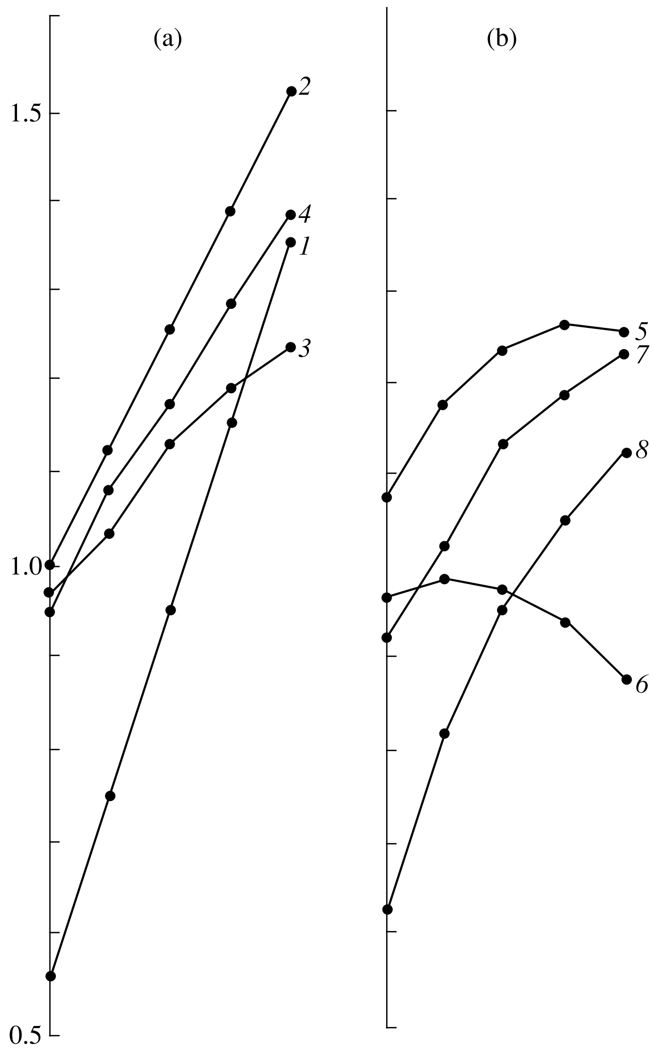

Fig. 1. Dependence of step length on changes in various factors: (a) elbow-joint extension; (b) angle of body undulation. See the text for designations (*1*)–(*8*).

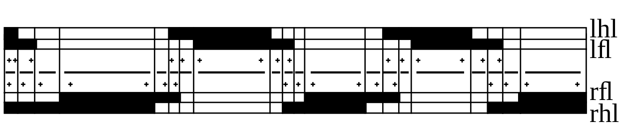

Fig. 2. Reference curve of a typical locomotion of New Guinea echidna. Limbs: lhl, left hind limb; lfl, left fore limb; rhl, right hind limb; and rfl, right fore limb. Shaded and unshaded ruler zones correspond to the phases of support and transfer, respectively. Patterns of limb support of the corresponding pace are shown between the rulers.

proved to be a normal pace in echidnas and New Guinea echidnas (Fig. 2). Therefore, a negative extension of the elbow joint is an adaptation to reduced instability of this stage of support.

Probably, different patterns of shoulder bone supination at the phase of transfer emerged at the earliest stages of evolution of tetrapods. In all respects, the retraction pattern of locomotion is superior to the protraction pattern. Therefore, the prohibition of shoulder retraction led to a nonadaptive pathway of locomotion development. The lack of stylopodia retraction in the pronation locomotion pattern gave rise to the appearance of adaptation mechanisms capable of compensating this disadvantage. This factor determined the emergence of different directions in locomotion adaptation (Table 1).

A substantial difference between these locomotion patterns is that the shoulder joint movement axis in retraction and pronation patterns is vertical and horizontal, respectively. This fact was of decisive importance for further progressive evolution of locomotion. Indeed, adaptation to the jumping pace appeared independently at least three times during the evolution of mammals. To provide shock-absorption upon landing after the jump, mammal limbs should be stretched down. This caused a gradual displacement of limbs to the parasagittal position, the shoulder-joint movement axis remaining horizontal. Thus, the parasagittal position of limbs and a huge diversity of available paces are historically due to a well-developed pronation locomotion with a horizontal axis of stylopodia movement. As a result, the primarily nonadaptive pathway of locomotion development in synapsids resulted in the emergence of the most perfect and diverse forms of locomotion in mammals without cardinal changes in the main axis of the shoulder-joint movement.

REFERENCES

1. Gambaryan, I.S., *Tr. Zool. Inst. Akad. Nauk SSSR*, 1990, vol. 215, pp. 9–37.
2. Gambaryan, P.P., *Beg mlekopitayushchikh* (Mammal Running), Leningrad: Nauka, 1972.
3. Kuznetsov, A.N., *Plany stroeniya konechnostei i evolyutsiya tekhniki bega u tetrapod* (Structural Patterns of Extremities and Evolution of Running Movements in Tetrapoda), Moscow: Mosk. Gos. Univ., 1999.
4. Sukhanov, V.B., *Obshchaya sistema simmetrichnoi lokomotsii nazemnykh pozvonochnykh i osobennosti peredvizheniya nizshikh tetrapod* (The General System of Symmetric Locomotion in Terrestrial Vertebrates and Characteristics of Movements of Lower Tetrapoda), Leningrad: Nauka, 1968.
5. Jenkins, F.A., Jr., *Science*, 1970, vol. 168, pp. 1473–1475.
6. Jenkins, F.A., Jr. and Goslow, G.E., *J. Morphol.*, 1983, vol. 175, pp. 195–216.
7. Gray, J., *Animal Locomotion*, London: Weidenheld and Nicolson, 1968.
8. Pridmore, P.A., *J. Zool. A.*, 1985, vol. 205, pp. 53–73.
9. Schaeffer, B., *Bull. Mus. Nat. History*, 1941, vol. 78, pp. 395–472.