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Analysis of limb movement synchronization in primates locomotion

Zofia Sikorska-Piwowska[1], Piotr Śliwka[2], Bogdan Ciszek[1]

[1]Department of Descriptive and Clinical Anatomy, Centre of Biostructure Research, Medical University of Warsaw, Poland
[2]Department of Mathematics and Natural Sciences, Cardinal Stefan Wyszyński University, Warsaw, Poland

Abstract: The authors present an original mathematical model based on features identified with discrete variables using vector and hierarchical cluster analysis in primates locomotion. Proposed model allows to formalize and analyze the synchronization variability of movements in given locomotion types of adaptation and specialization in monkeys, apes and humans. The material covers observations of 102 forms including 9 species of primates: the chimpanzee, bonobo, orangutan, gibbon, gelada, mandrill, brown capuchin and ring–tailed lemur. The studies included also the synchronization of locomotory movements in man. The sequences of moves of pectoral and pelvic limbs, right and left, were studied in four categories: walking, running, jumping and brachiation. The locomotion movements depend on the brain centers and allow to find phylogenetic relations between examined forms in the evolution process. The knowledge of the pattern of movements is used in the treatment of paraplegia and paraparesis in humans.

Key words: evolution process of primates bipedality, vector analysis, hierarchical cluster analysis, pattern of movements, treatment of human paraplegia and paraparesis.

Introduction

The aim of this work is to verify phylogenetic relation and contributes to the explanation of man's biped posture. As a tool, the vector analysis and hierarchical cluster analysis, based on formalized traits regarding the synchronization of locomotive movements of the primate limbs, were used.

These studies explained the mechanism of origin of foot and hand gaits examined by many researches and hadn`t to be identified in this analysis.

The evolution variability of synchronization limb movement in terms of locomotion of primates depends on types of their adaptation and specialization in particular environmental conditions. An adaptation type means the state of adaptive traits of extremities correlated with traits of all organisms. These traits ensure an optimal solution of locomotory functions of extremities in the habitat. Specialization types are selected structural functional differentiations of extremities due among others to intensification of given locomotory functions.

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Transition from plantigrade to digitigrade in quadrupedal adaptation is an instructive example.

Primates belong to the order of mammals. Zoological taxonomy divides this order into two principal groups: Strepsirrhini and Haplorrhini. Strepsirrhini are represented in our study by lemurs (*Lemur catta* L.) which climb trees with four limbs having prehensile hands and feet. Haplorrhini are composed of broad nose monkeys (Platyrrhini) and narrow nose ones (Catharrhini). Platyrrhini, like capuchin (*Cebus capucinus* L.), live in South America and climb from one branch to another hanging with pectoral extremities. Additionally, some of them use their prehensile tails while locomotion. The Catharrhini were divided into Cercopithecidae monkeys and Hominoidea. The locomotion of the Cercopithecidae, like baboons (*Papio papio* Desm.) or mandrills (*Mandrillus sphinx* L.), effects quadrupedally with prehensile hands and feet on branches or on the ground. Hominoidea like gibbons (*Hylobates lar* L.) and apes like chimpanzee (*Pan troglodytes* L.) and bonobo (*Pan paniscus* L.) brachiate hanging on branches or step on the ground quadrupedally (Sikorska-Piwowska et al. 2015). Their pectoral extremities are very elongated in relation to the pelvic ones.

In the present paper, the locomotion of man was compared with those of monkeys and apes. Human extremities evolved in a different way than those of other primates, because human pelvic legs are very elongated in biped locomotion, and pectoral ones are shortened. In the human hand, the thumb is capable of real opposition to other fingers enabling precise movements.

The evolution of primates locomotion was examined by Videan and McGrew (2002) as well as by Williams (2010). According to these authors, bipedalism evolved to increase the visual horizon as a strategy against greater predators and competition in savanna-woodland habitats. Richmond (2001) assumed that human bipedalism originated from arboreal quadruped ancestors. Moreover, there were anatomical similarities in the human and baboon hand structures. Carvalho (2012) claimed that the climate changes reduced forested areas forming selective pressure to lead hominine's ancestors to modify their posture to include a larger component of bipedality. Occasional bipedality occurs among wild great apes linked to food carrying with males transporting more often than females (Richmond 2001). Niemnitz (2010) described the evolution of the upright posture and gaits. Oscillatory movements of the limbs during locomotion of vertebrates were also considered by physicists and mathematicians such as Collins and Steward (1991) in terms of their diverse inter-relations. According to Crompton (2008), in the evolution of the locomotion system from the earliest hominids to modern *Homo sapiens* has to be explained how flexed postures of the hind limb could have preadapted the body for the apes acquisition of straight-legged erect bipedality. Hildebrand (1967) analyzed walking and running gaits of 26 genera of primates and described typical support sequences of them. Schmitt (2003) considered that primates including human showed patterns of locomotion and locomotor control different from all other mammals. According to this author, hominid bipedalism evolved in arboreal climbing primates.

Type of movement is generated by the spinal cord centers both for pectoral and pelvic limbs. Long-lasting research indicated that they play a significant role in coordinating primates' locomotion movements (Carvalho et all. 2012; Dietz 2002). This knowledge is being used in the treatment of paraplegia and paraparesis in humans - victims of spinal cord injuries. This research is focused on activation of peripheric spinal neurons coordinating pelvic limbs activities. This can be done by spinal cord stimulation or by modification of rehab programs and the usage of limbs' exoskeletons (van den Brand et al. 2015). These categories are the measure of brain evolution and allow to find phylogenetic relations between examined forms. Particular limb movement patterns are supposed to be invariable within the populations studied which are considered to be independent forms.

Material and methods

Observations were carried out in the Chimpanzees Sanctuary in the Sweetwaters Game Reserve in Kenya, in the Orangutans Sanctuary in Sumatra and Tsaratanana Strict Nature Reserve in Madagascar. This research was complemented in zoos in Warsaw and Gdansk.

Eight species of primates were observed at the following numbers: ring-tailed lemur (14), tufted capuchin monkey (14), baboon (14), mandrill (14), gibbon (10), orangutan (12), chimpanzee (12) and bonobo (12). In total information about 102 specimens was collected. The observed results were analyzed.

Table 1 presents four types of movements considered: walking, running, jumping and brachiation with information on the left and right chest and pelvic limb synchronization for all analyzed primates, including man. This synchronization was indicated by the sequence of the movements represented by numbers from 1–4 where 1 denotes the first movement, 2 second one, and so on. If the movements occur at the same time, they are denoted by the same number. The sequence allows to estimate the differences or similarities between the studied forms in the types of movements. For example, in walking moves of the chimp, the right chest limb (RC}, which is the first to move is numbered 1, next moves the left pelvic limb (LP) that is numbered 2, after that moves the left chest limb (LC) numbered 3 and finally the right pelvic limb (RP) numbered 4. So its sequence of movements was represented in Table 1 denoted by (3,1,2,4). There is also 0 in the table which indicates the lack of the type of movement.

In the rows of the table there are groups of stages of the movement tabulated. The 16 stages are divided between all types of movement as walking, running, jumping and brachiation. This way, every species is described by 16 stages of movements which compose a vector $x_i=\{x_{i1}, ..., x_{iN}\}$ determining a location of a given species in a multi-dimensional vector space with information about their synchronization (N=4 or N=16).

These 16 stages of movements divided into 4 types of movements: walking - W, running - R, jumping - J and brachiation – B were considered to be discrete characteristics which characterize each of the primate forms. These vectors generate matrix X (dim: 9x4 or 9x16)

$$X = \{x_1, ..., x_Q\}$$

consists of movement stages vectors for all species ($i \in Q$, Q = 9 - number of species of monkeys and human).

The lack of a particular type of movement in the examined species was customarily designated by the value of 0. As an example the lack of brachiation occurs both in humans and in the mandrill and baboon.

Table 1. Synchronization order of the limbs movement for the examined primates

Limbs	Walking				Running				Jumping				Brachiation			
Forms	LC	RC	LP	RP	LC	RC	LP	RP	LC	RC	LP	RP	LC	RC	LP	RP
L	1	3	4	2	1	3	4	2	2	2	1	1	1	3	2	4
CM	3	1	2	4	3	1	2	4	2	2	1	1	2	1	3	4
BA	2	4	3	1	4	2	3	1	2	2	1	1	0	0	0	0
MN	2	4	3	1	4	2	3	1	0	0	0	0	0	0	0	0
G	0	0	1	2	0	0	0	0	3	2	1	1	2	1	0	0
O	3	1	2	4	3	1	2	4	2	3	1	1	2	1	3	4
CH	3	1	2	4	3	1	2	4	2	3	1	1	2	1	3	4
BO	3	1	2	4	0	0	1	2	0	0	0	0	2	1	3	4
M	1	2	2	1	1	2	2	1	1	2	2	1	0	0	0	0

Legend: Limbs: LC-left chest, RC-right chest, LP-left pelvien, RP-right pelvien. Forms: Lemur (L), Capuchin (CM), Baboon (BA), Mandrill (MN), Gibbon (G), Orangutan (O), Chimpanzee (CH), Bonobo (BO), Man (M). Number from 1 to 4 represent the order of movements, 0 – lack of movement. Source: own calculations.

Preliminary analysis of all phases and types of movements was done by means of Spearman`s rank correlation coefficient ρ in the form:

$$\rho_{emp} = 1 - \frac{6}{N(N^2-1)}\sum_{k=1}^{N}(R_{ik} - R_{jk})^2$$

where: R_{ik}, R_{jk} is rank, k is index describing the type of limb in given stages and types of movement , i,j∈Q,

but ρ only shows correlations between pairs of species and they do not allow unique grouping of species with phylogenetic relationships. For this purpose, a hierarchical cluster analysis with the agglomeration method (merging smaller clusters into larger clusters) and the Ward measure of the inequality between clusters were applied (Murtagh and Legendre 2014).

Two steps were done:
- first, the Euclidean distance between clusters that uses the variance analysis approach to minimize the sum of the squares of the deviations within the clusters was estimated,

$$d_{x_i x_j} = \sqrt{\sum_{k=1}^{N}(x_{ik} - x_{jk})^2}$$

where: d_{xixj} – Euclidean distance between pairs of species x_i and x_j for each limb, k-index describing the type of limb in a given phase and type of motion, i,j ∈Q,

- second, a pair of clusters was selected that, after the merging approach the focus of the minimum differentiation by the ESS (error sum of squares):

$$ESS = \sum_{i=1}^{m}(x_i - \bar{x})^2$$

where: m is the number of species (m=1 to m=9).

The classic “elbow method” (also known as the “scree plot”, Thorndike 1953) is used to select the number of clusters based on the rule: find such $Var(C_1)+\ldots+Var(C_m)$ that adding a new cluster C_{m+1} with new variance $Var(C_{m+1})$ does not significantly changes the sum

$(\Sigma_{i=1,..,m} \mathrm{Var}(C_i) / \Sigma_{i=1,..,m+1} \mathrm{Var}(C_i) \approx 1)$.

In the graph with the increase in the number of clusters on the abscissa, we observed on the ordinates a "gentle descent" of the sum of variance

$$T_m = \sum_{i=1}^{m} \mathrm{Var}(C_i)$$

where: T_m - index of the number of clusters, C_i – i-th cluster, Var (C_i) - value of variance within the i-th cluster, m - optimal number of clusters.

Based on the T_m index and the type of movement, homogeneous groups were identified that best describe the phylogenetic relationships between species. In the next step each type of movement was analysed.

Results

Two types of analysis were done: first, detection of the numbers of clusters, and second, dendrograms of the connection between the examined forms based on separate types of movements such as walking, running, jumping and brachiation and all types of movements together. The visualization of the number of clusters (vertical line on graphs) and dendrograms on Figures 1 and 2 were presented (the species name abbreviations identical as those in Table 1).

In the type of walking locomotion four groups were formed. Apes, represented by the chimpanzee, orangutan and bonobo (Catarrhini), and the capuchin as a representative of the broad nose monkeys (Platyrrhini) in the dendrogram, formed one group, because their pelvic limbs, which are used to walk on the ground, have a similar form as that of the quadrupedal apes, but unlike them, they knuckle-walk on the elongated chest limbs. Quadrupedalism of the mandrill and baboon is similar to the quadrupedalism of the lemur, which is a primordial form of the primates, whereas the gibbon and the man diverge from the others. Gibbons walk on two limbs keeping their balance with their arms outstretched, and man uses the upper limbs as pendulums moving in the rhythm of the lower limbs.

In the type of running locomotion four groups were formed. The order of movement of the limbs resembles the previous type; however, bonobos and gibbons are distinguished from the others and form a common group, while the rest of apes are similar. Lemur as a primary form is linked, on the one hand, to mandrill and baboon, and on the other hand, with man.

In the type of jumping locomotion, two groups were formed. Bonobo and mandrill jump similarly. The orangutan, chimpanzee, gibbon, baboon, capuchin and lemur form one group, while man jumps in his own way. This dendrogram points out to the uniformity of the arboreal quadruped adaptation of the lower limbs of all examined primates, except for man who represents the type of bipedal adaptation.

In the type of brachiation two groups were formed. Brachiators, like the apes and capuchins, come from primitive forms represented by lemur, thus forming the same group. The second one consisted of humans, baboons, mandrills and gibbons. Human pectoral limbs have lost their locomotion function but retained the features of the primordial arbority, which allows to link humans to the baboon and the mandrill. The gibbon, which is a type of brachiator different than the ape and capuchin due to the well-developed thumb and occasional bipedalism, is also assigned to this group.

In the case of all type of movements, five groups were formed. Lemur is in the initial position for all examined forms. Apes form one group with capuchin except for the gibbon, whose locomotion developed in a different direction than that of the others. Proof of this is its hand-built construction with a fully developed thumb, which allows for acrobatics while hanging on the branches. Other brachiators have a reduced thumb. Man specialized in bipedalism as illustrated by the extension of the lower limbs, as opposed to brachiators with lower limbs shorter than the upper ones. However, man's bipedalism was a type of quadrupedal primitive adaptation for climbing, which is characteristic for the mandrill and baboon. Bonobo is a separate case, incorrectly considered to be the closest form to a human being.

Discussion

Locomotive adaptation types, such as primitive climbing, primitive hanging (brachiation) and human bipedness predispose the ways of limb movement syn-

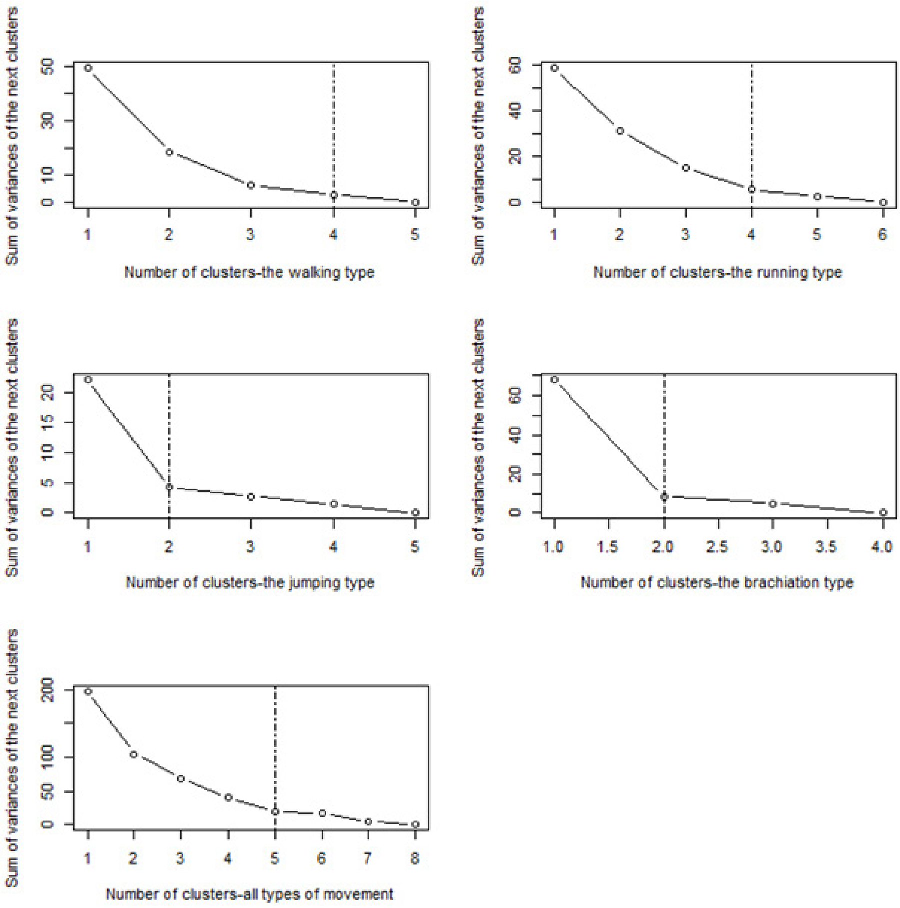

Fig. 1 Dendrograms of the numbers of clusters of examined species in defined types of movements in the locomotion. Source: own calculations.

chronization in walking, running, jumping and brachiation. Adaptations types were described by Sikorska-Piwowska (1984).

Lemurs, considered as a primary group of primates (Hofstetter 2002; Kay et all. 1997; Ross et all. 1998), have been added to the examined species. We can assume that this group forms a pluripotential variety which are linked in each quadrupedalism to mandrill and baboon on the one hand and to man on the other hand.

In the group of monkeys and apes the most distant connections are related to the gibbon. Cooper (1999) confirmed gibbon`s distinct specialization in the locomotor movement. It allows to assume that gibbon`s evolution line has separated from the other examined species.

During locomotion the chimpanzee, orangutan and capuchin monkey have a similar movements synchronization. One can assume that this is the result of a parallel evolution of apes and broad-nosed monkeys that took place on the two

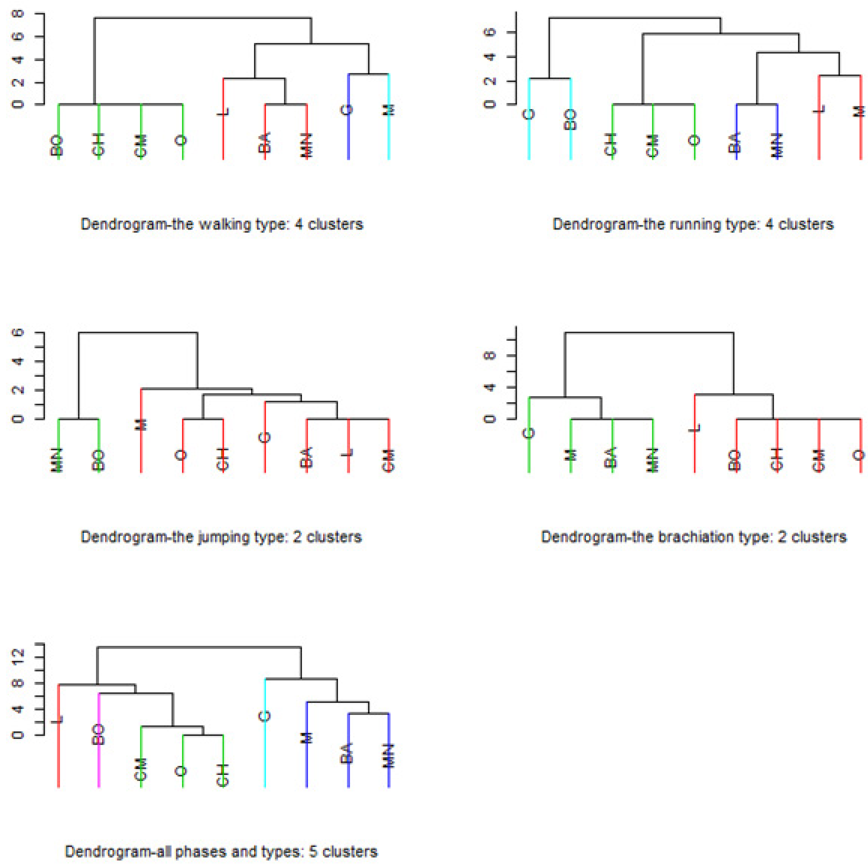

Fig. 2 Dendrograms of multilateral connections between the groups of examined species in defined types of movements in the locomotion (abbreviations identical to those in Table 1). Source: own calculations.

continents separated from each other - Africa and Asia - formed from the former Pangea (Fleagle 2013). This similarity of locomotion between these two groups was already noticed by Sikorska-Piwowska (1974) in her work concerning the ossification order of upper limb bases. Moreover, it is perhaps the plane of the moves or the centre of gravity which determines this.

The bonobo is a species which is clearly separated from both apes and man. Perhaps this species has started a new locomotive tendency. This is in opposition to Videan`s work (2002).

Man, in the course of his phylogenetic development, has also gone through the process of leaving the life in trees (Osborn and Homberger 2015), which is currently marked in his movement synchronization characteristic of baboons in all movement types possible for these species (with the exception of brachiation, Vallois 1956). Relict feature of this relation is the possibility of full opposition of the thumb to the other fingers observed in the baboon. These facts may suggest that movement patterns present in earlier evolution stages of primates could be introduced to rehabilitation programs (especially for incomplete damages like para and tetraparesis). Also modification of rehabilitation programs in ischemic strokes with half-deficit could take into account locomotive evolution of primates.

The forms studied represent the apex of the phylogenetic tree cut by the plane of the present times. Evolutionary connections between them based on locomotive movement synchronization could be evidence of their similarity on the one hand and diversity in their adaptation and specialization on the other hand.

Conclusions

Our study on primates' locomotion created a new algorithm which allows us to define the movement patterns for examined species. The obtained results allow better understanding multidimensional relations between examined traits of the primate locomotor apparatus. This study may be used to verify phylogenetic relation and contributes to the explanation of man's biped posture, as well as in the treatment of paraplegia and paraparesis in humans by modification of rehab programs and the usage of limbs' exoskeletons.

Authors' contributions

ZS-P conceived a paper, provided material for analysis, interpreted results, wrote draft manuscript, PS performed statistical analyses and interpreted results, BC discussed study results. All authors have read and approved the final version of the manuscript.

Conflict of interest

The authors have no conflicts of interest to declare.

Corresponding author

Zofia Sikorska-Piwowska, Department of Descriptive and Clinical Anatomy, Centre of Biostructure Research, Medical University of Warsaw, Chałubińskiego 5, 02-004 Warsaw, Poland
E-mail: zofiasikorska@poczta.onet.pl

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