http://dx.doi.org/10.1590/1519-6984.25512 Original Article

Histochemistry profile of the biceps brachii muscle fibres of capuchin monkeys (*Cebus apella, Linnaeus*, 1758)

*Bortoluci, CHF.[a], Simionato, LH.[a], Rosa Junior, GM.[a], Oliveira, JA.[b], Lauris, JRP.[c], Moraes, LHR.[d], Rodrigues, AC.[d] and Andreo, JC.[d]**

[a]Physiotherapy Department, Universidade do Sagrado Coração – USC, Rua Irmã Arminda, 10-50, Jardim Brasil, CEP 17011-160, Bauru, SP, Brazil

[b]Department of Basic Sciences, School of Dentistry of Araçatuba, Universidade Estadual Paulista "Júlio de Mesquita Filho" – UNESP, Rua José Bonifácio, 1193, CEP 16015-050, Araçatuba, SP, Brazil

[c]Department of Pediatric Dentistry, Orthodontics and Collective Health, Faculty of Dentistry of Bauru, São Paulo University – USP, Alameda Octávio Pinheiro Brisolla, 9-75, CEP 17012-901, Bauru, SP, Brazil

[d]Department of Biological Sciences - Anatomy, Faculty of Dentistry of Bauru, São Paulo University – USP, Alameda Octávio Pinheiro Brisolla 9-75, CEP 17012-901, Bauru, SP, Brazil

*e-mail: jcandreo@usp.br

Received: November 26, 2012 – Accepted: May 31, 2013 – Distributed: November 30, 2014
(With 1 figure)

Abstract

A general analysis of the behaviour of "*Cebus"* shows that when this primate moves position to feed or perform another activity, it presents different ways of locomotion. This information shows that the brachial biceps muscle of this animal is frequently used in their locomotion activities, but it should also be remembered that this muscle is also used for other development activities like hiding, searching for objects, searching out in the woods, and digging in the soil. Considering the above, it was decided to research the histoenzimologic characteristics of the brachial biceps muscle to observe whether it is better adpted to postural or phasic function. To that end, samples were taken from the superficial and deep regions, the inserts proximal (medial and lateral) and distal brachial biceps six capuchin monkeys male and adult, which were subjected to the reactions of m-ATPase, NADH-Tr. Based on the results of these reactions fibres were classified as in Fast Twitch Glycolitic (FG), Fast Twitch Oxidative Glycolitic (FOG) and Slow Twitc (SO). In general, the results, considering the muscle as a whole, show a trend of frequency FOG> FG> SO. The data on the frequency were studied on three superficial regions FOG=FG>SO; the deep regions of the inserts proximal FOG=FG=SO and inserting the distal FOG>FG=SO. In conclusion, the biceps brachii of the capuchin monkey is well adapted for both postural and phasic activities.

Keywords: biceps brachii muscle, histoenzimologic, muscle fibre types, capuchin monkeys, primates.

Perfil histoquímico das fibras do músculo bíceps braquial do macaco-prego (*Cebus apella, Linnaeus*, 1758)

Resumo

Uma análise geral do comportamento do "*Cebus apella*" mostra que este primata quando desloca para se alimentar ou realizar outra atividade apresenta diferentes maneiras de locomoção. Estas informações mostram que o músculo bíceps braquial deste animal é freqüentemente usado nas suas atividades de locomoção, mas deve ser lembrado ainda que este músculo é usado também para desenvolvimento de outras atividades como esconder-se, procurar objetos, vasculhar arboredos, além de cavar o chão. Considerando-se o exposto acima decidiu-se pesquisar as características histoenzimológicas do músculo bíceps braquial do macaco-prego com o objetivo de comparar se este músculo esta melhor adaptado para funções posturais ou físicas. As amostras foram retiradas das regiões superficiais e profundas; inserções proximais (medial e lateral) e distal de seis macacos-prego machos e adultos, os quais foram submetidos às reações de m-ATPase, NADH-Tr. Baseado nos resultados das reações, as fibras foram classificadas em *Fast Twitch Glycolitic* (FG), *Fast Twitch Oxidative Glycolitic* (FOG) e *Slow Twitch* (SO). Quanto à área dos diferentes tipos de fibras, os resultados encontrados foram semelhantes em todas as amostras estudadas, e as fibras de contração rápida foram sempre maiores do que as de contração lenta (FG=FOG>SO). Os dados obtidos sobre a frequência foram: nas três regiões superficiais estudadas FOG=FG>SO; nas regiões profundas das inserções proximais FOG=FG=SO e na inserção distal FOG>FG=SO. Baseado nestes dados pode-se concluir que o músculo bíceps braquial do macaco-prego está bem adaptado tanto para atividades posturais como físicas.

Palavras-chave: músculo bíceps braquial, histoenzimologia, tipos de fibras musculares, macaco-prego, primatas.

1. Introduction

The use of primates in biomedical research has increased very rapidly (De Oliveira, 1988). This interest has steadily grown due to their anatomic, biochemical and behavioural similarities to human beings. In some cases another advantage that can be added to the above is the fact that they have reduced physical size, which provides inexpensive maintenance and ease in handling (Coimbra-Filho et al., 1976). They have been used to study the motor control mechanism of the movements of the upper limbs, for instance elbow flexion and extension (Evarts, 1982).

The locomotion of non-human primates presents a different evolution from that of other quadrupeds (Schmitt and Lemelin, 2002). The most remarkable events in this evolution were the development of the erect position of the trunk of these animals and the structural reorganisation of the scapular waist, which allowed these animals to climb, hang on branches and engage in ways of hominid locomotion in some atelinae monkeys of the New World (Schmidt and Schilling, 2007). Between these two events, the latter became mostly responsible for the increased mobility of the forelimbs of these animals (Miller, 1932; Erikson, 1963; Oxnard, 1963; Ashton and Oxnard, 1964; Rose, 1973, 1989; Corruccini and Ciochon, 1976; Jenkins Junior et al., 1978; Schön Ybarra and Schön III, 1987; Isler, 2005).

Besides the anatomical structural modifications that occurred in the shoulder region of the primates, it is important to remember that functional alterations also took place in some muscles of this region. They changed from stabilisers to mobilisers, which may be observed microscopically, both in the architecture of the muscle fibres and in the composition of the different types of muscle fibres (Schmidt and Schilling, 2007).

Several studies in mammals have investigated the relationship between the locomotor behaviour and the composition of the fibre type of the muscles of the members. For instance, the slow loris and the sloth have muscles formed only by fibres of slow contraction speed, but which are resistant to fatigue (Sickles and Pinkstaff, 1981a; Kimura et al., 1987). In contrast, small species with the ability for fast movement have a high proportion of fibres of fast contraction speed in most of their muscles (Ariano et al., 1973; Sickles and Pinkstaff, 1981a; Jouffroy et al., 2003). Studies in primates have shown that the population of the fibre type in the muscle varies according to the predominant way of locomotion of each species (Ariano et al., 1973; Plaghki et al., 1981; Sickles and Pinkstaff, 1981a, b; Moriyama, 1983; Anapol and Jungers, 1986; Petter and Jouffroy, 1993; Jouffroy et al., 1999).

A general analysis of the behaviour of the *Cebus apella* shows that when they move to feed, this species walks upright as quadrupeds or jumps, 40% and 22% of the time, respectively. This species also presents other ways of locomotion such as running, climbing trees or branches and jumping from branch to branch or tree to tree. When the animals of this species travel their movements are the same, but the period of time through which they keep doing these movements changes (Wright, 2007).

The biceps brachii muscle of the capuchin monkey is frequently used in its activities of locomotion, but it is important to remember that these animals are agile and perform other activities such as hiding, looking for food, searching in the woods and digging in the soil, activities in which the biceps brachii is also used.

Taking the latter into consideration, it was decided to study the histoenzymologic characteristics of the biceps brachii muscle of the capuchin monkey in order to observe whether it is better adapted to postural or phasic functions.

2. Material and Methods

Six adult capuchin monkeys, from the Breeding Centre of Capuchin Monkeys at the State University "Júlio de Mesquita Filho" (UNESP) – Araçatuba *Campus*, were anesthetised by intraperitoneal injection of sodium thiopental, using a dose of 30 mg/Kg of body weight, for the collection of samples from superficial and deep regions, at the proximal (lateral - LP and medial - MP heads) and distal (D) insertions of the biceps brachii muscle. This study was approved by the Ethics Committee of the University of the Sacred Heart.

The samples were frozen with liquid nitrogen and then stored in a cylinder containing liquid nitrogen until the moment they were subjected to the histochemical treatment (Werneck, 1981).

Several sections, 12 μm thick, were obtained from the muscle samples using a Leica cryostat – Model CM 1850.

The sections were stained with Hematoxilin and Eosin (Behmer et al., 1976) to assess quality of freezing material, and then subjected to the reactions of m-ATPase, as well as to alkaline (pH 10.75) and acid pre-incubation (pHs 4.35 and 4.55) (Padykula and Herman, 1955; Brooke and Kaiser, 1970); and Nicotinamide Adenine Tetrazolium Reductase (NADH-Tr) (Pearse, 1968; Dubowitz and Brooke, 1973).

The images of the blades were captured through a photomicroscope Olympus BX 50, connected to a microcomputer Pentium III with an Image Analysing System, Image Model Pro-version 4.1.

Through the images of the same field of reactions of m-ATPases and NADH-Tr, 100 fibres of each insert studied were classified in Fast Twitch Glycolitic (FG), Fast Twitch Glycolitic Oxidative (FOG) and Slow Twitc (SO) (Peter et al., 1972).

Following the classification, the fibres were quantified and their areas were calculated using the image analysing system previously mentioned.

ANOVA, for repeated measures in a criterion, and Tukey's Test were used in calculating the percentage of the area in cross-section and the frequency of each fibre type, for the comparison among the fibre types in each portion and depth and among the portions in each fibre type and depth. The paired t-test was used for the comparison among the depths in each fibre type and portion.

Regarding the fibre area, the comparison among the fibre type and the portions and depths were performed through ANOVA, for measures repeated to three criteria, and Tukey's Test. In all these tests the significance level adopted was 5% ($p<0.05$).

The tests were executed utilising the Statistic program for Windows v. 5.1 (Stat Soft Inc., USA).

3. Results

The results of the histochemical reactions presented by the samples collected at the different parts of the biceps brachii muscle of the capuchin monkey were similar. These results are presented in Table 1, and they may be also observed in Figure 1.

The data regarding the frequency and area of the different fibre types in the regions of the biceps brachii muscle of the capuchin monkey are presented in Tables 2 and 3, respectively.

The data in Table 2 show that:

a) in the deep region in only one insertion (distal) the FOG fibres have higher frequency than those of the types FG and SO;
b) in the superficial region the FG and FOG fibres there is higher frequency than those of the type SO in all the studied insertions;
c) in the comparison of the frequency of the same types of fibre in the same insertions, but between the different regions (superficial and deep), there is an increase in the frequency of type SO fibres from the superficial to the deep region only in the distal insertion;
d) in the comparison of the same type of fibre between the insertions, in the same region, there is an

Table 1. Results of the reactions of m-ATPase and NADH-Tr to which the samples of the biceps brachii muscle of the capuchin monkey were subjected.

FIBRES	m-ATPase pH10.35	m-ATPase pH 4.55	m-ATPase pH 4.35	NDH-Tr
SO type	+	+++	+++	+++
FOG type	+++	+	+	++
FG type	+++	++	+	+

+ low reactivity ++ moderate reactivity +++ high reactivity.

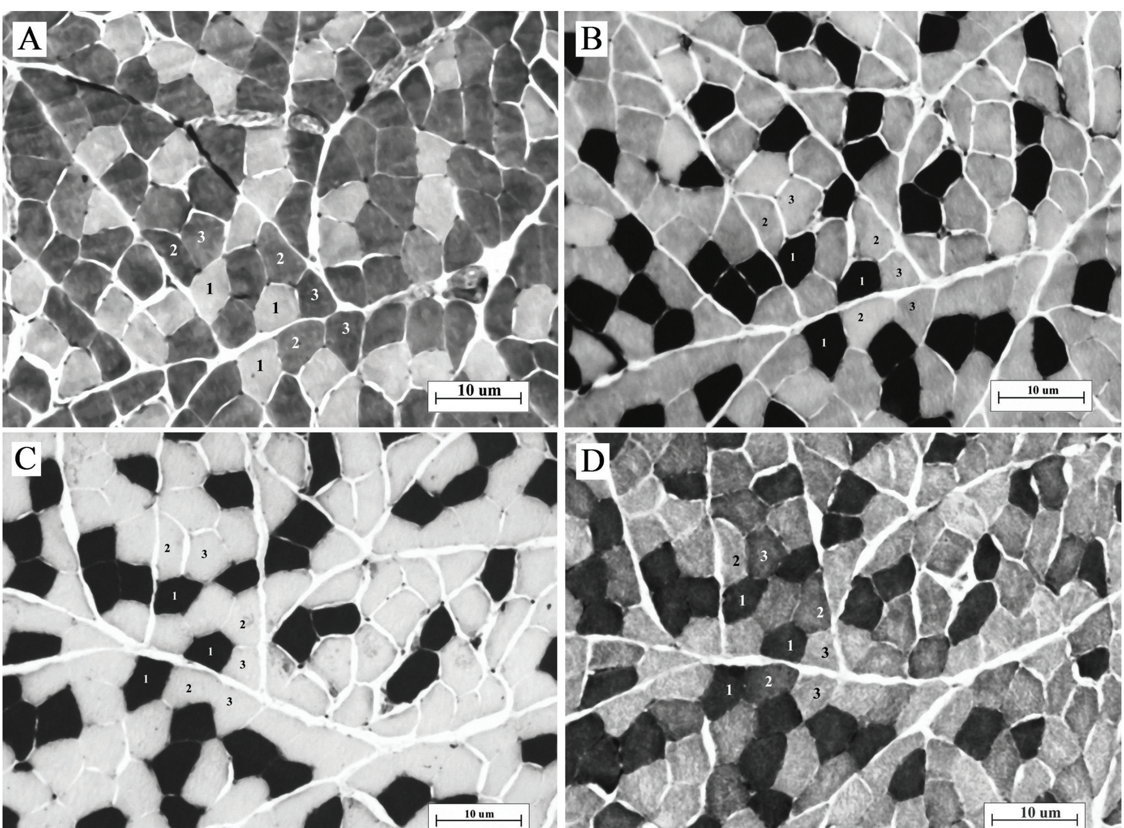

Figure 1. Result of the histoenzymologic reactions of the sample (insertion of the medial region of deep) of biceps brachii muscle of capuchin monkeys. A-) m-ATPase pH10.35; B-) m-ATPase pH 4.55; C-) m-ATPase ph 4.35 and D-) NDH-Tr. The number 1 indicates the type SO fibres, number 2 indicates the type FOG fibres and number 3 indicates the type FG fibres.

increase in the frequency of type SO fibres from the distal to the proximal insertion, in the surface region.

The following criteria were used to interpret the data in Tables 2 and 3:

Different letters indicate a statistically significant difference:

χ and β – comparison among the different fibre types in each portion (distal, lateral proximal and distal proximal) within each region (surface and deep) – horizontally.

A and B – comparison between the surface and deep regions in each portion (distal, lateral proximal and distal proximal), for each fibre type – vertically.

a and b – comparison among the portions (distal, lateral proximal and distal proximal), within each region (surface and deep), for each fibre type – vertically.

The data in Table 3 show that the area of the type FG and FOG fibres is always larger than that of the type SO fibres in all the studied insertion.

4. Discussion

It is commonly known that skeletal muscles respond to the functional demand that is required of them, and their contractile properties are determined by the composition of their different types of muscle fibres. This fact may also be observed in the muscles responsible for the locomotion of primates (Schmidt and Schilling, 2007).

The biceps brachii muscle is considered to be an elbow flexor and, in the *Macaca mulatta*, this muscle is also considered to be a flexor of the articulations of the elbow and shoulder, as it crosses these two joints (biarticular) (Singh et al., 2002).

The capuchin monkey presents eight categories of locomotion activities (Wright, 2007). According to the description of these movements, it is observed that in only one of them does the biceps muscle participate less actively. It is also important to remember that, when the primates are not moving, they use the forelimbs to perform other activities, such as digging in the soil, searching and breaking open objects and searching in the woods (Gasc et al., 1985).

The literature referred to gives special emphasis to type I (SO) and IIB (FG) fibres, such as indicators of postural activities (antigravitational) or muscle explosion in the movement propulsion, respectively (Jouffroy et al., 2003) .

As general characteristics of propelling and postural muscles, it is considered that the first have a homogenous distribution of the types of fibres over their cross-sectional area, whereas the second present an intra-muscular separation of the SO and FG- fibres in different regions. The deep regions are mainly composed of SO fibres, indicating a stabilising function, whereas the surface regions have a higher proportion of FG fibres and are therefore most appropriate for mobilisation (Schmidt and Schilling, 2007). These characteristics of muscle fibre type distribution are true both for the muscles of the members, as well as for those of the trunk (Ariano et al., 1973; Collatos et al., 1977; Armstrong, 1980; Burke, 1981; Roy et al., 1984; Petter and Jouffroy, 1993; Jouffroy et al., 1999; Schilling, 2005; Schmidt and Schilling, 2007).

Some researchers state that the biceps brachii of rats evidence low activity of the oxidative enzymes of the fibres in the surface region of this muscle due to the fact that they do not need to act as antigravitational muscles in this

Table 2. Mean and standard deviation of the percentage (%) of the different fibre types found in the samples of the biceps brachii muscle of the capuchin monkey.

Regions	Insertions	Fibre Type - %		
		FG	FOG	SO
Deep	D	$30.50 \pm 5.01^{aA\chi}$	$51.17 \pm 7.93^{aA\beta}$	$18.33 \pm 4.02^{aB\chi}$
	LP	$35.67 \pm 7.92^{aA\chi}$	$40.17 \pm 6.58^{aA\chi}$	$24.17 \pm 7.83^{aA\chi}$
	MP	$34.50 \pm 7.94^{aA\chi}$	$43.17 \pm 7.71^{aA\chi}$	$22.33 \pm 3.33^{aA\chi}$
Superficial	D	$43.00 \pm 6.90^{aA\beta}$	$47.00 \pm 8.37^{aA\beta}$	$10.00 \pm 5.02^{aA\chi}$
	LP	$37.17 \pm 5.38^{aA\beta}$	$47.17 \pm 4.71^{aA\beta}$	$15.67 \pm 6.09^{abA\chi}$
	MP	$35.00 \pm 7.92^{aA\beta}$	$44.67 \pm 6.19^{aA\beta}$	$20.33 \pm 11.16^{bA\chi}$

D = Distal, LP = Lateral Proximal and MP = Medial.

Table 3. Mean and standard deviation of the area (μm^2) of the different types of fibres found in the different regions of the biceps brachii muscle of the capuchin monkey.

Regions	Insertions	Type of Fibres (μm^2)		
		FG	FOG	SO
Deep	D	$2,777.44 \pm 556.84^{aA\beta}$	$2,755.95 \pm 538.68^{aA\beta}$	$2,033.45 \pm 399.35^{aA\chi}$
	LP	$2,505.31 \pm 344.94^{aA\beta}$	$2,490.72 \pm 301.28^{aA\beta}$	$1,826.47 \pm 324.21^{aA\chi}$
	MP	$2,867.67 \pm 857.36^{aA\beta}$	$2,828.23 \pm 889.36^{aA\beta}$	$2,243.94 \pm 992.95^{aA\chi}$
Surface	D	$2,658.13 \pm 704.68^{aA\beta}$	$2,570.85 \pm 702.09^{aA\beta}$	$1,958.67 \pm 851.95^{aA\chi}$
	LP	$2,762.07 \pm 463.67^{aA\beta}$	$2,713.19 \pm 461.31^{aA\beta}$	$1,960.99 \pm 350.59^{aA\chi}$
	MP	$2,982.42 \pm 651.65^{aA\beta}$	$2,948.94 \pm 515.26^{aA\beta}$	$2,147.32 \pm 555.53^{aA\chi}$

D = Distal, LP = Lateral Proximal and MP = Medial Proximal.

animal (Matsumoto et al., 2007). Others state that larger mammals have a higher percentage of type I fibres due to the need to support their heavier weight (Kawai et al., 2009). In the biceps of the capuchin monkey, it is observed that there is a tendency towards an increase in the percentage and in the area of type SO fibres from the surface to the deep region in the studied location, but not a prevalence of this fibre type in this region; however, it may be the correct balance for the execution of any postural activity in this animal, which does not present heavy body weight.

In some animals, for instance in horses, the biceps brachii muscle is more complex and its two heads may be useful for different functions, since the lateral contributes to postural functions, whereas the medial participates in phasic activities such as walking, trotting and running (Hermanson and Hurley, 1990).

Regarding the fact that the biceps brachii muscle of the capuchin monkey acts as a propellor, it is known that in quadrupeds the hindlimbs are better adapted to execute this task during locomotion (Niki et al., 1984; Merkens et al., 1993; Payne et al., 2004; Dutto et al., 2004, 2006).

In the description of the eight categories of locomotor activities of the capuchin monkey (Wright, 2007), it is observed that propulsion movement is made predominantly by the hindlimbs of this animal, but in some activities the participation of the forelimbs is very important; for instance, when they are climbing a tree branch or trunk, since they usually are found in the top of the tree (Chiarello, 1995). This fact could explain the higher percentage of the frequency and area of the FG fibre in relation to the SO fibres in all the portions studied in the surface region of the biceps brachii muscle of the capuchin monkey, in addition to a tendency towards an increase in the percentage of FG fibres from the deep to the surface region in the three portions examined in this study.

The role represented by the FG fibres of fast contraction speed is also related to other phasic activities of short fast movements developed by the primates, such as "burrowing" (disappearing, hiding, and seeking), in which fibres with oxidative metabolism are not necessary. This type of activity was described in other primates, but it must be highlighted that it is common in the capuchin monkey as well (Gasc et al., 1985).

The literature referred to shows that FOG fibres and other subtypes of fibres of fast contraction speed are normally not involved in the description of the regionalisation of the muscles . Whereas percentages of FG and SO fibres vary from surface to deep regions within a certain muscle (Schmidt and Schilling, 2007), the percentage of FOG fibres remains constant in these regions as is observed in the cynomolgus monkey (Roy et al., 1984; Singh et al., 2002) and in the biceps brachii of the capuchin monkey in this study.

In the studies found, the descriptions of the percentage and area of FOG fibres alone do not seem to demonstrate an important participation of this type of fibre in the functional performance of a muscle, but together with other types of fibres is it observed that they are important in the activities developed by a muscle or a group of muscle.

Fibres with high oxidative capacity are capable of balancing contraction with fatigue (Burke and Tsairis, 1974; Sickles and Pinkstaff, 1981a,b). Based on this fact, some researchers state that the abundance of FOG fibres in the muscles of the hindlimbs of the *Macaca mulatta* (Singh et al., 2002), which present high oxidative capacity, together with the presence of SO fibres provide this species with fibres that are capable of sustained contractions (Sickles and Pinkstaff, 1981a, b). Others state that this fact is also well illustrated in the common tree shrew, in which the fibres of fast contraction speed often contain similar oxidative capacity or, in some cases, higher oxidative capacity than the fibres of slow contraction speed. The high oxidative capacity of the muscle fibres of fast contraction speed is also present in the slow loris (a mammal of nocturnal habit), which explains the continuous activity of fibres of both fast and slow contraction speed (FOG and SO), and the combination of these two types of fibres would be important in postural activities, for instance in animals that move by hanging on branches and develop swinging activities, observed in some species of primates (Sickles and Pinkstaff, 1981a, b). It must be remembered that the capuchin monkey also performs these hanging and swinging activities.

Sickles and Pinkstaff (1981 a, b) ensure that animals have arboreal habitat require more energy for maintenance of locomotion and posture, and one would assume that a rise in the amount of oxidative fibres would be needed in the limb muscles of this animal. In the studied locations of the biceps brachii of the capuchin monkey, the sum of the oxidative fibres (FOG + SO) is greater than 50% of the total fibres observed in the cross-sections of this muscle. Based on the literature data, and on this information regarding the biceps brachii of the capuchin monkey, it is possible to reinforce the idea that this muscle is adapted for postural functions (antigravitational activities).

Considering the sum of the fibres of fast contraction speed (FG and FOG) in the studied locations of the biceps brachii of the capuchin monkey, it is observed that they represent over 70% of the fibres identified in the cross-sections, and it is important to note that the area of these types of fibres was always greater than that of the type SO, strengthening even more the speed aspect of this muscle. In addition to the activities previously described which would use these types of fibres, it is important to remember other tasks such as digging, working the soil and creating openings , which the capuchin monkey performs and that the biceps brachii muscles participate in. These activities demand faster, longer movements, and in this situation the FOG fibres can assist the FG fibres, allowing the regeneration of glycogen during the recovery of the glycolytic process stage, similar to what happens in other animals (Jouffroy et al., 2003) .

Observing the literature data and the data obtained from the samples of the biceps brachii muscle of the capuchin monkey, and considering only type FG and SO fibres, it would be difficult to state whether this muscle is predominantly a propelling or postural muscle. However, considering the type FOG fibres together with each one of the other two types of fibres, it is observed that it can demonstrate both postural and phasic functions.

References

ANAPOL, FC. and JUNGERS, WL., 1986. Architectural and histochemical diversity within the quadriceps femoris of the brown lemur (Lemur fulvus). *American Journal of Physical Anthropology*, vol. 69, no. 3, p. 355-375. http://dx.doi.org/10.1002/ajpa.1330690308. PMid:3706515

ARIANO, MA., ARMSTRONG, RB. and EDGERTON, VR., 1973. Hindlimb muscle fiber populations of five mammals. *The Journal of Histochemistry and Cytochemistry*, vol. 21, no. 1, p. 51-55. http://dx.doi.org/10.1177/21.1.51. PMid:4348494

ARMSTRONG, RB., 1980. Properties and distribution of the fibre types in the locomotory muscles of mammals. In SCHMIDT-NIELSEN, K., BOLIS, L. and TAYLOR, CR. (Eds.). *Comparative physiology of primitive mammals*. Cambridge: Cambridge University Press.

ASHTON, EH. and OXNARD, CE., 1964. Locomotor patterns in primates. *Proceedings of the Zoological Society of London*, vol. 142, no. 1, p. 1-28. http://dx.doi.org/10.1111/j.1469-7998.1964.tb05151.x.

BEHMER, OA., TOLOSA, EMC. and FREITAS NETO, AG., 1976. *Manual de técnicas para histologia e patologia*. São Paulo: Edart.

BROOKE, MH. and KAISER, KK., 1970. Muscle fiber types: how many and what kind? *Archives of Neurology*, vol. 23, no. 4, p. 369-379. http://dx.doi.org/10.1001/archneur.1970.00480280083010. PMid:4248905

BURKE, RE., 1981. Motor units: anatomy, physiology, and functional organisation. In BROOKS, VB. (Ed.). *Handbook of Physiology*. New York: Oxford University Press. Section I. The Nervous System, vol. II. Motor Control, Part I.

BURKE, RE. and TSAIRIS, P., 1974. Trophic functions of the neuron. II. Denervation and regulation of muscle. The correlation of physiological properties with histochemical characteristics in single muscle units. *Annals of the New York Academy of Sciences*, vol. 228, p. 145-159. http://dx.doi.org/10.1111/j.1749-6632.1974.tb20507.x. PMid:4152274

CHIARELLO, AG., 1995. Density and habitat use of primates at an Atlantic forest reserve of southeastern Brazil. *Revista Brasileira de Biologia*, vol. 55, no. 1, p. 105-110. PMid:7569145.

COIMBRA-FILHO, AF., ROCHA, ND. and PISSINATTI, A., 1976. Gestação quádrupla de triplo-híbridos em Callithrix duplo-híbrida (Callitrichidae, primates). *Revista Brasileira de Biologia*, vol. 36, no. 6, p. 675-681. PMid:828285.

COLLATOS, TC., EDGERTON, VR., SMITH, JL. and BOTTERMAN, BR., 1977. Contractile properties and fiber type compositions of flexors and extensors of elbow joint in cat: implications for motor control. *Journal of Neurophysiology*, vol. 40, no. 6, p. 1292-1300. PMid:925731.

CORRUCCINI, RS. and CIOCHON, RL., 1976. Morphometric affinities of the human shoulder. *American Journal of Physical Anthropology*, vol. 45, no. 1, p. 19-37. http://dx.doi.org/10.1002/ajpa.1330450104. PMid:822725

DE OLIVEIRA, JA., NICCOLI FILHO, WD., LEITE, HF., SIMÕES, S. and MADEIRA, MC., 1988. Anatomic aspects of the facial nerve of the capuchin monkey (Cebus apella). *Revista Brasileira de Biologia*, vol. 48, no. 4, p. 785-788. PMid:3241889.

DUBOWITZ, V. and BROOKE, M., 1973. *Muscle biopsey: a modern approach*. London: Sauders.

DUTTO, DJ., HOYT, DF., CLAYTON, HM., COGGER, EA. and WICKLER, SJ., 2006. Joint work and power for both the forelimb and hindlimb during trotting in the horse. *The Journal of Experimental Biology*, vol. 209, no. Pt 20, p. 3990-3999. http://dx.doi.org/10.1242/jeb.02471. PMid:17023593

DUTTO, DJ., HOYT, DF., COGGER, EA. and WICKLER, SJ., 2004. Ground reaction forces in horses trotting up an incline and on the level over a range of speeds. *The Journal of Experimental Biology*, vol. 207, no. Pt 20, p. 3507-3514. http://dx.doi.org/10.1242/jeb.01171. PMid:15339946

ERIKSON, GE., 1963. Brachiation in New World monkeys and in anthropoid apes. *Symposia of the Zoological Society of London*, vol. 10, p. 135-164.

EVARTS, EV., 1982. Pyramidal tract neurones and mechanisms for recovery of function following lesions of motor cortex. *Electroencephalography and Clinical Neurophysiology. Supplement*, vol. 36, p. 147-152. PMid:6186471.

GASC, JP., RENOUS, S., CASINOS, A., LAVILLE, E. and BOU, J., 1985. Comparison of diverse digging patterns in some small mammals. In DUNCKER, HR. and FLEISCHER, G. (Eds.). *Functional morphology in vertebrates*. Stuttgart: Fischer.

HERMANSON, JW. and HURLEY, KJ., 1990. Architectural and histochemical analysis of the biceps brachii muscle of the horse. *Acta Anatomica*, vol. 137, no. 2, p. 146-156. http://dx.doi.org/10.1159/000146875. [Basel] PMid:1690494

ISLER, K., 2005. 3D-kinematics of vertical climbing in hominoids. *American Journal of Physical Anthropology*, vol. 126, no. 1, p. 66-81. http://dx.doi.org/10.1002/ajpa.10419. PMid:15386239

JENKINS JUNIOR, FA., DOMBROWSKI, PJ. and GORDON, EP., 1978. Analysis of the shoulder in brachiating spider monkeys. *American Journal of Physical Anthropology*, vol. 48, no. 1, p. 65-76. http://dx.doi.org/10.1002/ajpa.1330480110. PMid:414626

JOUFFROY, FK., MEDINA, MF., RENOUS, S. and GASC, JP., 2003. Immunocytochemical characteristics of elbow, knee and ankle muscles of the five-toed jerboa (Allactaga elater). *Journal of Anatomy*, vol. 202, no. 4, p. 373-386. http://dx.doi.org/10.1046/j.1469-7580.2003.00167.x. PMid:12739615

JOUFFROY, FK., STERN JUNIOR, JT., MEDINA, MF. and LARSON, SG., 1999. Function and cytochemical characteristics of postural limb muscles of the rhesus monkey: A telemetered EMG and immunofluorescence study. *Folia Primatologica*, vol. 70, no. 5, p. 235-253. http://dx.doi.org/10.1159/000021703. PMid:10567829

KAWAI, M., MINAMI, Y., SAYAMA, Y., KUWANO, A., HIRAGA, A. and MIYATA, H., 2009. Muscle fiber population and biochemical properties of whole body muscles in Thoroughbred horses. *The Anatomical Record*, vol. 292, no. 10, p. 1663-1669. http://dx.doi.org/10.1002/ar.20961. PMid:19728360

KIMURA, T., KUMAKURA, H., INOKUCHI, S. and ISHIDA, H., 1987. Composition of muscle fibres in the slow loris, using the m. biceps brachii as an example. *Primates*, vol. 28, no. 4, p. 525-532. http://dx.doi.org/10.1007/BF02380866.

MATSUMOTO, A., NAGATOMO, F., MORI, A., OHIRA, Y. and ISHIHARA, A., 2007. Cell size and oxidative enzyme activity of rat biceps brachii and triceps brachii muscles. *The Journal of Physiological Sciences*, vol. 57, no. 5, p. 311-316. http://dx.doi.org/10.2170/physiolsci.RP008907. PMid:17971264

MERKENS, HW., SCHAMHARDT, HC., VAN OSCH, GJ. and VAN DEN BOGERT, AJ., 1993. Ground reaction force patterns of Dutch warmblood horses at normal trot. *Equine Veterinary Journal*, vol. 25, no. 2, p. 134-137. http://dx.doi.org/10.1111/j.2042-3306.1993.tb02923.x. PMid:8467772

MILLER, RA., 1932. Evolution of the pectoral girdle and forelimb in the primates. *American Journal of Physical Anthropology*, vol. 17, no. 1, p. 1-56. http://dx.doi.org/10.1002/ajpa.1330170113.

MORIYAMA, K., 1983. Functional differentiation of fore and hindlimb muscles in macaca fuscata determined on the basis of enzymatic activities. *Primates*, vol. 24, no. 1, p. 94-108. http://dx.doi.org/10.1007/BF02381457.

NIKI, Y., UEDA, Y. and MASUMITSU, H., 1984. A force plate study in equine biomechanics 2. The vertical and fore-aft components of floor reaction forces and motion of equine limbs at walk and trot. *Bulletin of Equine Research Institute*, vol. 21, p. 8-18.

OXNARD, CE., 1963. Locomotor adaptation of the primate forelimb. *Symposia of the Zoological Society of London*, vol. 10, p. 165-182.

PADYKULA, HA. and HERMAN, E., 1955. The specificity of the histochemical method for adenosine triphosphatase. *The Journal of Histochemistry and Cytochemistry*, vol. 3, no. 3, p. 170-195. http://dx.doi.org/10.1177/3.3.170. PMid:14381606

PAYNE, RC., VEENMAN, P. and WILSON, AM., 2004. The role of the extrinsic thoracic limb muscles in equine locomotion. *Journal of Anatomy*, vol. 205, no. 6, p. 479-490. http://dx.doi.org/10.1111/j.0021-8782.2004.00353.x. PMid:15610395

PEARSE, AE., 1968. *Histochemistry: theoretical and applied*. Baltimore: Williams and Wilkins.

PETER, JB., BARNARD, RJ., EDGERTON, VR., GILLESPIE, CA. and STEMPEL, KE., 1972. Metabolic profiles of three fiber types of skeletal muscle in guinea pigs and rabbits. *Biochemistry*, vol. 11, no. 14, p. 2627-2633. http://dx.doi.org/10.1021/bi00764a013. PMid:4261555

PETTER, A. and JOUFFROY, FK., 1993. Fibre type population in limb muscles of Microcebus murinus. *Primates*, vol. 34, no. 2, p. 181-196. http://dx.doi.org/10.1007/BF02381389.

PLAGHKI, L., GOFFART, M., BECKERS-BLEUKX, G. and MOUREAU-LEBBE, A., 1981. Some characteristics of the hindlimb muscles in the leaping night monkey *Aotus trivirgatus* (Primates, Anthropoidae, Cebidae). *Comparative Biochemistry and Physiology*, vol. 70, no. 3, p. 341-349. http://dx.doi.org/10.1016/0300-9629(81)90188-2.

ROSE, MD., 1973. Quadrupedalism in primates. *Primates*, vol. 14, no. 4, p. 337-357. http://dx.doi.org/10.1007/BF01731356.

ROSE, MD., 1989. New postcranial specimens of *catarrhines* from the Middle Miocene Chinji Formation, Pakistan: descriptions and a discussion of proximal humeral functional morphology in anthropoids. *Journal of Human Evolution*, vol. 18, no. 2, p. 131-162. http://dx.doi.org/10.1016/0047-2484(89)90067-5.

ROY, RR., BELLO, MA., POWELL, PL. and SIMPSON, DR., 1984. Architectural design and fiber-type distribution of the major elbow flexors and extensors of the monkey (cynomolgus). *The American Journal of Anatomy*, vol. 171, no. 3, p. 285-293. http://dx.doi.org/10.1002/aja.1001710305. PMid:6517031

SCHILLING, N., 2005. Characteristics of paravertebral muscles - fibre type distribution pattern in the pika, Ochotona rufescens (Mammalia: Lagomorpha). *Journal of Zoological Systematics and Evolutionary Research*, vol. 43, no. 1, p. 38-48. http://dx.doi.org/10.1111/j.1439-0469.2004.00295.x.

SCHMIDT, M. and SCHILLING, N., 2007. Fiber type distribution in the shoulder muscles of the tree shrew, the cotton-top tamarin, and the squirrel monkey related to shoulder movements and forelimb loading. *Journal of Human Evolution*, vol. 52, no. 4, p. 401-419. http://dx.doi.org/10.1016/j.jhevol.2006.11.005. PMid:17289114

SCHMITT, D. and LEMELIN, P., 2002. Origins of primate locomotion: gait mechanics of the woolly opossum. *American Journal of Physical Anthropology*, vol. 118, no. 3, p. 231-238. http://dx.doi.org/10.1002/ajpa.10048. PMid:12115279

SCHÖN YBARRA, MA. and SCHÖN III, MA., 1987. Positional behavior and limb bone adaptations in red howling monkeys (Alouatta seniculus). *Folia Primatologica*, vol. 49, no. 2, p. 70-89. http://dx.doi.org/10.1159/000156310. PMid:3454342

SICKLES, DW. and PINKSTAFF, CA., 1981a. Comparative histochemical study of prosimian primate hindlimb muscles. I. Muscle fiber types. *The American Journal of Anatomy*, vol. 160, no. 2, p. 175-186. http://dx.doi.org/10.1002/aja.1001600204. PMid:6455915

SICKLES, DW. and PINKSTAFF, CA., 1981b. Comparative histochemical study of prosimian primate hindlimb muscles. II. Populations of fiber types. *The American Journal of Anatomy*, vol. 160, no. 2, p. 187-194. http://dx.doi.org/10.1002/aja.1001600205. PMid:6791489

SINGH, K., MELIS, EH., RICHMOND, FJR. and SCOTT, SH., 2002. Morphometry of Macaca mulatta forelimb. II. Fiber-type composition in shoulder and elbow muscles. *Journal of Morphology*, vol. 251, no. 3, p. 323-332. http://dx.doi.org/10.1002/jmor.1092. PMid:11835368

WERNECK, LC., 1981. O valor da biopsia muscular em neurologia (Análise de 290 exames a fresco e pela histoquímica). *Revista Brasileira de Clínica e Terapêutica*, vol. 10, p. 2-24.

WRIGHT, KA., 2007. The relationship between locomotor behavior and limb morphology in brown (Cebus apella) and weeper (Cebus olivaceus) capuchins. *American Journal of Primatology*, vol. 69, no. 7, p. 736-756. http://dx.doi.org/10.1002/ajp.20391. PMid:17253617