Proposed actions of bi-articular muscles and the design of hindlimbs of bi- and quadrupeds

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Abstract

In contemporary textbooks on functional anatomy, the actions of muscles which cross more than one joint are often described according to the degrees of freedom which they might influence about the joints crossed. Such actions, however, might in principle also be performed by sets of mono-articular muscles crossing the same joints. In the past centuries many authors have provided convincing evidence that muscles which cross more than one joint are able to perform unique actions that could by no means be realized by sets of mono-articular muscles.

This paper provides an overview of the literature from these previous centuries. The major action of bi-articular muscles appears to be their capacity to couple movements in adjacent joints. The consequences of this action (which was already identified more than three centuries ago) can be explained in various different contexts. Examples are presented which may help to understand the principles which underly the general design of the hindlimb of man, hoofed animals and predators.

"Nature, just in everything, has made the size of the muscles to accord with the usefulness of the actions they must perform".

De usu partium, I 171 Galen (131–201 AD)
(transl. by May, 1968)
1. Introduction

Since Aristotle (384–322 BC) wrote his *De incessu animalium*, the functional anatomy of animals has received considerable attention. This is especially true with respect to the musculoskeletal design of the extremities.

When focussing on muscles which are primarily responsible for movements in the sagittal plane, the global design of the hindlimb shows a striking similarity across different bi- and quadrupeds. As outlined in Fig. 1, hindlimbs mostly contain sets mono-articular antagonists at the hip, knee and ankle joints and a set of bi-articular antagonists at both sides of the femur. Especially in quadrupeds with long metatarsi (as is the case in most hoofed animals) one can also observe a set of bi-articular antagonists along the tibia. In animals with short metatarsi (such as primates), however, the cranial one is absent. The only major differences in hindlimb design among different animals are the relative lengths of the femur, tibia and especially the metatarsi relative to the total leg lengths and the extent to which the distal muscles contain active muscles fibres.

![Diagram of hindlimb design](image)

Fig. 1. Outline of the general design of the hindlimb of bi- and quadrupeds. The peroneus tertius is bi-articular in a limited number of animals (e.g. springbok, horse) but is mono-articular in many other animals.
The functional significance of the sets of mono-articular muscles seems rather unambiguous. Since muscles can only pull, one needs at least one set of antagonists to control the flexion-extension degree of freedom in the sagittal plane (Galen, 131-201 AD). The functional significance of muscles which cross two joints is much less clear, especially if one tries to imagine which actions might be performed by these muscles which could not be performed by a set of mono-articulars crossing the same two joints (henceforth referred to as unique actions of bi-articular muscles). Contemporary textbooks on functional anatomy or kinesiology do not contain much information about this question. Bi-articular muscles are classified according to their extending or flexing influence with respect to the two joints that are crossed. The gastrocnemius for example, is said to be a knee flexor and a plantar flexor. With such a description it is difficult to understand why this muscle is highly active in explosive leg extensions in which hip, knee and ankle joints are simultaneously stretched (Bobbert and Van Ingen Schenau, 1988). Apart from an explanation of the so-called Lombard’s paradox (which deals with the observation that co-activation of hamstrings and rectus femoris will result in hip and knee extension due to differences in their level arms at both joints) one will find surprisingly little information about actions of these muscles which could not be performed by mono-articular muscles. This is surprising since the literature of especially the last two centuries contains convincing examples of such unique actions. Since most other contributors of this special issue will focus their paper on recent findings and in order to prevent too much overlap with other publications of our group (Bobbert and Van Ingen Schenau, 1988; Van Ingen Schenau, 1989; Van Ingen Schenau et al, 1992a; Jacobs and Van Ingen Schenau, 1992; Van Ingen Schenau and Bobbert, 1993; Rozendal, this issue; Bobbert and Zandwijk this issue), this paper will discuss opinions and observations published in the previous centuries and some possible explanations of the differences in the design of the hindlimb among different mammals based on these and more recent insights in the unique actions of bi-articular muscles.

2. From Aristotle to Borelli

One of the very first extensive descriptions of the musculo-skeletal design of animals was published by Aristotle (384–322 BC). His *De inessu animalium* can be judged as one of the first textbooks of functional
anatomy. Although he states in this book that “Nature created nothing without purpose”, Aristotle did not pay special attention to muscles which cross more than one joint. In the present author's reading, Galen (131–201 AD) seems to be the first scientist who explicitly described the existence of bi-articular muscles. Galen, who was a physician and surgeon at the school of gladiators in Pergamo, published more than 500 scientific treatises without being guilty of what nowadays is indicated as “salami-publishing”. His most known merit concerns his identification of the role of the brain and peripheral (motor and sensory) nerves in the control of movements. He described various bi-articular muscles. With respect to the rectus femoris he remarks that its major action (“the sake for which it was made”) is knee extension but also: “... when it is tensed, it naturally not only draws up the tibia toward itself, but also flexes the femur, ...” and: “In fact, Nature acted providently in making this muscle grow out from above the diathrosis at the groin in order to provide another extra movement necessary to the animal” (De usu partium, II, p. 373; translated by May, 1968). Galen did not indicate why such an “extra movement” could not be performed by two mono-articular muscles. He deserves, however, credit for his statement that “the usefulness of the parts of an instrument must be related to the actions of the whole instrument” (De usu partium, I 183) arguing that we will fail to understand the function of muscles if we do not study that function in a natural context. In fact, one might state that the description of muscular actions as can be found in most contemporary textbooks is only valid for an animal in a weightless condition floating in space without any contact with the environment where muscles are stimulated one at a time (as approached by Duchenne through his muscle stimulation experiments; Duchenne, 1867). Galen already recognized that (as will be demonstrated in many of the papers of this special issue) if one tries to understand the role of muscles one should study the action of muscles during movements of the entire organism in its (mechanical) interaction with the environment.

After Galen, there was hardly any progress in the knowledge about bi-articular muscles for more than 1000 years (as was the case in most sciences). Important progress in functional anatomy and (muscle) physiology was not made until the 16th and 17th centuries. Due to the work of for example Canape (1541), Vesalius (1543), Harvey (1627) and Stensen (1662, 1667), the contractile capacity of muscle fibres was recognized and the functional significance of their (architectural) arrangement relative to the passive tendinous structures was indicated (see Foster, 1901, for an extensive review of this period).
Based on these important predecessors and on the mathematical/physical line of approach advocated by Galilei (1564–1642) and Descartes (1596–1650), Borelli wrote his famous De motu animalium (1680/1681; published in two parts after his death) which was recently translated into English. Due to this important work, Borelli can be judged as the founder of what we now would define as the interdisciplinary science of human and animal movement. Borelli was the first who attempted to quantify muscular loads in complex movements; he discussed various types of locomotion (e.g. walking, swimming, skating, flying), and aspects of motor control and motor learning, ventilation, blood circulation and nutrition.

With respect to the action of muscles which cross over more than one joint, he gave a nice example of a poly-articular tendinous muscles in birds which allows these birds to flex their digits around a tree branch under the influence of their own body weight leading to a stable posture which can be maintained without metabolic costs (Borelli, 1680/1681, propositions CXLIX and CL). Apart from the fact that he seems to realize that bi-articular muscles cause some coupling between the actions in the joints crossed, Borrelli does not provide more evidence for actions of bi-articular muscles which are advantageous when compared to two mono-articular muscles. His calculations of muscular loads even seem to prove the opposite (propositions LIII and LIV). He gives an example of a man (120 pounds) who carries a load of 120 pounds on his neck with flexed hip and knee joints (Fig. 2). If these loads are to be opposed by the gluteus maximus, a vastus and the soleus only, Borelli calculated a “total load” of the muscles of 5336 pounds (Fig. 2a). With the bi-articular rectus femoris and gastrocnemius (Fig. 2b) and assuming that the load of the knee extensors and plantar flexors is shared according to their cross-sectional areas, Borelli calculates a “total load” of 6040 pounds. His calculations are based on some type of inverse dynamics. Although a formal definition of force and the existence of reaction forces were unknown in his time (and as consequence one can easily dispute the magnitudes of his calculations), his conclusion that the sum of all muscle forces is larger in the second case is correct. This is due to the opposing effects of the bi-articular antagonists at the hip and the knee joints which have to be compensated by higher (summed) forces of the hip and knee extensors in order to obtain the same net extending moments in these joints. So, based on these analyses, co-activations of mono-articular agonists and bi-articular antagonists might seem to be disadvantageous; although it is not clear how exactly the sum of muscle forces is related to metabolic costs. However, as will be illustrated
Fig. 2. As Borelli correctly argued, the total muscle load necessary to maintain this posture is larger if the bi-articular rectus femoris and gastrocnemius muscles are involved (Fig. 2b) when compared to the situation where only mono-articular muscles are activated (after Borelli, 1680/1681).

in the following part of this paper, co-activations of mono-articular agonists and their bi-articular antagonists are proven to be highly efficient in most dynamic tasks.

3. From Borelli to the first half of the present century

After Borelli, the bi-articular muscles were left in peace until about the middle of the 19th century. In the following 100 years, however, considerable evidence was provided by a large number of authors that these muscles do indeed perform unique actions which could by no means be performed by sets of mono-articular muscles spanning the same joints. Even when judged on the basis of our present knowledge derived with sophisticated mechanical analyses and model simulations, this evidence is so convincing that it is difficult to understand why this knowledge has not been incorporated in our present textbooks. A reason might be that movement scientists of the second half of our present century are on
average less familiar with mechanical concepts than movement scientists in previous centuries, possibly as the result of a reaction on the highly mechanistic approaches used by most scientists even in the humanities until a few decades ago. The actions of muscles and especially poly-articular muscles, however, often have to be described in a terminology which relies strongly on mechanical and energetical concepts of a rather hypothetical nature (Fischer, 1927). Since an overview of the major hypotheses of the authors from this period was presented before (Van Ingen Schenau, 1990), only the major papers will be summarized here.

Since Borelli (1680/1681), many authors have argued that bi-articular muscles may couple the movements in the joints crossed (Hüter, 1863, 1869; Cleland, 1867; Duchenne, 1867; Fick, 1879; Langer, 1879; Hering, 1897; Fischer, 1902; Lombard, 1903; Von Baeyer, 1921, 1922; Fischer, 1927; Fenn, 1938; Elftman, 1939). In fact, almost all of the various descriptions of unique actions of these muscles discussed by these and later authors can be seen as consequences of this coupling action. The most complete overviews in this respect were published by Cleland (1867) and Fick (1879). The coupling action per se can easily be imagined with the help of a bi-articular tendinous gastrocnemius as illustrated in Fig. 3 (an example which is valid for most hoofed animals). Since the strain of a tendon is limited, it will be

Fig. 3. With a tendinous gastrocnemius, knee extension is always coupled to plantar flexion. Due to this tendinous action of bi-articular muscles, such as the knee extensors, can do work about joints that are not crossed by these muscles.
clear that in this design a knee extension is always coupled to a plantar flexion. In animals which also have a bi-articular muscle or tendon in front of the tibia (Peroneus tertius; Fig. 1), such a coupling is also present between knee flexion and dorsal flexion. This means that the ankle joint can be moved on the basis of actions of muscles which do not pass that joint. These “indirect actions” (Cleland, 1867) are of course also present if these bi-articulars contain muscle bellies. To a certain extent one can judge such active bi-articular muscles in this context as tendons whose lengths can be adjusted and whose actions can be timed (options which are not present in passive tendons). To indicate this coupling effect of both active bi-articular muscles and passive bi-articular tendons, Cleland (1867) speaks of the “tendinous” actions of bi-articular muscles. The advantages of these tendinous actions can be expressed in various ways. Many authors argued that due to the “indirect” control of distal joints most of the muscle mass of the legs can be located close to the trunk leading to slender legs with low moments of inertia (Cleland, 1867; Fick, 1879; Von Baeyer, 1921). Another argument often used is that in simultaneous extensions of both joints which are crossed, bi-articular muscles will have a lower shortening velocity (and thus higher force) than two mono-articulars would need to have (Duchenne, 1867; Fick, 1879; Fenn, 1938). This is one of the reasons why for example the plantar flexion moments in explosive tasks such as jumping can be considerably larger than what is measured in mono-articular plantar flexions at the same angular velocities (Bobbert and Van Ingen Schenau, 1990). In the studies of our own group we mostly used an energetical approach. In an inverse dynamical analysis as originally applied by Elftman (1939) one can calculate the net moments at the joints of a model which is supposed to consist of rigid links. By applying power equations to these rigid links one can prove that the available external power is equal to the sum of joint powers (Aleshinsky, 1986; Van Ingen Schenau and Cavanagh, 1990) where joint power is equal to the product of net joint moment and joint angular velocity. If one applies this approach to the example of Fig. 3, it will be clear that the joint power calculated for plantar flexion cannot be liberated by the bi-articular tendon but has to be delivered by the knee extensor muscles. Since the gastrocnemius tendon will decrease the net moment in the knee, its effect on the net joint powers will be a decrease of knee joint power and an increase of ankle joint power. We defined this effect (which of course is also present with active bi-articulars) as a “proximo-distal transport of power”. Although the reasoning based on these rather hypothetical joint powers may easily cause some confusion
(Pandy and Zajac, 1991; see also our response in Van Ingen Schenau et al., 1990 and Van Soest et al., 1993), even this concept appeared not to be new: Cleland (1867), Fick (1879), Lombard (1903) as well as Fenn (1938) already indicated such effects of bi-articular muscles.

In this context Cleland stated about bi-articular muscles that “they convey from one joint to another the effects of the contractions of other muscles” which has the advantage that the “total amount of muscle power is made available for overcoming the total amount of resistance whichever be the joint on which that may to the greatest extent fall”. For a simultaneous hip and knee extension Fick (1879) states: “es leisten also Gluteus Maximus und Adductor Magnus durch den Rectus mehr Arbeit am Kniegelenk als der Rectus durch eigene Contraction leisten würde”.

Lombard (1903) speaks of energy which is transmitted and Fenn (1938) argues with respect to this movement: “Presumably the gluteus muscle would be used to extend the hip, in which case the hip extensor might be said to be doing work in extending the knee, its force being transmitted through the rectus femoris muscle”.

Although we performed the search for this older literature after our group had already worked in this field for many years, I feel that these authors (especially Cleland and Fick) deserve the credit to be referred to as the founders of our present hypotheses about unique actions of bi-articular muscles. In fact most of the present views with respect to this subject can be seen as applications of these basic concepts.

4. Bi-articular muscles and some differences in hindlimb design between various species

As stated above, the major differences in the hindlimb design outlined in Fig. 1 concern the relative segmental lengths and the extent to which the distal muscles contain active muscle bellies.

Table 1 shows the global segments lengths ratios, femur : tibia : metatarsus, for some species (note that the total foot length is always larger than the length of the longest metatarsus). Man (and most other primates and some other animals like bears) have relatively short metatarsi while most hoofed animals have a total foot length which is considerably larger than the length of the tibia or the femur. Man, monkeys and bears may as plantigrades easily walk or stand on two legs (and climb trees), but they are bad long distance runners and bad sprinters. The most specialized long
Table 1
Segment lengths of tibia and metatarsus relative to femur length

<table>
<thead>
<tr>
<th></th>
<th>Femur:</th>
<th>Tibia:</th>
<th>Metatarsus</th>
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<tbody>
<tr>
<td>Man</td>
<td>1</td>
<td>1</td>
<td>0.15</td>
</tr>
<tr>
<td>Rodents</td>
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<td>0.3</td>
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<td>Predators</td>
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<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td>Hoofed animals</td>
<td>1</td>
<td>1</td>
<td>0.7</td>
</tr>
</tbody>
</table>

(Parly from Alexander and Goldsping, 1977).

distance runners can be found among the hoofed animals while predators appear to be specialized to achieve a very large acceleration from stance which is an important prerequisite to cover a short distance in a minimal time interval. These two specializations can to a certain extent be seen as contradictory with respect to the optimal hindlimb design. With respect to the mechanical requirements in running, sprinting and jumping tasks two major leg functions can be distinguished: rotation of the entire leg relative to the trunk and flexion and extension of all joints. This can easily be illustrated with help of Fig. 4. Without technical equipment such as wheels or skates, the velocity and acceleration of the trunk is almost entirely determined by the velocity difference and its time derivative between the hip and the (fixed) position of the point of contact between foot and

![Fig. 4](image_url)

**Fig. 4.** The major movements of the hindlimbs in sprinting and running are a rotation of the entire leg relative to the trunk which is necessary in maintaining a high speed and a lengthening (and shortening) of the distance between the hip and the toes important in sprinting and jumping from rest.
The velocity \( v \) of this ground contact point relative to the hip can be resolved into two components \( v_r \) and \( v_e \). The vector \( v_r \) is predominantly dependent on the rotational velocity of the entire leg relative to the trunk while \( v_e \) depends on the extension velocities in all joints. When comparing hoofed animals with predators, it appears that the hindlimb design of hoofed animals is suitable to a high \( v_r \) at low metabolic costs while predators are predominantly suitable to realize a high \( v_e \) and a high acceleration \( dv_r/dt \).

As stated above, most hoofed animals have tendinous lower leg muscles and relatively long metatarsi. This means that most of the muscle mass is located close to the trunk. This leads to relatively low moments of inertia which is very important in running since the majority of the metabolic energy liberated during running is necessary for the backward (and forward) rotational acceleration and deceleration of the leg associated with \( v_r \) (Alexander and Goldspink, 1977). A clear disadvantage of such a design is that due to the bi-articular lower leg tendons, the knee and ankle joints cannot be moved independently which allows only a rather limited repertoire of stereotyped movements. Most predators have active mono- and bi-articular lower leg muscles, relative larger lever arms of the plantar flexors and relative shorter metatarsi. These global differences are outlined in Fig. 5. This leads to considerable larger moments of inertia. Based on data provided by Hildebran and Hurley (1985) it can be calculated that from the two fastest quadrupeds, the cheetah and the pronghorn (both having a body mass of about 30 kg), the cheetah needs about 2–3 times more energy than the pronghorn in rotating the hindleg at the same top speeds of about 100 km/hour despite the fact that the pronghorn has a total leg length which is about 30% longer than that of the cheetah (Van Ingen Schenau, 1992). The fact that the cheetah can (albeit for only a short time period) achieve the same peak velocity as the pronghorn is due to a larger amount of muscles which this animal can mobilize. In contrast to hoofed animals who use their frontlegs merely to support their body weight, predators also use their frontlegs for propulsion and moreover the flexion–extension movements of their back also contribute significantly to their speed. In this context it should also be noted that a dissection study of a doctoral student of our group revealed that the cheetah may not be a typical example for the general design of predators (Aarts, 1992). The lower leg muscles of this animal appeared to be almost entirely tendinous. This is in sharp contrast to for example lions, panthers and cats who do have substantial muscle bellies in their lower leg muscles. As a conse-
Fig. 5. The hindlimbs of hoofed animals have relatively low moments of inertia due to their long metatarsi and the absence of active muscle mass in the lower leg muscles. This allows them to maintain a high running speed. Predators, however, can realize much higher push off forces due to their shorter metatarsi, their large ratios between the lever arm of the plantar flexors and the shortest distance (a) between the ankle joint and the line of action of the ground reaction force and more work due to their active calf muscles. Consequently, these predators seem more specialized to realize a large $v_e$ and $dv_e/dt$. Due to the stronger and shorter metatarsi, their larger lever arms of the calf muscles and their active bi-articular lower leg muscles, they can realize considerably larger initial accelerations from stance than hoofed animals. This is not only due to the possibly larger ground reaction forces (Fig. 5) but also to the possibility to realize a proximo-distal sequence in the timing of the onset of joint extension which has been shown to be important for the total energy production in explosive leg extensions (Bobbert and Van Ingen Schenau, 1988; Jacobs and Van Ingen Schenau, 1992b).

For a proper understanding of the unique actions of bi-articular muscles as discussed above, it is important to realize that tendinous bi-articulars can only convey power from one joint to another. The total amount of energy delivered in a leg extension movement, however, is equal to the time integral of the (instantaneously) summed joint powers. This means that tendinous bi-articulars may be necessary for the most effective distribution of the available muscle power over the joints but clearly they cannot increase the total amount of energy whereas active bi-articular muscles can.
Fig. 6. In the leg extension during a jump, sprint or gallop an animal often has to push off while only the hindlegs make contact with the ground. In order to preserve the angular momentum of the entire animal, the ground reaction force has to point more or less in the direction of the body centre of gravity (bcg). This can only be realized through the combination of a net extending moment in the hip, a plantar flexing moment in the ankle and a net flexing moment in the knee joint (during knee extension!). In such a complicated movement, eccentric contractions can be minimized through activation of the bi-articular hamstrings. The knee extensors can even contribute to work as long as the required net flexing moment in the knee is maintained by their bi-articular antagonists.

The bi-articular upper leg muscles of bi- and quadrupeds are never tendinous, obviously due to the fact that walking and running would hardly be possible in such a design. The major differences in these muscles between species is the relative size of the rectus femoris and hamstrings. Quadrupeds appear to have considerable larger bi-articular hamstrings (up to over 30% of the total leg muscle mass) than bipeds such as man while their rectus femoris is relatively less well developed. This is most likely associated with the important role of these bi-articular muscles in the regulation of the distribution of the net moments and joint power over the hip and knee joints (Van Ingen Schenau, 1989). As recently demonstrated for man, these muscles appear primarily responsible for the control of the direction of the external force on the ground (Van Ingen Schenau et al., 1992a; Jacobs and Van Ingen Schenau, 1992b). For example, if an animal wants to push slightly backwards in order to realize a ground reaction force which points more or less in the direction of its body center of gravity (Fig. 6), the net joint moments necessary to realize this force direction are a combination of a (large) extending moment in the hip, a flexing moment in
the knee (associated with the fact that the line of action runs in front of the knee) and a plantar flexing moment.

Since all joints are extended in such a jumping or galloping movement, it would be highly inefficient to activate a mono-articular knee flexor. To avoid eccentric contractions, the hamstrings are activated instead, leading to the required distribution of net moments and joint powers. The mono-articular knee extensors can even be activated in order to contribute to the total work done in the leg extension as long as the hamstrings can adjust the required net flexing moment (note that the power produced by these muscles now appears as part of the hip joint power). Humans appear to de-activate the hamstrings and to activate the rectus femoris if a forward directed external (action) force is required. From the results of animal studies it seems likely that the roles of these bi-articular antagonists do not differ between man and quadrupeds (Van Ingen Schenau and Bobbert, 1993).

In order to prevent a rotation of the entire animal, the line of action of the resultant of the ground reaction forces has to point more or less in the direction of the body centre of gravity. In quadrupeds the centre of gravity lies more in front of the hip and knee joints than in bipeds. This means that if quadrupeds push off with the hind legs only, which is the case in jumping, sprinting and galloping, the situation of Fig. 6 will often occur. In humans, however, the line of action will mostly point at the trunk and thus run between the hip and knee joints with occasional deviations to both sides. This means that quadrupeds rely much more on their bi-articular hamstrings and much less on the rectus femoris than humans which explains the differences in the relative size of these bi-articulars between these species.

The cheetah even appears to have a hamstring muscle which can control the required net moments in the task of Fig. 6 with one actuator only (Fig. 7). The biceps femoris of this animals insert not only on the tibia but also, via a tendon, on the calcaneus (Aarts, 1992). This interesting actuator seems to exist in some other predators as well.

This was an example of just one out of many possible fields where the insights in the unique actions of bi-articular muscles may help to understand questions concerning the design of the musculo-skeletal system. Of course there are many other possible fields of interest where these insights may have considerable impact.

As substantiated by previous papers (e.g. Van Ingen Schenau et al., 1992a,b; Jacobs and Van Ingen Schenau, 1992a) and other contributions to
Fig. 7. Animals like the cheetah have a biceps femoris the active part of which is bi-articular but which is also coupled to the calcaneus via a strong tendon. This bi- and tri-articular actuator helps to realize the combination of a net hip extending knee flexing and plantar flexing moment necessary for the complicated task outlined in Fig. 6.

this issue, this is certainly true for theories on motor control but even for fields like robotics. Robots appear to have considerable problems with the type of tasks as illustrated in Fig. 5 (Bizzi et al., 1992). As indicated before (Gielen and Van Ingen Schenau, 1992) this might be associated with the absence of bi-articular actuators in contemporary robotic devices.

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