Aristotle’s Physiology of Animal Motion: On Neura and Muscles

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Abstract: Aristotle had a developed theory of animal motion with an elaborate physiological component. In this paper we present the physiological component in which the main role is assigned to structures called *neura* that operate on the bones to which they are attached. We demonstrate that *neura* exclude muscles and we propose an explanation for Aristotle's curious failure to observe the actual role of muscles in producing limb motion. Also, we try to identify the main *neura* specified by Aristotle, we show that he conceived of their operation on the bones in producing limb motion in much the same way as we conceive of the operation of muscles, and we point out the main difficulties for his account.

Keywords: locomotion, physiology, mechanics, joints, tendons

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The fact that animals move from one place to another, without any apparent external cause and often in complicated and unpredictable ways, fascinated Aristotle. It was not only a universally recognized manifestation of life that a sound theory of living beings needed to account for, but it also raised a serious problem for his theory of eternity of motion developed in *Physics* VIII. Apart from *de Anima*, in which Aristotle took several chapters to explain what it is about the soul that accounts for motion of animals, he dedicated two separate treatises to animal motion. In *de Motu Animalium* he explored the general principles of all animal motion and explained how the soul moves the body, and in *de Incessu Animalium* he investigated each type of animal motion, such as walking, flying, swimming and crawling. In addition, numerous references to bodily parts involved in animal motion are found in his other biological works, notably in *Historia Animalium* and *de Partibus Animalium*.

These treatises contain a robust theory of animal motion, rich in psychological and physiological detail. What is likely to surprise a modern reader about the physiological part of the theory is that it makes no mention whatsoever of muscles, the tissues whose contraction is known to produce voluntary movements of limbs. In fact, the Greek word for muscle (μῦς) is used in that sense only twice in the Aristotelian corpus, both times in the same passage from *Problemata* (885a38–b1), a work generally believed to have been composed after Aristotle. One may find it hard to imagine that a systematic thinker and a careful observer of animals like Aristotle could possibly have overlooked the role of muscles in effecting animal motion. Instead of muscles, central to Aristotle's explanation of limb motion were structures he called *neura* – usually translated as 'sinews' or 'tendons' – which cannot be identified with muscles.

The aim of this paper is to examine the details of Aristotle's physiology of animal motion and to explain his neglect of muscles. In Section 1 we begin with a sketch of Aristotle's physiology of animal motion, we show why *neura* cannot be identified with muscles, and we discuss two main functions ascribed to *neura*. In Section 2 we examine Aristotle's general account of *neura* in *Historia Animalium* III 5, we try to identify the structures he singled out as the main *neura*, and we offer an explanation of why he failed to observe the actual role of muscles in producing animal motion. Finally, in Section 3, we show that although Aristotle conceived of the operation of *neura* in much the same way as we conceive of the operation of muscles, he made some fundamental physiological assumptions which rendered his physiology of animal motion problematic.

1 The elements of Aristotle's physiology of animal motion

According to Aristotle, the heart is the central organ, both spatially, insofar as it is located roughly in the middle of the chest, and functionally. The heart is central for the activity of nutrition and growth, at first because it governs the development of the embryo, and later because blood is produced in the heart at the final stage of the digestive process, and from there it is distributed all over the body. The heart is central also for the activity of perception, because perceptions take place only when certain alterations transmitted from the peripheral sense-organs, via 'channels' and blood-vessels, arrive at the heart. Some perceptions – notably those of objects which are good or bad for the animal, such as nutrients or predators – are accompanied by thermic alterations ('heatings and chillings'). These thermic alterations, it has been argued elsewhere, should be identified with sensations of pleasure and pain as well as with desires, typically the desire to go for what is pleasant and to avoid what is painful.[1] Finally, the heart is central also for animal motion, because thermic alterations in the heart, produced by perceptions and representations of pleasant or painful objects, cause the connate *pneuma* inside the heart to expand or contract.

Aristotle's notion of the connate *pneuma* is multifaceted and controversial, but for our purpose it will suffice to describe it as warm air which is not taken in from the outside by breathing, but which is generated together with the animal and maintained inside it, primarily in the heart.[2] The connate *pneuma* has a constitution which enables it to react to perceptual alterations accompanied by thermic alterations so as to expand and contract, and to do so repeatedly and non-uniformly, i.e., expanding in some regions and contracting in others. And as the connate *pneuma* in the heart expands and contracts, it pushes and pulls the *neura* inside the heart. This mechanical impulse is, arguably, transmitted to the other *neura* that operate on the system of bones so as to produce movements of limbs.

This is a bare sketch of Aristotle's physiology of animal motion which might tempt modern readers to think that Aristotle's *neura* are in fact muscles, or at least include them, since we know that it is muscles that operate on the system of bones when they contract. Indeed, scholars often assume, tacitly or expressly, that *neura* are or include muscles. For example, A. Preus writes: 'For Aristotle, the *neura* are all the stringy parts – muscles, sinews, and nerves – he does not distinguish.'[3] However, muscles are soft, supple, and vascularized. As such they would be identified as flesh (σάρξ) in Aristotle's division of bodily parts at the most basic level, whereas *neura* are said to be hard, solid, and elastic.[4] So the most basic description of *neura*, in terms of their elementary properties, puts *neura* in a different category of bodily parts than muscles. Second, Aristotle says that *neura* can be cut lengthwise but not crosswise, whereas flesh can be cut in any direction.[5] These properties also suggest that there is no overlap between *neura* and muscles. Third, flesh is the sense-organ (or, more precisely, the connate medium) of the sense of touch, whereas *neura*, by their very

1 For a fuller account of Aristotle's theory, and specifically for the identification of thermic alterations in the heart with desires and feelings of pleasure and pain, see Corcilius and Gregoric (2013).

2 More on the constitution and operations of the connate *pneuma* can be found in Gregoric (forthcoming). For a selected bibliography of modern studies on the connate *pneuma*, see Freudenthal (1995), 107 nn. 2 and 3. See also Berryman (2002); Corcilius (2008), 332–43; Buddensiek (2009).

3 Preus (1981), 81; cf. Nussbaum (1978), 281 and 284; Bos (2003), 37; De Groot (2008), 62.

4 *HA* I 1, 487a1–10; *PA* II 2, 647b10–20; *GA* II 6, 743b3–5

5 *HA* III 5, 515b14–16 and III 16, 519b30–2 constitution, are insensitive, for 'no bloodless part is sensitive.'[6] Fourth, Aristotle says that *neura* do not grow back together after they have been cut,[7] whereas vascularized parts, such as flesh, have regenerative potential.

Finally, to show that Aristotle includes muscles under flesh and overlooks their actual role in effecting bodily movements, we adduce a passage from *de Partibus Animalium* in which Aristotle explains the physiological peculiarities of the human being with reference to its erect posture. One of the peculiarities is that 'mankind has fleshy legs, both thighs and shanks, while all the others have fleshless legs … that is to say, they have sinewy, bony and spiny legs.'[8] The reason why the lower parts are fleshy in human beings, and this certainly refers to various muscles in the buttocks, upper and lower legs, is *not*, as we would expect, to make legs move, but something else: 'In order that it may easily carry the upper parts, which are light, nature, taking the corporeal constituent from the upper parts, added the weight to the lower parts. This is why it made the haunches, thighs, and calves fleshy. At the same time, the nature of the haunches is rendered useful for taking rests.'[9] So the lower extremities are fleshy for the sake of the corporeal constituent's distribution that facilitates erect bipedal gait, not for the sake of producing it.

The quoted passages give us reasons to think that *neura*, in Aristotle's mind, do not comprise muscles and that he is not aware of the actual role of muscles in producing limb motion. Before we can clinch these points, we should return to our sketch of Aristotle's physiology of animal motion and substantiate some of its crucial elements.

The presence of *neura* in the heart, mentioned in the sketch, is well-attested in Aristotle's writings: 'The heart also has many *neura*, and this is reasonable. For the movements are from this part, and are accomplished through pulling and relaxing; so the heart needs such equipment and strength.'[10] In *Historia Animalium* III 5, 515a28–31, Aristotle specifies the middle cavity of the heart as the one containing *neura*. The middle cavity is the most important one of the three recognized by Aristotle, since it is connected with both of the remaining two cavities ('a common source for the other two'[11]), and the blood in it is said to be very pure and of the mean temperature and quantity, which seems to be important for perception

6 *PA* II 10, 656b19; cf. *de An* II 11, 423b12–26; *HA* I 4, 489a23–30; *PA* II 1, 647a19–24.
7 Lones (1912), at 109 remarks that 'it is probable that Aristotle copied this from Hipppocrates,' referring the reader to *Aphorisms* VI 19 (Littré vol. 4, 568.3–4) and VII 28 (Littré vol. 4, 584.2–3).
8 *PA* IV 10, 689b7–10 (trans. J. G. Lennox)
9 *PA* IV 10, 689b12–16 (trans. J. G. Lennox, slightly modified)
10 *PA* III 4, 666b13–16 (trans. J. G. Lennox); cf. *HA* I 17, 496a13 and *GA* V 7, 787b10–788a18.
11 *PA* III 4, 666b33

and thermic alterations that produce expansion and contraction of the connate *pneuma*.[12] The most likely structure that Aristotle has in mind when referring to the *neura* in the heart are the *chordae tendineae*, the small tendons which connect the papillary muscles with the valves.[13] They fit his elementary description of *neura* quite well and they look like miniature versions of the larger tendons which Aristotle calls *neura*, as we shall see presently. We should like to add that the *chordae tendineae* are clearly visible in the hearts of larger domestic animals such as oxen, sheep and pigs which Aristotle may have dissected himself.[14]

Our sketch also mentioned a system of bones upon which the tendons operate. This requires further explication. Bones are said to form a continuous system the origin of which is the spine or its analogue in invertebrates. With the exception of the bones of the head, which are connected by sutures, other parts of the skeletal system are connected by *neura*: 'All the bones which are attached to one another are bound together by *neura*.'[15] The function of *neura*, as Aristotle clearly sees, is not merely to join the bones, but to do so in such a way as to enable one bone to change its position relative to another bone. He writes that two bones of the same limb can be used 'both as one and continuous and as two and divided for the purpose of flexion.'[16] That is to say, one bone can change its relative position to the other bone, when the limb is being flexed or extended ('the bones are used as two and divided'), or one bone can keep the same relative position to the other bone, as when the whole straightened limb is being moved ('the bones are used as one and continuous'). This is possible, Aristotle claims, because *neura* are 'scattered around the joints of the bones.'[17]

This function of *neura* is very important for animal motion. All types of animal motion, according to Aristotle, require fixed points inside the body as much as fixed points outside the body. A fixed point outside the body is a surface offering resistance against which the limbs can be supported when the animal displaces itself. A fixed point inside the body is a resting part of the joint which serves as a prop for the adjacent part of the joint which is moved. This is what Aristotle means by 'using the joint as two'.[18] Of course, a joint can also be 'used

12 *PA* III 4, 666b30–667a6; cf. II 10, 656b1–7 and III 10, 672b14–19; for controversies concerning the identification of Aristotle's three cardiac cavities, see Harris (1973), 122–33.

13 See Lones (1912), 137 and Moraux (1985), 343 n. 18; cf. Harris (1973), 161.

14 See Aristotle's remarks on bulls' hearts at *GA* V 7, 787b15–19. A picture of an open heart of a sheep, with the *chordae tendineae* clearly visible, can be found at: http://www.hometraining-tools.com/heart-dissection-project/a/1318/ (accessed 7 May 2013).

15 *HA* III 5, 515b11–13

16 *PA* II 9, 654a35–b2; cf. *IA* 9, 708b22–4; *MA* 1, 698a18–b1; 8, 702a22–6; 9, 702b30–1.

17 *HA* III 5, 515b4

18 *MA* 8, 702a23–4; cf. n. 16 above.

as one', when no division of labor between the resting and the moved parts takes place, i.e., when no flexing or extending occurs.

Whether a joint is used 'as one' or 'as two' depends not only on the operation of *neura* on the bones connected at the joint, but also on the momentary disposition of certain parts around the joints. As Aristotle notes in *de Motu Animalium* 8, 702a7–10: 'It is reasonable that the inner parts around the origins of the instrumental parts <i.e., around the joints of the limbs> are constructed so as to change from solid to supple and from supple to solid, from soft to hard and *vice versa*.' Presumably, this is reasonable because there has to be something that prepares the joints for different kinds of movements. By growing solid and hard, this bodily part turns one portion of the joint into the fixed point of support against which the other portion will be moved, thus enabling flexion and extension of the limb. By growing supple and soft again, it removes the differentiation within the joint, thus enabling other movements of the limbs, e.g., movement of the whole straightened arm as opposed to bending the elbow.

It is hard to see what else this bodily part 'constructed so as to change from solid to supple and from supple to solid' could be but flesh,[19] or what we would identify as muscles. The change of this bodily part's disposition seems to be another effect of thermic alterations in the heart, and this effect could be transmitted by blood, given that flesh is vascularized. Although this series of conjectures hardly amounts to strong evidence, it suggests that muscles might have a secondary or background role in animal motion, namely insofar as their hardening and softening creates and dissolves fixed parts of the joints, thus enabling different kinds of movements of the limbs.

In any case, one function of *neura* is to connect bones and secure joints, and it is a precondition for successful execution of the second function of *neura*, which is to make limbs move. How a limb is moved – whether as a whole, or in a flexing or extending motion – depends on the disposition of the relevant joint and on the operation of *neura* on the relevant bones. As we shall see later, some *neura* have to pull the bones while others have to be relaxed.

The execution of the second function of *neura* starts in the heart. We take Aristotle to be saying in *de Motu Animalium* 10, 703a18–23, that as *pneuma* in the heart expands, it pushes the *neura* in the heart and thus relaxes them, and as it contracts, it pulls the *neura* in the heart.[20] These pushes and pulls of the

19 Cf. Corcilius and Gregoric (2013), 70–1.

20 We follow the manuscript tradition of this passage. The addition of τε καὶ ἐκτεινομένη and the change of βιαστικὴ into ἑλκτικὴ at a22, as proposed by Farquharson with weak manuscript support and subsequently accepted by Nussbaum, is unnecessary. The point of the lines in a large majority of manuscripts, we take it, is that the connate *pneuma* contracts ἀβίαστος, i.e., *neura* in the heart are then transmitted to the *neura* which operate on the bones so as to make limbs move. In *de Motu Animalium* 7, 701b2–10 the system of bones and *neura* that operate on them is compared with the internal parts of automatic puppets responsible for their movements:

> The movement of animals is like that of automatic puppets, which are set moving when a small motion occurs, the ropes being released and striking against one another … Animals have instrumental parts that are of the same kind: the *neura* and bones, the latter are like the wooden parts and iron in our example and the *neura* like the ropes; when these are released and relaxed the animal moves.[21]

We shall return to this essential passage in Section 3, once we have examined Aristotle's account of *neura* more closely and identified the *neura* he mentions.

2 Aristotle's account of *neura*

We have seen that Aristotle takes one type of structure, *neura*, to perform two distinct functions crucial to animal motion. In modern anatomy, these two functions are performed by several different structures. The structures primarily responsible for binding the bones and stabilizing the joints are ligaments and articular capsules, while tendons bind the bones only indirectly. The structures which enable the movement of limbs, on the other hand, are muscles, with tendons as their terminating parts attached to the bones. All major ligaments, articular capsules and tendons, however, fit Aristotle's description of *neura* very well. They are all hard, solid, and elastic, more easily cut lengthwise than sidewise.

With these results in mind, let us look at Aristotle's account of *neura* in *Historia Animalium* III 5. He states, quite correctly, that 'the greatest number of *neura* is found around the feet, the hands, the ribs, the shoulder-blades, the neck, and the arms.'[22] More specifically, he writes: 'The largest portion of *neura*

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not under external pressure, whereas when it expands, it exerts force and pushes (βιαστικὴ καὶ ὠστική). That the contraction and expansion respectively produce pulling and pushing is evident from the preceding sentence in which Aristotle says that pushing and pulling are the basic locomotory operations (cf. *Phys* VII 2, 243a16–244b14; *de An* III 10, 433b25–6; *PA* III 4, 666b14–15; *IA* 2, 704b22–3). That these operations take place on the *neura* in the heart is clear from the passages cited in n. 10 above.

21 Translation based on the manuscript reading. Nussbaum has κρουόντων ἄλληλα τῶν ξύλων instead of κρουόντων πρὸς ἀλλήλας τὰς στρέβλας; see Nussbaum (1976), 150–1.

22 *HA* III 5, 515b21–3. Although Aristotle's account of *neura* is meant to be general, it is based largely on human anatomy, or at any rate that is what we assume in our attempts on the following pages to identify the main *neura*.

is found in the part which is in charge of jumping (that is called the "ham"); another *neuron*, a doublefolded one, is the *tenōn*, and those which are useful for feats of strength, the *epitonos* and the *ōmiaia*.'[23]

'The part in charge of jumping', or the 'ham' (ἰγνύη), seems to refer to the back of the knee, where the tendon of the biceps femoris is readily observable on the lateral side,[24] and the two tendons, one of the semitendinosus and the other of the semimembranosus muscle, on the medial side. Aristotle seems to think, then, that these three tendons bring about the act of jumping, whereas we know that their function – or rather the function of their respective muscles – is to control the motion of legs, e.g., to enable us to slow down when walking downhill, to land from jumps, or to come to a halt from sprinting. The act of jumping is in fact produced by the contraction of the quadriceps muscle at the front of the upper leg, which extends into a strong tendon and patellar ligament that connects patella to the tibia. Later on, we shall suggest how Aristotle might envisage the tendons of the ham to produce the act of jumping.

Next, Aristotle mentions a double *neuron* called the *tenōn*. In the Hippocratic corpus the word *tenōn* can designate any tendon in the body, but in ordinary Greek ὁ τένων refers to the paradigmatic tendon, that is the thickest, strongest and most prominent tendon – the calcaneal tendon, popularly known as the 'Achilles' tendon'. However, this tendon is not 'doublefolded' (διπτυχές) in any obvious way, which has led D'Arcy Thompson to suggest that Aristotle refers to the great ligament of the neck (*ligamentum nuchae*), based on the Homeric usage of the word τένων. It is more likely that the adjective διπτυχές, which occurs only at this place in the Aristotelian corpus, refers to the bifurcation of the Achilles' tendon into two heads of the gastrocnemius muscle, in the shape of 'Y', which is easily observable, especially in men of athletic build that Aristotle could see in sport arenas.

It is even more difficult to identify 'the *epitonos* and the *ōmiaia*'. The latter suggests that he has in mind tendons in the shoulder area (ὦμος), although these are hardly distinguishable from the salient muscles that control the motion of the arm, especially the deltoid muscle and the pectoralis major.[25] The reference of *epitonos* is even more uncertain. D'Arcy Thompson is content with the statement that its anatomical meaning is unknown, whereas A. L. Peck ex-

23 *HA* III 5, 515b6–10

24 The Hippocratic author refers to this tendon as ὁ ἔξω τένων ὁ παρὰ τὴν ἰγνύην; cf. *de Fracturis* 37 (Littré vol. 4, 542.1) and *Vectiarius* 1 (Littré vol. 4, 340.7–8).

25 D'Arcy Thompson (1910) *ad loc.* says that *ōmiaia* 'is probably the deltoid muscle.'

plains that the term *epitonos* is used of the great sinews of the shoulder and arm at Plato's *Timaeus* 84e.[26] Here is the relevant passage:

> And often, when flesh disintegrates inside the body, air is produced there, but is unable to get out. This air then causes just as much excruciating pain as the air that comes in from outside. The pain is most severe when the air settles around the *neura* and the veins there and causes them to swell, thereby stretching backwards the "back stays" [τοὺς ἐπιτόνους] (the great sinews of the shoulder and arm) and the *neura* attached to them. It is from this phenomenon of stretching [τῆς συντονίας], of course, that that the diseases called *tetanus* ("tension") and *opisthotonus* ("backward stretching") have received their names.[27]

It is likely that Aristotle borrows the term from this passage. In their interpretation of *epitonous* at 84e6 both A. L. Peck and D. Zeyl seem to follow A. E. Taylor, who has the following remark in his commentary *ad loc*.: 'The word [viz. *epitonos*] properly means the "back stays" of a mast. Hence its use, by a natural metaphor, for the great sinews of the shoulder and arm, Aristot. *Hist. Animal.* Γ. 515^{b}6…' It is unclear how Taylor arrived at his interpretation of *epitonos*. Given that he seems to have based it on our passage from Aristotle's *Historia Animalium*, perhaps he took 'the *epitonos* and the *ōmiaia*' to be synonymous terms referring to the same thing, which would explain why he understood *epitonous* in the *Timaeus* to refer to the 'great sinews of the shoulder and arm'. However, there is no need to suppose that Aristotle uses the two terms as synonyms for the same structure. On the contrary, the context of the passage, in which Aristotle enumerates the main *neura*, gives us every reason to believe that *epitonos* does not refer to the structures in the shoulders (*ōmiaia*).

Cornford's translation of the *Timaeus* passage reads: '… the air, gathering and swelling up round the sinews and the small veins there, makes them stretch backwards the tendons of the back and the sinews attached to them.' In the accompanying note, Cornford says that *epitonoi* 'seem to mean whatever tendons or sinews were supposed to hold the back erect, like the back-stays of a mast.'[28] This interpretation looks more promising than Taylor's, given that Plato mentioned *epitonoi* in the context of *tetanus* and *opisthotonus*. Clinically, what characterizes tetanus is a descendent appearance of symptoms: from facial spasms and trismus to opisthotonus – the specific spasm of paravertebral muscles that forces the patient to acquire arch-like posture because of overstretching. Plato's *tetanus* could very well mean both the facial and pectoral spasm, meaning that the *neura* around the shoulders could be attacked by the disease, but the term 'stretching backwards the "back-stays"' almost certainly signifies paravertebral

26 Peck (1965), 188 n. *a*
27 *Tim.* 84e2–9 (trans. D. Zeyl)
28 Cornford (1937), 341 n. 1

muscles that keep the body erect, in particular the *erector spinae* group of muscles. In such spasms these and other paravertebral muscles become contracted so forcefully that Aristotle could easily be led to identify them as *neura*. Indeed, these muscles visibly contract during walk and unsupported upright sitting, which makes the mistake all the more likely. It is difficult to say whether or not Plato took *epitonos* to be the same type of tissue as *neura* when he spoke of 'the *epitonous* and the *neura* attached to them', but Aristotle certainly thinks that *epitonos* is a kind of *neuron*. This, together with our tentative identification of the *ōmiaia*, leads us to conclude that some muscles which look elongated and become hard when contracted, thereby acquiring external similarity with tendons, Aristotle would be inclined to identify as *neura*. This does not mean, however, that Aristotle revises his basic description of *neura* as hard and solid in order to be able to classify some muscles as *neura*, but rather that he confuses some prominent muscles with *neura* due to his limited knowledge of internal human anatomy.

In contrast with these few prominent *neura* which have proper names and which all seem to produce limb movements, Aristotle says that 'those around the joints of the bones have no name.'[29] Presumably, the latter group of nameless *neura* includes all those with the function of connecting the bones and stabilizing the joints, that is the ligaments and articular capsules, as well as some of those that produce motion but happen to be less prominent or smaller, such as the tendons on the upper side of the hand or foot.[30]

There were various parts of the body which Aristotle calls *neurōdes* or 'sinewy'. Some of them were thus called because they actually contained *neura*, as in the case of the upper part of the hand or foot,[31] and hence we may suppose that their being *neurōdes* is connected with their being mobile or their having mobile parts, such as fingers and toes. Other parts, however, are called *neurōdes* on account of manifesting some structural similarity with *neura*, such as hardness, tightness, or fibrousness, without thereby implying either of the two functions crucial for limb motion. For instance, the aorta is said to be a sinewy vessel, with extremities which are 'entirely sinewy'.[32] Similarly, Aristotle speaks of the penis as sinewy,[33] of the ductus deferens as a 'thicker and more sinewy

29 *HA* III 5, 515b10–11
30 In the Hippocratic corpus, e.g. in the *de Fracturis* and *de Articulis*, the word *neuron* is used for both ligament and tendon, much like in Aristotle. However, in the Hippocratic corpus we find the word *tenōn* used unequivocally for tendons, to the exclusion of ligaments.
31 *HA* I 15, 494a2–3, 13–14
32 *HA* III 5, 515a30–1
33 *PA* IV 10, 689a21–31

passage',[34] or of the flesh in the calf as 'sinewy and containing blood-vessels'.[35] If one supposes, very reasonably, that the flesh in the calf refers largely to the gastrocnemius muscle, one might deduce that calling it *neurōdes* might suggest that it plays a role in moving the foot. That is not necessary, however, since the basis for calling the flesh in the calf *neurōdes* might be merely that, when the gastrocnemius is contracted, it becomes very hard and looks like a *neuron*. The bodily parts here adduced as examples share only some structural similarities with *neura*, primarily their hardness and tightness; they were not *neura* and we have no reason to think that they were involved in causing the limbs to move.

At *HA* III 5, 515b16–18 Aristotle observes: 'Around the *neura* a mucous liquid is formed, which is white and glutinous; the *neura* are nourished by this, and we can see them being formed out of it.' This seems to be a reference to the synovial fluid. The inside of articular capsules is moist from the synovial fluid which lubricates the articular cartilage to reduce friction. Additionally, several tendons, e.g., the tendon of the long head of the biceps brachii muscle, have synovial sheaths which produce the synovial fluid, whereas other tendons are in close proximity to bursae, small cushions that contain synovial fluid and decrease friction at places where tendons traverse bony parts of the joints. The primary purpose of the synovial fluid is to lubricate the joint, and although it does indeed nourish avascular parts of the tendons, it generates neither tendons nor ligaments, contrary to Aristotle's claim that *neura* are 'formed out' of the mucous fluid. This is an interesting observation for our present purpose because muscles, being soft and vascularized structures, are nourished and generated by blood, which supplies yet another point of dissociation of *neura* from muscles.

A further reason for dissociating *neura* from muscles is the following. When Aristotle speaks of the connection between bones and flesh, he says that flesh grows 'around the bones, attached to them by thin fibrous threads.'[36] There is no indication whatsoever that these 'thin fibrous threads' (λεπτοῖ καὶ ἰνώδες δεσμοῖ) count as *neura*. Aristotle probably has in mind the fusion of muscle fasciae and periosteum, e.g., in the calf where deep muscle fascia is connected to tibia covering its subcutaneous surface. There is no mention of the connection between flesh and *neura*, and hence no grounds for supposing that the flesh is responsible for moving the *neura* and thus exerting force on the bones.

Let us pause here to take stock. It is certain that limb motion, according to Aristotle, is achieved by the hard and solid structures in the body, that is bones and *neura*, the former being 'brittle' (θραυστόν) and the latter elastic or 'pull-

34 *HA* III 1, 510a16–18
35 *HA* I 15, 494a7
36 *PA* II 9, 654b28

able' (ἑλκτόν).[37] Although Aristotle does not attempt a terminological distinction between different kinds of *neura*, it is clear that he assigns two distinct functions to them, that of connecting the bones and stabilizing the joints, and that of operating on the bones by pulling or being released. Although Aristotle probably misidentifies some muscles in their contracted state as *neura* on account of their external structural similarities, muscles either play no role in producing limb motion, on Aristotle's picture, or perhaps they play the secondary role of creating and dissolving fixed portions of the joints, depending on whether or not flexing and extending movements are to take place.

One wonders how Aristotle could overlook the fact that tendons are appendages of muscles, the fact anyone eating a chicken drumstick can plainly see.[38] It is more likely than not that Aristotle was aware of that fact, but the juncture of tendons and muscles was not something that troubled him enough to make him rethink his basic assumptions concerning the structures which are in charge of moving the body. He probably thought that these junctures could be explained one way or another, without upsetting his basic assumptions. What was important to him was that there clearly were some structures connected to the bones and well suited for the purpose of moving the bones, i.e., structures which could produce and withstand considerable force. And it was perfectly reasonable to think that such structures should be naturally solid and hard rather than soft and supple, as muscles in their relaxed state are. Of course, muscles can readily turn from soft and supple into hard and solid, as Aristotle must have observed, but again he may have seen no need to suppose that this very change is what produced movements of limbs. After all, muscles can very well be contracted without causing any limb motion, as when one flexes his biceps to impress the audience.

It is our contention, then, that Aristotle overlooked the actual role of muscles in producing animal motion because of his commitment to a set of theoretical assumptions about the necessary characteristics of the bodily structures in charge of moving the limbs, assumptions governed by his approach to the analysis of parts of animals and embedded in his general theory of matter. It is probable that he found some confirmation of these assumptions in empirical

37 *GA* II 6, 743b4–5

38 Or as the author of the Pseudo-Aristotelian *de Spiritu* clearly saw, when he wrote at 484a18–20: '…' '*neura* are attached to the bones, but not on the other side, because they end in flesh.' Incidentally, this quotation shows that identifying muscles as 'flesh' would not be peculiar to Aristotle. Although Bos (2008) has recently attempted to defend the Aristotelian authorship of the *de Spiritu*, against an almost universal scholarly consensus to the contrary, we are not at all convinced by his arguments.

data gathered through palpation, observation of emaciated and muscular persons, inspection of slaughtered animals, and by his own dissections of animals. Whether he has encountered evidence suggesting that it was the muscles that actually did the job of pulling the bones, or what sort of evidence he has encountered, it is extremely hard to say.[39] But even if he did have some evidence to that effect, we imagine he could find ways of interpreting it to suit his own assumptions or else to dismiss it.[40]

3 The mechanics of animal motion

Now that we have shown that Aristotle was unaware of the actual role of muscles in causing the limbs to move, we should like to examine how he thought *neura* accomplished the task.

Interestingly, the underlying mechanical principles of animal motion are the same in Aristotle's and in modern physiology. We know that muscles contract and relax. When a skeletal muscle contracts, it exerts force so as to pull the bone to which it is connected by a tendon. When it relaxes, it exerts no force, i.e., it does not push the bone, but only passively stretches as the bone is pulled in the opposite direction by another muscle or by some force such as gravitation. Given that (i) all the mechanical work is done by the contraction of muscles, whereby they pull the bones to which they are attached, it is necessary to have (ii) a plurality of appropriately arranged muscles around the bones, and (iii) joints which allow the connected bones to change their relative positions in a variable yet sufficiently stable way, in order to achieve the complex movements of limbs whereby animals move themselves from one place to another.

We submit that all these three principles are shared by Aristotle. Regarding (i), whenever Aristotle speaks of the operation of *neura*, he always speaks of pulling and relaxing or releasing, never of pulling and *pushing*. For instance, at *PA* III 4, 666b13–15, Aristotle writes: 'The heart also has many sinews, and this

39 Some Hippocratic treatises, such as *de Fracturis* and *de Articulis*, contain a more detailed picture of the skeletal system and make a clear distinction between ligaments, tendons and muscles. Some passages seem to suggest that the Hippocratic authors were aware of the actual role of muscles – e.g., *Art.* 30 (Littré vol. 4, 140.8–142.4), *Fract.* 30 (Littré vol. 3, 538.7–10) – but Hynek Bartoš convinced us that they present no conclusive evidence to that effect. Even if these treatises were written by Aristotle's time, which is uncertain, he does not seem to have been familiar with them; cf. Oser-Grote (2004), 64–7, 294.
40 For Aristotle's attitude to empirical data, as well as for his sources thereof, see Lloyd (1978) and (1987).

is reasonable. For the movements are from this part, and are accomplished through pulling and *relaxing* (διὰ τοῦ ἕλκειν καὶ ἀνιέναι).' In the analogy with automatic puppets, in *MA* 7, *neura* are compared to the ropes the release of which sets the puppets in motion (λυομένων 701b2, λυομένων καὶ ἀνιεμένων 9–10). To be sure, the *pneuma* in the heart does its work by pulling and *pushing*, but the effect of the *pneuma* pushing the tendons in the heart (or perhaps pushing the walls to which the tendons are attached, from the opposite side) is their relaxation. Aristotle never implies that *neura* themselves do any pushing.

This is not a problem, as long as Aristotle holds something like (ii) and (iii). As we have seen in Section 2, when we discussed joints and the *neura* that we would identify as ligaments, Aristotle does hold (iii). Indeed, he places great emphasis on joints in the *de Motu Animalium*, where they figure as a sort of 'origin' (ἀρχή) of animal motion. As for (ii), Aristotle says that the greatest number of *neura* are located in hands, feet, arms, and shoulders, i.e., in connection with parts of the body that are capable of complex movements in many directions, which suggests that he thinks it necessary to have a multitude of tendons to produce such complex movements, presumably for the same reason we think it necessary to have opposing muscles.

One might object to this by pointing out that it is difficult to understand how Aristotle could say that the *neura* in the back of the knee are 'in charge of jumping' – if pulling is indeed all that *neura* can do, like muscles. By being pulled, these tendons can bring about only the bending of the leg in the knee. Aristotle's idea might be that by bending the knee, the (hypothetical) tendon in the front of the leg gets pulled, so that the release of the tendons in the ham causes the frontal tendon to spring.[41] Presumably, the frontal tendon would have to be very strong, but that would explain why we would need as many as three tendons in the ham. Also, it would not be entirely unjustified to say that these three tendons are 'in charge of jumping', if their pulling first bends the knee in order to bring the body into position for jumping, if they thereby tighten the frontal tendon, and if it is their sudden release that then enables the frontal tendon violently to pull the upper part of the leg against the lower part set on the ground, thus effecting the explosive straightening of the leg that constitutes the act of jumping.

This is very much the way automatic puppets work. The 'heart' of the automatic puppet that Aristotle probably had in mind was a cylinder with a rope wound around it and a weight attached to the end of the rope. There were pegs

41 Although Aristotle does mention the kneecap (μύλη, *HA* I 15, 494a5), which is embedded in the patellar tendon that connects the quadriceps femoris to the tibia, we admit that Aristotle does not explicitly mention any tendon in the front of the leg.

on the cylinder, and as the cylinder rolled under the pull of the weight, these pegs would pull and release the ropes attached to the other parts of the automaton, thus setting them in motion.[42] The shape and ordering of the pegs on the main cylinder determined which other parts will be moved and in which sequence. In addition, there must have been a blocking mechanism, e.g., another rope which counterbalanced the force conferred to the cylinder by the weight. When this other rope was *released*, the cylinder would start rolling as the rope around it unwounded under the pull of the weight. Various sophistications of this basic design were available, by which the work produced by the weight could be sequenced, transferred and amplified with the use of various levers and pulleys.[43] Thus one simple motion, namely the release of the rope that blocked the mechanism, would bring about diverse movements of the automatic puppet.

This is the sort of design to which Aristotle compares animal bodies in *de Motu Animalium* 7, 701b2–10. Let us quote the passage again:

> The motion of animals is like that of automatic puppets, which are set moving when a small motion occurs, the ropes being released and striking against one another … Animals have instrumental parts that are of the same kind: the *neura* and bones, the latter are like the wooden parts and iron in our example and the *neura* like the ropes; when these are released and relaxed the animal moves.

The point we would like to emphasize here is that the analogy with automatic puppets does not seem to be introduced merely to shed light on some limited aspect of the target phenomenon; rather, it appears to be a heuristic analogy which discloses the principles at work in the target phenomenon. That is to say, Aristotle takes the mechanics of animal bodies to be essentially the same as the mechanics of automatic puppets, with functionally corresponding parts: bones correspond to the wooden and iron parts of the frame, cylinders, axles, pegs and the like, whereas *neura* correspond to the ropes.[44] And the way ropes operate on wooden and iron parts of automatic puppets is essentially identical to the way *neura* operate on the bones.[45]

42 Cf. Nussbaum (1976), 146–52; De Groot (2008), 55–6.
43 Such devices are described in the *Automatopoietica* of Hero of Alexandria (1st century AD).
44 These are the *neura* that we would identify as tendons, not those that we would identify as ligaments.
45 We should acknowledge the fact that the automatic puppet analogy occurs in conjunction with the analogy with a cart featuring wheels of unequal size on two sides, for which see De Groot (2008). Aristotle uses both analogies also to contrast inanimate mechanisms, in which no alteration occurs, from animals, in which alteration – starting with perceptual alteration that in

Aristotle uses the automatic puppet analogy again in his *de Generatione Animalium*, to explain how semen can fashion parts of the body in the embryo without itself having these parts in actuality.[46] Just as an automatic puppet, once the engineer winds it up, has a stored potential until 'something external moves the first part' (e.g., when the rope of the blocking mechanism is released) which triggers a chain of motions without any help of the engineer – semen has a potentiality, bestowed upon it by the male parent, such that when certain conditions in the womb are met, a chain of motions is triggered whereby parts of the embryo are fashioned. In both cases we find an external cause of a preprogramed causal sequence which remains potential until activated by an external agent or circumstance, but requiring no external help from that point on. It seems that here too 'the cases compared are instances of the same general law,' to quote Geoffrey Lloyd's elucidation of Aristotle's characteristic use of analogies.[47]

In any case, the picture of animal motion which emerges from the analogy with automatic puppets is very similar to the one found in Plato's *Timaeus*:

> Moreover, the god thought that bone as such was rather too brittle and inflexible, and also that repeatedly getting extremely hot and cold by turns would cause it to disintegrate and to destroy in short order the seed within it. That is why he contrived to make *neura* and flesh. He bound all the limbs together with *neura* that could contract and relax (ἐπιτεινομένῳ καὶ ἀνιεμένῳ), and so enabled the body to flex about the pivots and stretch itself out. The flesh he made as a defense against summer's heat and as protection against winter's cold, and also, as protection against injuries, he made the flesh so that it would give way softly and gently to bodies like the felted coverings we wear.[48]

Like Aristotle, Plato in this passage assigned two functions to *neura*, that of binding the bones and that of operating on the bones, and the way *neura* operate on the bones is by being tightened and released. Clearly, *neura* do not perform any pushing on Plato's account. Cornford's remarks that 'Plato never used the word muscle (μῦς),' and that most probably he 'thought of flesh as simply a covering and attributed all muscular action to the "sinews"' holds equally of

some cases leads to thermic alteration which in turn brings about expansion and contraction of the *pneuma* – does occur.

46 *GA* II 1, 734b9–17; cf. II 5, 741b5–9 and Philoponus *in GA* 77.14–78.4. This analogy seems to be found also in the Ps.Aristotelian *de Mundo* 6, 398b14–16, where it is stated that God can 'produce all kinds of result easily by means of a single motion – just like the operators of machines, who produce many varied activities by means of the machine's single release mechanism' (trans. D. Furley).

47 Lloyd (1966), 378

48 *Tim.* 74a7–c1 (trans. D. Zeyl, slightly modified)

Aristotle, as we have seen.[49] So it seems that Aristotle's picture was largely inherited from Plato.

However, there is a grave problem with Aristotle's picture. As Aristotle himself observes, *neura* did not form a continuous system: '*Neura* are not of a nature continuous from a single origin, as blood-vessels are … If they were of a continuous nature, the continuity of them all would be evident in emaciated persons.'[50] Observation of emaciated animals and humans was one of Aristotle's chief methods of acquiring anatomical knowledge, and it enabled him to establish that blood-vessels do and *neura* do not form a continuous system. But if the system of *neura* is discontinuous, how does mechanical impulse travel from one segment of the body to another?[51]

This problem has two distinct facets. First, there is no connection between the *neura* in the middle chamber of the heart and the *neura* associated with the system of bones. Aristotle says that the heart is connected to the windpipe by fatty, cartilaginous and fibrous connective tissues, the windpipe to the esophagus and the esophagus to the spine, both by membranous connective tissues, not by *neura*.[52] There seems to be no promising way of making the heart continuous with the spine and the rest of the system of bones and tendons.[53] Galen rebuked Aristotle for claiming that the heart is the origin of *neura* (which Galen took to refer to the nerves), precisely because of this discontinuity: 'Even if one should agree with Aristotle that the connective tissues in the heart were *neura*, none can be seen to pass from them to any other part of the body, as they pass to all other parts from the brain and the spine.'[54]

Some scholars have tried to save Aristotle by appealing to the continuity of the vascular system, in conjunction with one of the following two ideas. The first idea is that *pneuma* spreads throughout the body with the blood and thus

49 Cornford (1937), 298

50 *HA* III 5, 515a32–b6

51 This problem has been correctly identified and helpfully discussed by Frampton (1991), at 321–5.

52 *HA* I 16, 495b12–24

53 Aristotle claims that horses and a certain kind of ox have a bone in the heart (*HA* II 15, 506a8–10; *GA* V 7, 787b17–19), so one might think that at least in these species the continuity between the heart and the system of bones is preserved. Unfortunately, Aristotle does not seem to entertain that possibility, but claims instead that the function of the cardiac bone is to provide support for the large hearts of these animals (*PA* III 4, 666b18–21); cf. Moraux (1985), 333–4.

54 Galen, *In Platonis Timaeum commentarii fragmenta*, 14.9–12 (Larrain); with slightly different wording in *de Placitis Hippocratis et Platonis* I 10.2–7 (de Lacy); cf. Solmsen (1961), 176 n. 43 and Moraux (1985), 334–5.

carries motor impulses from the heart.[55] However, the role of *pneuma* in animal motion is restricted to its workings inside the heart. Namely, *pneuma* converts thermic alterations that accompany perceptual alterations into mechanical impulse, and that conversion can occur only in the heart because that is where perceptual alterations occur.[56] Mechanical impulse is produced in the heart, and *pneuma* is not a viable agent of its transmission. The second idea is that motor impulses are transmitted by the blood-vessels themselves, given that some of them are explicitly said to be 'sinewy' (νευρώδες)[57] and they extend to the farthest reaches of the body.[58] Certainly, blood-vessels extend to the flesh, but flesh plays no role in the production of animal motion, and we hear nothing of the connection between blood-vessels and *neura*. Indeed, we should not expect to hear anything about this connection, given the constitution of *neura* and the fact that they were said to be nourished by the white and glutinous mucous fluid,[59] not by blood.

So, one facet of the problem of discontinuity concerns the transmission of mechanical impulse generated in the heart to the periphery. The other facet concerns the transmission of mechanical impulse from interior to exterior parts of the periphery. Of course, it is not necessary for two tendons to be in direct contact for one to act on another, as we have seen in our proposal of the way the knee works in Aristotle's theory: pulling the tendons of the ham brings about tightening of the frontal tendon, which then springs into action when the tendons of the ham are released. None of this requires any direct connection between the tendons of the ham and the frontal tendon. It is sufficient that the tendons be attached to the same bone. However, for the tendons of the ham to produce tightening of the frontal tendon, they have to move the bone to which they are all attached (tibia): unless the tendons of the ham flex the lower leg, the frontal tendon will not be tightened. On this principle, one would not be able to flex one's wrist without moving one's forearm (radius and ulna), which in turn would require moving one's upper arm (humerus), etc. This may be how automatic puppets work, but certainly not how animal bodies work.

The correct explanation of animal motion relies on our knowledge of the central nervous system, which originates in the brain and extends, among other parts of the body, to muscles. Because skeletal muscles are connected with parts of the

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55 See, e.g., Freudenthal (1995), 135–6; Peck (1942), 579.

56 Cf. *MA* 9, 702b20–5 and 10, 703a11–16.

57 *HA* III 4, 514b21; III 5, 515a30

58 This is proposed by Ogle (1882), 196–7 and Ogle (1912), n. *ad* 666b13; cf. Lones (1912), 162 and Harris (1973), 162.

59 *HA* III 5, 515b16–18

nervous system which are under conscious control, we can move individual muscles, or groups of muscles, independently of all the others. Aristotle did not have such a resource, and the attempt to take his cardiovascular system as a proxy for our nervous system, as we have seen, does not work. The whole complexity of animal motion had to be explained with reference to mechanical impulse generated by the connate *pneuma* operating on the *neura* in the middle chamber of the heart, and then transmitted to the periphery. Aristotle could appeal to the large number of *neura* in the heart and to the ability of *pneuma* to 'change shapes' (τὰ σχήματα μεταβάλλειν, *MA* 7, 701b14), which is best interpreted as the ability of the *pneuma* in the heart to expand and contract variably in different regions, thus simultaneously pulling some and pushing other *neura* in the heart. With this, the complexity of the effects of the original mechanical impulse is considerably increased, and that certainly makes Aristotle's account richer.

However, regardless of how complex the effects of the original mechanical impulse may be, they would have to be transmitted to the periphery in some way. And even if the continuity of *neura* were somehow established, Aristotle would need an extremely large number of *neura* in the heart – certainly more than he could empirically verify – to account for the fact that we can, for example, bend our finger without moving the rest of the arm. This would require continuity between the *neura* in the heart and the exterior part of the finger independently of the whole finger, of the hand and of the arm, and likewise for any section of the body which we can move independently of the other sections. This means that the middle chamber of the heart would have to house, literally, hundreds of *neura*.

In addition to the problem of transmission, there is also the problem of amplification of mechanical impulse. The tiny *neura* in the heart may get pulled and relaxed in a certain sequence and combination, but this could hardly suffice to move the bulk of a straightened leg, for instance. Aristotle does not explain how the amplification of the mechanical impulse generated in the heart is achieved, but he must think that some sort of leverage mechanism is at work. This is indicated by a memorable passage in *de Motu Animalium* 7: 'A small change occurring in an origin sets up great and numerous differences at a distance, just as, if the rudder shifts a hair's breadth, the shift in the prow is considerable.'[60] Of course, the rudder acts as a lever.[61] More explicitly, in *Physics* VIII 6 Aristotle says that the soul moves the body by leverage: 'The cause of moving oneself is moved by itself, albeit only accidentally. For the body changes place, so that what is in the body <viz. the soul> also changes place,

60 *MA* 7, 701b24–8 (trans. M. C. Nussbaum)

61 See Ps.Aristotle, *Mech* 5, 850b28–851a37.

moving itself by leverage.'[62] Lever is what enables 'great weight to be moved by a small force'[63] and it was exploited widely, in various forms, by ancient engineers. Aristotle probably believed that animal bodies contained parts that exploited the lever principle, and it was by means of such parts that the initial mechanical impulse was amplified.[64] And in thinking so, Aristotle would not be far off the mark, since all three classes of levers can indeed be found in the system of bones and muscles of humans and most higher vertebrates.

Apart from the transmission and amplification of the mechanical impulse at the origin, it is likely that Aristotle also supposes that it gets diversified in the periphery. Diversity of movements is made possible by the joints and *neura*, that is by the ligaments and tendons attached to the bones that dictate the range of movements that the limb can perform, depending on which tendons are being pulled and which relaxed. Although Aristotle does not specify how diversification of the initial mechanical impulse is achieved, we suspect that he would point to the engineering solutions found in the cleverly designed automatic puppets and repeat his well-known dictum that art imitates nature. In other words, seeing that there were engineering solutions to the problems of transmission, amplification and diversification of mechanical impulse generated at the origin in automatic puppets, Aristotle could feel confident that some such solutions must be at work in animals too, which seemed sufficient for the purpose of a general account of animal motion.

4 Conclusion

Aristotle failed to observe that muscles produce movements of limbs, because he took them to be flesh, the soft and vascularized tissue whose main functions were to provide the medium for the sense of touch and to protect the bones and other internal parts of the body. If he assigned any role to muscles in animal motion, it was only the secondary role of preparing the joints for different kinds of movements, by creating and dissolving fixed points in the joints.

62 *Phys* VIII 6, 259b17–20

63 Ps.Aristotle, *Mech* 3, 850a30–2; cf. 1, 847b11–15 and 18, 853a38.

64 De Groot (2008) finds another hint at lever in Aristotle's otherwise surprising mention of the cylinders at *MA* 7, 701b6, in connection with the cart analogy. No doubt Aristotle had in mind cylinders of unequal bases, the smaller base of which is 'like a center.' This is an illustration, De Groot argues, of the principle that points along a moving radius all move at different speeds in proportion to their distance from the center, which explains of the functioning of lever in the *Mechanica*.

The chief role in producing limb movements was assigned to *neura* – solid, hard and elastic structures whose main functions were, on the one hand to connect the bones and stabilize the joints, and on the other to act on the bones. *Neura* acted on the bones by pulling them in one direction, or by being released so as to allow the bones to be pulled in other directions by the opposing tendons. The way Aristotle envisaged *neura* to act was in principle identical to the way we know skeletal muscles to act. However, Aristotle did not have a substitute for the central nervous system, something that would enable him to claim that the heart can move any individual *neuron* or group of *neura* at the periphery independently of the others. Consequently, he was stuck with the idea that all movements originate in the heart, with the connate *pneuma* acting on the tiny *neura* in the heart. Moreover, he was convinced on empirical grounds that there was no continuity in the system of *neura*, which made the transmission of movements a major difficulty.

Aristotle's picture of the physiology of animal motion largely relied, as we have argued, on his appreciation for the engineering genius that went into the construction of automata. If men can construct contraptions such that a small initial impulse can produce large and versatile movements of the whole, certainly nature can do so too. Aristotle did not identify the structures responsible for the transmission, amplification and diversification of mechanical impulses generated in the heart, but he seems to have been confident that they could be found. For if they could be found in automata, so much more could they be found in animal bodies.[65]

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