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REVIEW

JOURNAL OF EXPERIMENTAL ZOOLOGY
PART B
MOLECULAR AND DEVELOPMENTAL EVOLUTION

Links between Evolution, Development, Human Anatomy, Pathology, and Medicine, with A Proposition of A Re-defined Anatomical Position and Notes on Constraints and Morphological "Imperfections"

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ABSTRACT

Surprisingly the oldest formal discipline in medicine (anatomy) has not yet felt the full impact of evolutionary developmental biology. In medical anatomy courses and textbooks, the human body is still too often described as though it is a "perfect machine." In fact, the study of human anatomy predates evolutionary theory; therefore, many of its conventions continue to be outdated, making it difficult to study, understand, and treat the human body, and to compare it with that of other, nonbipedal animals, including other primates. Moreover, such an erroneous view of our anatomy as "perfect" can be used to fuel nonevolutionary ideologies such as intelligent design. In the section An Evolutionary and Developmental Approach to Human Anatomical Position of this paper, we propose the redefinition of the "human standard anatomical position" used in textbooks to be consistent with human evolutionary and developmental history. This redefined position also simplifies, for students and practitioners of the health professions, the study and learning of embryonic muscle groups (each group including muscles derived from the same/ontogenetically closely related primordium/primordia) and joint movements and highlights the topological correspondence between the upper and lower limbs. Section Evolutionary and Developmental Constraints, "Imperfections" and Sports Pathologies continues the theme by describing examples of apparently "illogical" characteristics of the human body that only make sense when one understands the developmental and evolutionary constraints that have accumulated over millions of years. We focus, in particular, on musculoskeletal functional problems and sports pathologies to emphasize the links with pathology and medicine. These examples demonstrate how incorporating evolutionary theory into anatomy education can be helpful for medical students, teachers, researchers, and physicians, as well as for anatomists, functional morphologists, and evolutionary and developmental biologists. *J. Exp. Zool. (Mol. Dev. Evol.) 0:1–10, 2016.* © 2016 Wiley Periodicals, Inc.

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The growing influence of evolutionary developmental biology (Evo-Devo) is evidenced by the recent emergence of numerous books, meetings, and even scientific journals specifically focused on this field. However, anatomy—as taught not only in medical schools but also in comparative anatomy and functional morphology and even in biological anthropology courses—has not yet embraced the contributions of Evo-Devo and of other, older fields such as evolutionary anthropology and even evolutionary biology. Teaching materials such as textbooks, movies and even specialized papers/chapters often present the morphological organization of our body as an example of a perfect machine (e.g., "Incredible Human Machine," National Geographic documentary, winner of two 2009 Emmy Awards; "The Perfect Human Machine"; Helsen and Missirlis, 2010). Our bodies, like those of all other living organisms, contain many examples of structures that are well adapted to the niche we occupy. However, most structures in the modern human body originated in ancestors that occupied very different niches and thus can only be understood in an evolutionary and developmental (Evo-Devo) context. In fact, most anatomical features of human embryos are common to all vertebrate embryos, and a legacy based on a pattern that emerged over 400 million years ago (Diogo et al., 2016).

The gaps between medicine, evolutionary biology/comparative anatomy, and developmental biology increased during the second half of the 20th century as many biologists and medical researchers began to subscribe to a more gene-centered approach. In fact, in the 19th and early 20th centuries many physicians and medical researchers were also comparative anatomists and/or evolutionary biologists. Rudolf Virchow (1821–1902) and Etienne Serres (1786–1868) are two particularly instructive examples of this good tradition. Fortunately, these gaps have been decreasing over the last few years as molecular genetics merges with Evo-Devo, and more recently with the rise of Evolutionary Developmental Anthropology and its subfield Evolutionary Developmental Pathology and Anthropology (Evo-Devo-P'Anth: Diogo et al., 2015). See Diogo et al. (2016) for further discussion of these points and the importance of a holistic approach to developmental and gross anatomy and pathology. In fact, understanding gross anatomy can inform pathology, which, combined with evolutionary and developmental information, can in turn make it easier to understand the human body.

AN EVOLUTIONARY AND DEVELOPMENTAL APPROACH TO HUMAN ANATOMICAL POSITION

One of the unfortunate heritages that resulted from the historical decoupling of medicine from evolutionary biology and comparative anatomy was the treatment of the human body and its maladies as distinct from those of other organisms. For this reason, most medical curricula—particularly medical gross anatomical courses—currently do not include evolutionary changes and constraints. The conventional human anatomical position (Fig. 1A) used by physicians, medical students, and researchers is an emblematic example of this problem and its profound implications for a correct understanding of the human body. Our system of anatomical terminology traces its roots to the field's infancy, many centuries ago (Singer, '57, '59). Although some terms have been changed, notably since 1895 (e.g., Terminologia Anatomica; FCAT, '98), many of those we still use today therefore reflect an obsolete, nonevolutionary way of thinking that is far from being the most logical, efficient way of understanding, teaching, and healing the human body.

In fact, there were attempts to change this way of thinking and to reflect that change in anatomical terminology, but most of these attempts failed. We obviously cannot provide here a detailed history of anatomical terminology, and would thus summarize a few examples; for more details, readers should refer to works focusing specifically on this subject, such as those of ORahilly ('89), Sakai (2007), Kachlik et al. (2008) and references therein. For instance, as stressed in those works (and by an anonymous reviewer, as well as by Tatjana Buklijas, who is writing a detailed review exclusively on this subject: pers. communication), committees did meet several times since the late 1800s to not only standardize terminology for anatomical features but to also discuss the best anatomical position for humans. This begun with the 1895 Ninth Congress of the Anatomische Gesellschaft in Basel, where the chosen standard anatomical position presented an Orthograde stance with the upper limb rotated, rather than the lower limb as is shown in Figure 1B of the present paper. This was termed the BNA position after the meeting, in the Basel Nomina Anatomica. However, a subsequent meeting in Jena (JNA), which included veterinarians, reverted to the use of a quadripedal (pronograde) stance in order to compare anatomical features of humans with those of other tetrapods, while a 1955 meeting by the International Anatomical Nomenclature Committee reverted to the orthograde stance. The problem is that despite all of these committees looking to standardize a "universal anatomical position," early versions of influential human anatomical atlases such as *Greys Anatomy* portray a human in a so-called "cadaver" pose, that is, in a supine position, which corresponds to the standard anatomical position consensually used in most textbooks nowadays. Thus, rather than choosing an anatomical position that represents—and for ease of learning—the evolutionary and developmental history and function of muscles, the choice of the current standard position was seemingly done for ease of examination of preserved humans, a practice that predated evolutionary theory. Thus, to make a very long story short, comparative and developmental anatomy did had input into discussions on the anatomical position at certain moments in time, but then were mainly voted out, unfortunately. As a result, medical students, researchers, and biologists continue to use conventional terms for joint movements and muscle groups that do not reflect

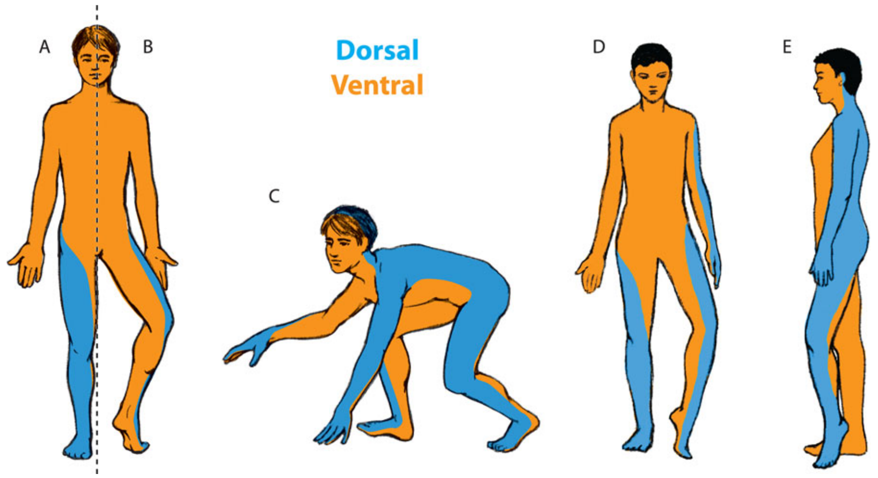

Figure 1. Diagram showing the "human standard anatomical position" (A), the redefined anatomical position with the lower limb rotated laterally almost 180° (B), and other positions that emphasize the evolutionary and developmental history of the human body (C–E). In (B), the flexor (ventral) musculature of both upper and lower limbs faces anteriorly, reflecting the true topological correspondence between the elements of the limbs. (C) A quadrupedal crouched posture similar to that of salamanders (Fig. 2), emphasizing our ancestry as tetrapods. Developmentally ventral structures (orange) mainly face inferiorly. (D–E) The left limbs in a position similar to that of an early embryo (Fig. 3A), with ventral limb structures facing medially, while the right limbs are in standard anatomical position. Illustration by Julia Molnar.

our true evolutionary and developmental history or the topological correspondences between the limbs (Diogo et al., 2013, 2016). For instance, in the current "human standard anatomical position" the developmentally ventral (flexor) sides of the lower limbs face posteriorly and those of the upper limbs face anteriorly (Fig. 1A). This inconsistency leads to a cascade of illogical definitions and terms that students are obliged to memorize.

Although adult humans are bipedal, the anatomy and function of our limbs reflects their ancient evolutionary and developmental origin: the salamander-like body plan of basal tetrapods and tetrapod embryos. In resting salamanders, all four legs are oriented in the same way, highlighting the topological correspondence between the elements of the upper and lower limbs (forelimb and hindlimb; Fig. 2). The humerus, radius, and ulna correspond to the femur, tibia, and fibula, respectively. The palm and sole of the foot, and the ventral (flexor) side of the entire limbs, face ventrally, and digit 1 of both sets of limbs ("thumb" and "big toe") point toward the head. A similar configuration can be seen early in human development, when patterns of innervation, muscle attachments, directions of joint movement, and many other aspects of anatomy are established (Fig. 3). Later, the upper limb rotates laterally and the lower limb rotates medially (Fig. 3; incidentally, this rotation of the limbs explains the spiral pattern of dermatomes in the skin of the lower limb; Sadler, 2011).

Continuing to use the "human standard anatomical position" in the face of our current knowledge of human evolution and development creates a set of terms and concepts that are particularly difficult for medical students to memorize because they have no logical basis. For example, moving the thigh anteriorly is designated "flexion" in current directional terminology, whereas the very same movement of the leg (anteriorly) is called "extension," and a similar movement of the foot is called "dorsiflexion." Furthermore, the conventional position obscures the topological correspondence between the upper and lower limb and the true developmental history of the muscles: all limb muscles develop from two initial muscle masses, ventral/flexor, and dorsal/extensor (e.g., Kardon, '98). Finally, this conventional position complicates comparative, evolutionary, and developmental studies of human anatomy and comparisons with embryological or veterinary/zoological texts, obscuring putative evolutionary relationships and generally slowing integrative works.

To solve the problem of inconsistency between medical/human anatomical terminology and that used in other anatomical fields, and to make this nomenclature logical and therefore much easier for students to understand and learn, we propose the following two main changes.

1. Human anatomical position should show the ventral aspects of the upper and lower limbs facing anteriorly and the dorsal aspects posteriorly. In view of the evolutionary and developmental history of humans and the topological correspondence between the components of the upper and lower limb, the depiction of the human body

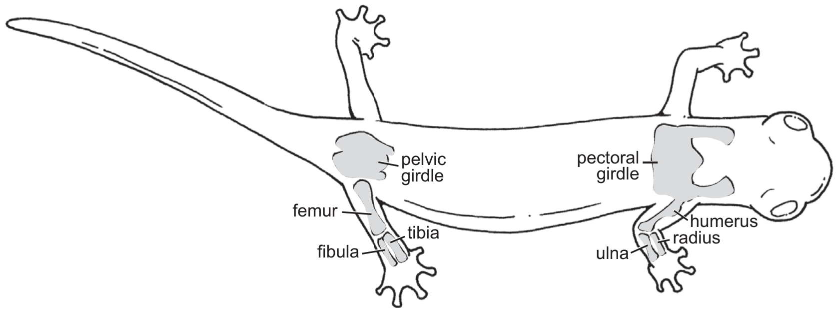

Figure 2. Limb anatomy of a salamander, representing the ancestral tetrapod body plan and showing topological correspondences between the fore- and hindlimb bones: humerus/femur, radius/tibia, ulna/fibula, and "thumb"/"big toe." Illustration by Julia Molnar.

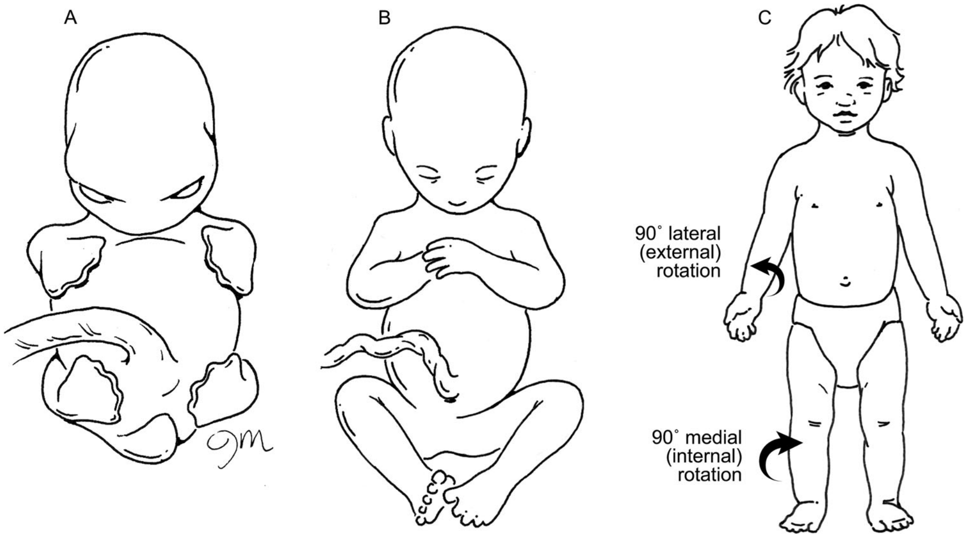

Figure 3. Stages of human embryology showing opposite rotations of upper versus lower limbs. (A) At about 19 weeks; the first digit of the upper limb (thumb) and lower limb (big toe) form on the cranial side of the developing limb, as they are in adult salamanders. (B) By about 23 weeks, the upper limb begins to rotate laterally and the lower limb begins to rotate medially. (C) At about 1 year, the limbs approach their adult configuration. In the "human standard anatomical position" shown in this figure, the upper limb is rotated 90° laterally so that the thumb lies on the lateral side. (Note, however, that in normal standing posture the rotation of the upper limb is less than 90°.) In both normal standing posture and the "human standard anatomical position," the lower limb is rotated 90° medially so that the big toe lies on the medial side. Illustration by Julia Molnar.

shown in Figure 1B is most scientifically accurate and, importantly, easiest to understand and study. The basic quadrupedal tetrapod body plan is in some ways similar to that displayed by humans in a crouched position (Fig. 1C), with the palms of the hands and soles of the feet—that is, the ventral/flexor side of this region of the limbs—planted on the ground, facing ventrally. However, we are bipedal tetrapods, so our anatomical position should also take into account this extremely important aspect of our evolutionary history. Figures 1D and E show a position representing the embryological stage during which many limb structures are formed, with the ventral/flexor side of the left upper and lower limbs facing medially. However, in this position the dorsal/ventral axes of the limbs are not aligned with the dorsal/ventral axis of the trunk and head. Therefore, the position shown in Figure 1B best reflects our basic tetrapod body plan, our developmental organization, the true topological correspondences between upper and lower limbs and our more recent, unique evolutionary history.

2. Embryonic ventral muscle groups flex the limbs and embryonic dorsal muscle groups extend the limbs. Following point 1 and using Figure 1B, it becomes obvious that the muscle groups located on the posterior (dorsal) side of the body (blue in Fig. 1) extend the limb, while those on the anterior (ventral) side flex the limb. Therefore, moving the limbs anteriorly relative to the redefined anatomical position should be called flexion, without exception. A few joint motions will need to be redefined to be internally consistent and reflect the evolutionary and developmental histories of the muscles responsible for them. First of all, the quadriceps femoris and other muscles innervated by the femoral nerve (dorsal muscles that move the thigh posteriorly relative to the redefined anatomical position shown in Fig. 1B) should be regarded primarily as extensors of the thigh (i.e., extensors at the hip joint), and the hamstring muscles (ventral muscles that produce the opposite motion) should be regarded primarily as flexors of the thigh, not vice versa. This designation will be consistent with that of ventral muscles such as the gastrocnemius, which move the leg anteriorly from the redefined position and are already designated flexors of the leg (despite being part of the "posterior" compartment of the lower limb in the "human standard anatomical position" shown in Fig. 1A). Similarly, anterior movement of the foot from the redefined position, performed by ventral muscles that are already called flexors (e.g., flexor hallucis longus), should simply be called flexion, not plantarflexion. Accordingly, the opposite movement (posterior, relative to the redefined position) should simply be called extension, not dorsiflexion. Among a multitude of illogical terms they have to learn, "dorsiflexion" is particularly confusing for students because they have previously been taught that the muscles responsible for this movement are extensors, for example, "extensor digitorum longus."

A possible objection to the redefined anatomical position shown in Figure 1B is that it is an unnatural posture for humans, while some could argue that the conventional position shown in Figure 1A is our "natural resting posture." There are two main problems with this argument. First of all, Figure 1A clearly does not represent a neutral resting posture because the palm of the hand faces anteriorly rather than medially. Rarely do people stand in such a posture if they are not specifically illustrating "anatomical position." Second, the purpose of anatomical position is not to show a "natural" or a "resting" posture, but to provide a convenient, consistent reference point for directional terminology. The conventional "human standard anatomical position" can be kept as a merely comparative reference because it reflects tradition and is deeply associated with the directional terms that have been used for centuries in human anatomy and functional morphology (e.g., anterior, posterior, superior, inferior, lateral). For instance, the artery that supplies the ventral (flexor) muscles of the leg is currently designated the "posterior tibial artery" based on the conventional position shown in Figure 1A. In the redefined position shown in Figure 1B, it actually lies on the anterior side of the body because, evolutionarily and developmentally, this artery and surrounding muscles are part of the true ventral—not dorsal—soft tissues of the limb. For this reason, we strongly suggest that students and health professionals always use a figure such as Figures 1A and B to show both the conventional position and the re-defined "correct" position, side by side. Ultimately, when the redefined anatomical position will be consensually accepted, a more dramatic change of the gross anatomical terminology will need to be done, to be consistent with this redefined position and the true evolutionary history of our body. For instance, this so-called "posterior tibial artery" is in reality – developmentally and evolutionarily – an anterior (ventral) artery, as the anterior rami are truly ventral rami (as is already – and correctly – reflected in current gross anatomical terminology).

In addition to being consistent with both the generalized tetrapod body plan and the specifics of human evolution and development, this redefined anatomical position also has profound practical implications. Above all, the redefined position makes it much easier for students to understand the topological correspondence between muscles of the upper and lower limbs, the embryonic development of the limbs, and the relationship between human anatomy and that of other tetrapods, including the model animals that play increasingly important roles in medicine. Furthermore, this evolutionary and developmentally correct anatomical position allows us to replace the current highly confusing set of definitions of muscle groups and joint movements with one that is straightforward, consistent, logical, and therefore more informative.

Among the benefits of adopting the redefined anatomical position, perhaps the most important is that it would reduce the amount of memorization required of anatomy students by eliminating unnecessary, counter-intuitive rules. As explained above, anatomy educators teach students that the function of the muscles of the extensor layer of the leg (e.g., *extensor digitorum longus*) is not to extend the foot but to "dorsiflex" it. As clearly shown in the redefined anatomical position, leg extensors are developmentally dorsal muscles that simply extend the foot; the developmentally ventral muscles are antagonists and thus flex it. Therefore, moving the thigh anteriorly from this redefined position should be called thigh *flexion*, exactly as anterior movement of the arm is called flexion. Once students understand the movements of the joints, they will be primed to easily learn the names of the many limb muscles that are named for the movements they produce (e.g., *flexor digitorum, extensor indicis, flexor carpi radialis).* Students will also be better able to understand the logic behind muscle innervation since all limb muscles develop from dorsal and ventral muscle masses (e.g., Kardon, '98; Diogo et al., 2016). For example, all intrinsic hand and foot muscles, which are both embryonic ventral muscle groups, are innervated by branches of the ventral nerve structures of the brachial and lumbosacral plexuses: the ulnar and median nerves in the hand and branches of the tibial nerve in the foot.

With the dorsal and ventral aspects of the upper and lower limbs in line, the correspondences between the two limbs become obvious. The arm flexor *biceps brachii* corresponds topologically to the thigh flexor *biceps femoris* (as explained above, anterior movement of the thigh in the redefined position should logically be termed "flexion"), and the *triceps brachii* corresponds to the *quadriceps femoris*. Using the redefined anatomical position will make it much easier for students to compare the upper and lower limbs and extrapolate the information they learn about one set of limbs to the other, focusing on the few differences between them rather than trying to learn each limb from scratch. By using a more consistent, logical system of anatomical terms, we can both speed up the learning process and improve retention because anatomy students will actually understand the system rather than learning it by rote memorization.

In addition to improving anatomy education, the adoption of a system that takes into account both that used in embryology and zoology and the more recent evolutionary transformations that produced our bipedal posture will make it easier to integrate these disciplines in areas such as Evo-Devo, evolutionary medicine, and medical research on model organisms. With the renaissance of anatomy brought about in a large part by the rise of these promising new research areas and the blossoming of evolutionary medicine as a new field with huge practical implications for human health, much swifter progress could be made if we collectively let go of outdated ideas about anatomical terminology and deploy a more holistic concept of the anatomical sciences that maximizes the application of current knowledge to reveal important and exciting new insights.

EVOLUTIONARY AND DEVELOPMENTAL CONSTRAINTS, "IMPERFECTIONS," AND SPORTS PATHOLOGIES

Having discussed a way to approach the human body in the context of its evolutionary and developmental history, we can now consider the "imperfections" that result from that history. In this section, we provide examples of features of the human body with important medical implications that can only be explained by the influence of evolutionary constraints.

Human evolutionary history has involved several dramatic reorganizations of the vertebrate body plan that required remodeling of preexisting anatomical structures. One such reorganization was the origin of tetrapods, or animals with limbs and digits, which occurred approximately 350 million years ago (Clack, 2012). Their new terrestrial mode of life spurred musculoskeletal changes in the descendants of these first tetrapods such as elongation of the neck and repositioning, reorientation, and elaboration of the appendages. Another reorganization occurred more recently with the adoption of bipedal posture in hominins a few million years ago. Because major alterations to the body plan are produced mainly by incremental modification of existing anatomical structures, human anatomy is constrained by the evolutionary history of our species (Diogo et al., 2016). In his book on evolutionary theory Richard Dawkins explains, "The human body abounds with what, in one sense, we could call imperfections but, in another sense, should be seen as inescapable compromises resulting from our long ancestral history of descent from other kinds of animal" (2010: 365). He points out several familiar examples of such "imperfections" in the human body, including the path of the left recurrent laryngeal nerve. In humans, this nerve takes a meandering course from the base of the brain through the neck and into the thorax where it passes beneath the arch of the aorta before ascending again to innervate the larynx. However, in fish (which lack a neck), the structures homologous with the larynx and aortic arch both lie in the head, so the original path of the "recurrent" laryngeal nerve in ancestral tetrapods was a direct one. According to Dawkins, because each step in the evolution of the human body plan from a fish-like body plan required only a tiny increase in the length of the recurrent laryngeal nerve, there was not enough selective pressure for the major reorganization that would have been necessary to change its path. Thus, historical contingency has produced a seemingly inefficient anatomical configuration in humans which in some cases, such as thyroid pathology, can be detrimental.

Other examples of seemingly inefficient paths taken by nerves and arteries in humans most likely due to our evolutionary history are less dramatic but often just as important to medicine. The pattern of forelimb muscle innervation by spinal nerves was established in fish, whose pectoral girdles were located ventrolaterally. Therefore, it makes sense that the shoulder girdle is innervated by ventral rami of spinal nerves. However, in humans the pectoral girdle is mainly located on the dorsal (posterior) aspect of the body, meaning that some ventral rami nerves must somehow pass through the dorsal region of the body to reach their muscular targets, in a configuration unlikely to make sense to any engineer (Diogo et al., 2016). The four "tricks" (i.e., evolutionary by-products of the evolutionary changes that occurred in our evolutionary history) that allow nerves from the ventral primary rami to innervate posterior (dorsal) shoulder (upperlimb) muscles (Fig. 4) are as follows: (1) the *dorsal scapular nerve* runs posteriorly from its origin and passes through the middle scalene to pass medially to the scapula and innervate the rhomboid major, rhomboid minor, and levator scapulae; (2) the *suprascapular nerve* passes through the suprascapular notch of the scapula to innervate the supraspinatus and infraspinatus; (3) the upper and lower *subscapular nerves* run inferiorly from their origin to pass anterior (ventral) to the scapula and innervate the subscapularis and teres major; (4) the *axillary nerve* passes through the "quadrangular space" between the subscapularis, teres

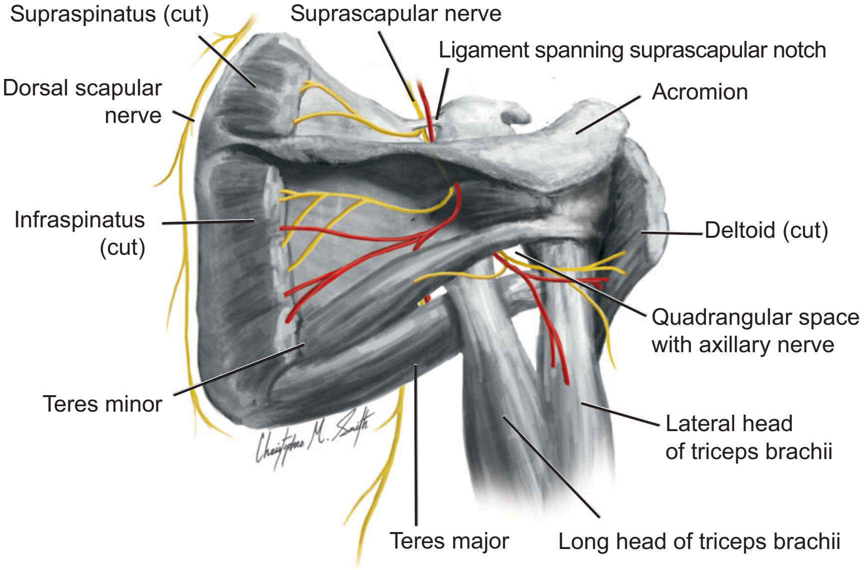

Figure 4. Posterior view of left shoulder showing paths of nerves from ventral rami. In an example of evolutionary constraints in the human body, the dorsal scapular, suprascapular, subscapular, and axillary nerves must travel through or around the scapula to reach their target muscles lying in the posterior (dorsal) region of the shoulder. Illustration by Christopher Smith.

major, long head of triceps brachii, and the surgical neck of the humerus to innervate the teres minor and posterior portion of the deltoid.

The "tricks" described above represent evolutionary trade-offs in Dawkins's sense because they make these nerves particularly vulnerable to sports injuries. As it passes through the quadrangular space, the axillary nerve (and accompanying posterior circumflex humeral artery) becomes vulnerable to compression. If the space is constricted by muscle hypertrophy, fibrosis, compression by dislocated humeral head, or other causes, the symptoms of *quadrilateral space syndrome* may appear. These include poorly localized pain, weakness and atrophy of shoulder muscles, and paresthesia (Safran, 2004). *Dorsal scapular nerve entrapment* is a similar condition in which the dorsal scapular nerve is compressed where it passes through the scalene muscle, causing pain, loss of sensation, and scapular winging (Sultan and Younis El-Tantawi, 2013). Likewise, *suprascapular nerve entrapment* can be caused by compression by the transverse scapular ligament as the suprascapular nerve passes through in the suprascapular notch; the nerve also may become entrapped in the spinoglenoid notch formed by the lateral edge of the scapular spine (Safran, 2004). In the latter case, only the infraspinatus is affected, but in the former case both the supraspinatus and the infraspinatus may result in atrophy, often causing shoulder weakness and pain during some scapular motions. All these conditions discussed in this paragraph are often found in baseball, tennis and volleyball players, and others who habitually use overhand throwing motions. Both quadrilateral space syndrome and dorsal scapular nerve entrapment are relatively rare, while suprascapular nerve entrapment is more common, reportedly affecting up to one-third of high-level volleyball players (Safran, 2004).

Another example of an apparently "illogical" configuration in the human body concerns the arteries of the limbs. Fish plesiomorphically have only a few muscles in each appendage, whereas tetrapods such as humans have more than 50 in the pectoral girdle and upper limb alone (Diogo et al., 2009). Therefore, the path of the brachial artery, which lies in the anterior compartment of the arm but supplies blood to all the arm, forearm, and hand muscles, is extremely convoluted. If the body was free from evolutionary and developmental constraints, it would be more logical to have a major artery on the anterior (flexor) side and a major artery on the posterior side of the arm. As this is not the case, in humans the brachial artery has to perform a "trick" to reach the triceps brachii and the other tissues of the posterior/extensor compartment (Diogo et al., 2016). The deep brachial artery branches from the proximal region of the brachial artery to enter the posterior arm compartment (in both the human standard and redefined positions shown in Figs. 1A and 1B). It courses around the posterior surface of the humerus, where it accompanies the radial nerve in the spiral (radial) groove and then gives rise to the radial collateral artery that anastomoses with the radial recurrent artery that branches from the radial artery. In the middle of the arm, the brachial artery gives rise to the superior and inferior ulnar collateral arteries. These two collateral arteries anastomose with the posterior and anterior ulnar recurrent arteries, respectively, which are branches of the ulnar artery.

Somewhat similar "tricks" are performed by the arteries of the lower limb. As the main arteries of this limb lie in the anterior (in the human standard anatomical position shown in Figure 1A, so corresponding to the developmentally dorsal side: see above) compartment of the thigh, how does the posterior (developmentally ventral) thigh receive blood? The deep femoral artery gives rise to the perforating branches of the deep femoral artery, which pass through the adductor magnus muscle to supply the posterior (developmentally ventral) thigh muscles. These two major arteries of the upper and lower limbs perform very different "tricks" to supply the distal limb structures. In the upper limb, an anterior branch of the major artery (the ulnar artery) gives rise to a branch (common interosseous artery), which divides to supply the anterior and posterior compartments of the forearm (anterior and posterior interosseous arteries). In contrast, the femoral artery passes through the adductor hiatus—an opening in the tendon of the adductor magnus muscle just above the knee—to reach in the posterior side of the knee region. Now called the popliteal artery, it gives rise to several branches and becomes the single major artery in the proximal region of the leg. Now the opposite problem occurs: the popliteal artery lies in the posterior (developmentally anterior) compartment of the leg, but it must still supply the anterior (developmentally posterior) leg muscles and surrounding tissues. It performs a second "trick", bifurcating in the proximal leg into the anterior tibial artery, which passes through the interosseous membrane to enter the anterior (developmentally posterior) side of the leg, and the posterior tibial artery, which continues in the posterior (developmentally anterior) side of the leg.

A major rearrangement of the body of our ancestors occurred in the last few million years with the emergence of habitual bipedal walking (Raichlen et al., 2010). Other primates move quadrupedally or by swinging by the arms (i.e., brachiation), a type of locomotion that requires a very large range of shoulder movement, and great apes thus have the unusual ability to abduct the arm a full 180° (Fig. 5). To allow this movement, the supraspinatus muscle in primates is located above the shoulder rather than behind the shoulder as in most other mammals (Diogo and Abdala, 2010; Diogo and Wood, 2012). Modern humans retain both the supraspinatus anatomy and shoulder abduction ability of our primate ancestors, although as terrestrial bipeds we seldom need to use this ability. Unfortunately, the superior location of the supraspinatus tendon, "sandwiched" between the spine and acromion of the scapula and the shoulder joint, puts it in a position to be impinged upon by surrounding structures. Supraspinatus impingement, often called *painful arc syndrome*, subacromial impingement syndrome, or thrower's shoulder, can be caused by thickening of the shoulder ligaments, joint capsule, or bursae and results in limited range of motion, pain, and weakness of the shoulder (Michener et al., 2004). It also is the most common cause of shoulder pain (Michener et al., 2004) and, like those conditions discussed in the previous paragraph, it is common in athletes who use overhead motions such as baseball, volleyball and tennis players, and swimmers.

Like the location of the supraspinatus in humans, the anatomical configuration of the lumbar region is an ancestral primate feature retained in modern humans despite our transition to a very different type of locomotion. It is also at least partially responsible for the lower back pain so common within our species. With the adoption of habitual bipedalism, the human vertebral column developed a deep lumbar curvature (lumbar

Figure 5. A brachiating spider monkey (modified from Jenkins et al., '78) demonstrating 180° abduction of the shoulder. While modern humans share this ability, the evolutionary trade-off is predisposition to painful arc syndrome, "rotator cuff" injuries, and other pathologies of the shoulder.

lordosis). However, other than lumbar lordosis the human back does not have any unique adaptations for bipedalism; moreover, bipedalism arose in hominids that weighed only about one-third as much as modern humans (Schilling et al., 2005). Therefore, forces that must be accommodated by the bones, muscles, and connective tissues of the lower back in modern humans have changed dramatically in a relatively short period of time. As the authors note, "the human back has had to fulfill functional demands, but it is also highly constrained by the physical properties of its components, for example, muscle, bone, and connective tissue, and its evolutionary history ... analyses of the human back and its problems should keep all three aspects in mind." (Schilling et al., 2005 p. 233–234).

A final example of historical constraints that relate to our species' adoption of bipedalism is the conflicting demands of locomotion and childbirth that have shaped the human female pelvis. On the one hand, humans have relatively large heads as newborns and have pelves with a "twist" between the pelvic inlet and outlet due to our bipedal posture, making a broad female pelvis necessary for safe childbirth (Rosenberg and Trevathan, 2014). On the other hand, bipedal locomotion is most efficient when the feet are placed directly beneath the center of mass rather than beneath the hip joint; accordingly, the femora angle lies medially, placing our knees and legs closer beneath our midline/center of mass. Bipedal walking and running consist mainly of phases of single-leg support, interspersed with double-leg support (walking) and aerial phases (running). During single-leg support phases, the body's center of mass must be approximately above the planted leg to avoid falling over, so widely spaced legs would require large shifts in center of mass from side to side that expend energy but do not contribute to forward progress. In human adults, the compromise is a relatively large valgus angle, or *Q*-angle (the angle between the thigh and the leg when viewed from the front) in females, about 17° as opposed to about 12° in males. However, a large valgus angle has been associated with higher risk for *patellofemoral syndrome*, a major cause of knee pain (Emami et al., 2007). With a large valgus angle, the line of action of the quadriceps femoris muscles moves lateral to the knee, meaning that these muscles tend to pull the patella laterally out of alignment. Patellofemoral syndrome is common in runners, bicyclists, basketball players, and young and/or female athletes in general (Emami et al., 2007).

These are only a few of the many examples of musculoskeletal structures in the human body that are best understood in the light of our evolutionary history. As noted in Rowe's (2015) divulgation article, the Greeks were obsessed with the idea of a mathematically perfect body, but "unfortunately for anyone chasing that ideal ...Evolution constructed our bodies with the biological equivalent of duct tape and lumber scraps." To illustrate his point, the author summarized 10 "flaws" in the human body including the curves and counter curves of our vertebral spine and our inside-out retinas, relatively inflexible knees, too narrow pelvis, crowded teeth, exposed testicles, meandering arteries, misrouted nerves, misplaced voice box, and "clumsy" brain that imperfectly combines old and new parts. Additional examples include the muscle *trapezius,* which is innervated by cranial nerves because it originated as a head muscle in fish and accordingly develops in the head region but then migrates caudally and actually lies on our back (Diogo and Abdala, 2010), and the highly variable forearm muscle *palmaris longus* thought to be vestigial as it has no known major function in modern humans but very likely aided in brachiation in arboreal primates (Diogo and Wood, 2012). In fact, anatomical variations are a crucial part of our evolutionary heritage that are too often neglected by medical teachers, students, and researchers (Diogo et al., 2015). While some of these anatomical incongruities do not cause problems, in many cases historical constraints in the musculoskeletal system predispose us to certain sports injuries or pathologies in general, as noted above. Therefore, athletes, trainers, physical therapists, and physicians would want to understand these constraints in order to best prevent, diagnose, and treat these injuries.

In summary, medical students, teachers, researchers, and the scientific community in general would work much more effectively if it is kept in mind that the human body is far from being a perfect machine. Intelligent design advocates cite blood clotting and vesicular transport as examples of "irreducible complexity" that could only result from design (Pennock, 2003), but they conveniently ignore "imperfections" such as those discussed above that clearly mark the human body as a product of evolution rather than engineering. A 2007 poll of almost 1,500 physicians by the Louis Finkelstein Institute for Social and Religious Research reported that, while 78% accepted evolution, 50% felt that schools should be allowed to teach the "controversy" of intelligent design (Evolution vs. Intelligent Design, 2007). This attitude may be spreading into Europe as well (Kutschera, 2003). We strongly agree with Pennock's (2003) argument that evolutionary theory should be integrated into human anatomy courses, as well as other biology courses. Only when we fully appreciate its evolutionary and developmental history will we be able to fully understand the intricacies, functions, and pathologies of the human body.

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