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Activity-Related Skeletal Changes

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Abstract

Since the end of the 19th century, biological anthropologists have looked for evidence of change in the skeleton in order to identify physical activities in the past. These activity-related skeletal changes form an extremely heterogeneous group, both in terms of types of changes and processes behind their development. This entry presents the wide spectrum of opinions regarding the degree of accuracy that can be achieved in such studies of past activities, and some examples of activity-related skeletal changes, as well as their specific importance and limitations.

Key Points/objectives box:

- Activity-related skeletal changes (ARSC) are skeletal adaptations or alterations related to biomechanical strains generated by physical activities
- There is a wide spectrum of opinions regarding the degree of accuracy that can be achieved in studies of past activities
- This entry presents the most commonly studied ARSC, as well as their specific importance and limitations

1 Introduction

Daily activities modify our body, including our skeleton, a living tissue that reacts to several stimuli, and in particular to the biomechanical strains generated by physical activities. These reactions—bone adaptation and sometimes bone alteration—are relatively well documented in sports and occupational medicine, and from experimental studies on animal models. Based on these findings, and using an actualistic approach, biological anthropologists look for evidence of change in the skeleton in order to identify physical activities in the past. This type of approach can take many different forms: some studies focus on the locomotor behaviors of fossil species, others are interested in the precise identification of activities or movements for a given individual, whereas others seek patterns in skeletal samples in order to address social organization— notably task divisions—within past human groups.

There is no agreement in biological anthropology for a name that would group together all the changes observed on the skeleton associated with activities practiced during life. In 1983, Merbs used “activity-induced pathology”, whereas the same year Kennedy introduced the term “skeletal markers of occupational stress” (Kennedy, 1983). Other expressions, such as “activity-related changes” (Knüsel, 2000) or “activity-related skeletal morphologies” (Molleson, 2009), were subsequently proposed, but none of them has really become widespread to the point of consensus. Here, the expression “activity-related skeletal changes” (hereafter ARSC) was chosen because it has the advantages of being relatively precise while not implying too direct a cause and effect relationship (i.e., not using the term “induced” or “markers”) and not being limited to one type of change (i.e., pathology).

2 Reconstructing Past Activities: An Overview

Brief Historical Background

Pioneer Studies

Looking for skeletal changes produced by the repetition of movements made during life is not really a novel approach: it was already a topic in its own right at the end of the 19th century. For example, as early as 1887, Manouvrier suggested that the medio-lateral flattening of the tibia (called platycnemia), regularly observed in prehistoric skeletons, was not an inherited trait (a hypothesis frequently put forward at the time) but more likely an individual variation related to an increased activity of *M. tibialis posterior*, particularly during running. A few years later, Charles (1893) described in a rather detailed study various appearances of the lower limbs of skeletons from India, in particular the presence of supernumerary articular facets on the talus, and associated them with the squatting position. Similar studies identifying potential ARSC flourished in the late 19th and early 20th centuries, and already circumscribed the main behavioral aspects that could be identified with this type of skeletal changes: forceful and/or repetitive movements, frequently adopted positions, and the practice of long-distance running, for example. Studies of ARSC from that time were often anecdotal and contradicted each other. They were also characterized by a direct and rather simplistic association between skeletal changes and specific behaviors, and lacked, for the most part, proper methodology to record the changes. However, those works laid the groundwork for more “standardized” studies to emerge.

The Blooming of Paleopathological Studies

The revival of ARSC studies, mainly focusing on paleopathological lesions, began in the late 1960s. They were characterized by (1) the analysis of larger samples, (2) more formalized approaches to record the changes, and (3) greater consideration of the archaeological, socio-cultural and environmental contexts of the population studied. These studies also greatly benefited from considerable advances in sports and occupational medicine, as well as from the development of medical imaging. One of the most iconic studies from that period is the work published by Merbs in 1983, entitled “Patterns of activity-induced pathology in a Canadian Inuit population”. Merbs recorded several degenerative and traumatic lesions (mostly osteoarthritis) in a sample of 91 adult skeletons of Hudson Bay Inuit, the Sadlermiut, a group who remained mostly isolated and kept traditional ways of life until they disappeared due to infectious disease in 1902–1903. The study revealed quite different patterns of lesion distributions and severity in males and females, which were interpreted in the light of archaeological contextual information, including recollections of informants and accounts of meetings with the Sadlermiut prior to their disappearance. Merbs thus linked, in a relatively cautious way, the pattern seen in males to harpoon-throwing and kayak-paddling, and the pattern seen in females with carrying heavy loads and the scraping, softening, cutting and sewing of skins.

Syntheses, Criticism, Seeking Standardization and New Research Directions

Since the 1980s, many avenues of research have been explored regarding ARSC. Some authors have attempted to classify and/or draw up exhaustive catalogues of the many skeletal changes claimed to be related to past activities (e.g., Capasso et al., 1999). Other researchers have focused on a particular ARSC in order to define a solid methodological and interpretative framework for study (e.g., Merbs (1996) for spondylolysis or Kennedy (1986) for auditory exostoses). On the other hand, a significant number of scholars expressed concerns or sometimes acerbic criticism regarding the reconstruction of past lifestyles from skeletal changes (e.g., Dutour, 1992; Jurmain et al., 2012). These concerns, depending on the author, focused on:

- The low replicability and the anecdotal nature of such studies;
- The fact that many changes considered as ARSC can be caused by conditions other than activity (i.e., the lack of specificity);
- The influence of many other factors (e.g., age or sex-related hormone levels) that participate, along with biomechanical stresses, in the appearance and development of changes.

In a more positive way, the last 50 years saw the development of much methodological research as well as the identification of new ARSC. In terms of improvement, the most successful is arguably the study of robusticity of long bones (for a review, see Ruff, 2018). Many efforts (e.g., Mariotti et al., 2004; Henderson et al., 2013) have also been

made to create reproducible methods to record changes seen at entheses (i.e., tendon and ligament attachment sites). More recently, new approaches, such as the measurement of the size of enthesal areas (e.g., Nolte and Wilczak, 2013; Karakostis and Harvati, 2021) or the quantification of trabecular bone quantity and orientation (e.g., Ryan and Shaw, 2012), have been developed. Finally, experimentation on animal models (e.g., Zumwalt, 2006; Wallace et al., 2022), studies of identified human skeletal collections (e.g., Villotte et al., 2010; Alves-Cardoso and Assis, 2021) and of living humans (e.g., Shaw and Stock, 2009; Macintosh et al., 2017) have multiplied in order to carefully test hypothetical skeletal reaction to mechanical stress in controlled settings.

From Pprecise Aactivities to Intragroup Aactivity Ppatterns

Among researchers who have taken an active interest in ARSC, there is a wide spectrum of opinions regarding the degree of accuracy that can be achieved in such studies of past activities.

Identification of Sspecific Aactivities in a Ggiven Iindividual

At one end of this spectrum are some scientists who consider that it is possible, for a given individual, to identify the practice of a specific activity. This approach is the most spectacular, but in order to remain credible, it must respect a set of strict conditions (Dutour, 1992): (1) The link between a physical activity and its consequences must be established based on current medical references, (2) the ARSC have to be as specific as possible to this activity, and (3) hypotheses must be compatible with the archaeological context.

While indispensable, the first criterion greatly limits the generalization of this approach. Very few current sports activities can be directly transposed to the past (javelin throwing, horse riding, archery and canoeing being the main examples), and technological changes (e.g., saddles, or bows) have likely generated varying biomechanical stresses over time. Moreover, nowadays very few scholars consider that a given ARSC is specific to only one activity.

Patterns of Llesions and Iidentification of Pprecise Aactivities in a Ggroup

In a variant of the previous approach, specific activities for a given individual are not the focus. Instead, patterns of lesions are associated with specific movements and then to activities known to be practiced in the studied group. This approach was notably applied, among other scholars, by Merbs (1983) and Hawkey and Merbs (1995). According to these authors (1995, p. 325), it requires (1) “a relatively large sample size with good skeletal preservation”, (2) “a relatively narrow time span”, (3) “cultural and genetic isolation”, and (4) “a limited number of specialized, but known, activities”. Unfortunately, such a sample probably seems more theoretical than realistic for most bioarchaeologists. Moreover, one may question whether it is worthwhile to study ARSC for such well-documented groups.

Gendered Ddivisions of Llabor

Most scholars use ARSC to formulate hypotheses about task division between males and females. They usually do link ARSC to possible activities, but often without putting too much emphasis on this point. The main criticism formulated against this type of study is the potentially narrow and stereotyped view of gender roles in the past. As noted by Robb (1998, p. 363), “it is common to ascribe hyperdeveloped arm and shoulder muscles in males to weapon use, while the same muscle markings in females are often explained as the result of plant processing or hide preparation.” Geller (2017, p. 162) criticized the strict gender boundaries drawn in such studies, as “they abide by the law of averages and discount overlap.” Indeed, it is true that authors tend to mention hypothetical gender-related tasks in a somehow simplistic way that suggests hermetic gender roles. However, the main result of these studies is unquestionably the strong evidence of gendered divisions of tasks in many of the analyzed groups. For instance, sexual differences in asymmetrical humeral robusticity are quite clear in many prehistoric groups in Europe, males being on average much more asymmetrical than females. This trend, that indicates a tendency of males (or at least some of them) being more preferentially involved in unimanual tasks than females, is not systematic but remains fairly widespread (e.g., Sparacello et al., 2017; Sládek et al., 2018) and supported by the diachronic study of other ARSC (Villotte and Knüsel, 2014).

Activity Ppatterns

Uniquely, the last approach considers that an ARSC can be associated with a wide range of cultural practices and not with a single task. Developed by Robb (1998), this approach does not consist of identifying any probable or possible activities, but instead seeks to understand the relationships among task divisions within the studied sample. From the study of enthesal changes in an Italian Iron Age sample, Robb (1998) highlighted relations between the specialization and intensity of activities on one hand, and the age-at-death, sex and associated grave goods of the deceased on the other hand. Remarkably, this analysis shed new light on the social organization in this early urban population, without setting hypotheses about the actual physical activities practiced by the individuals.

3 Key Issues: Types of ARSC — Potential and Limits

Classifications

The “atlas of occupational markers on human remains”, one of the most complete syntheses in this field of research, reports approximately 140 ARSC (Capasso et al., 1999). In fact, they form an extremely heterogeneous group, both in terms of types of changes and processes behind their development. This great variety implies application of very different methods to record the changes and affects the interpretations and hypotheses formulated, as these are based on very different theoretical frameworks. Consequently, the methodological and interpretative limitations are also very diverse: even if osteoarthritis of the elbow and platycnemia are both potentially relevant to discussions of past activities, the recording of their presence, the statistical analysis of the data and the resulting interpretations are very different, simply because they represent two clearly distinct biological phenomena. Yet scholars in this field tend to downplay or even ignore these fundamental differences, which does not facilitate dialogue between defenders and proponents of ARSC.

Considering this great heterogeneity, it is difficult to offer a classification that encompasses all the variation seen in this group of morphological changes. One can, arbitrarily though, group the ARSC according to:

- (1) The type of skeletal response (adaptation versus alteration);
- (2) The anatomical area affected (i.e., teeth, joints, muscular attachment sites, bone itself).

Based on these criteria, the following sections briefly present some examples of ARSC, as well as their specific importance and limitations.

Skeletal Adaptation

The ability of an individual skeleton to adapt in response to environmental changes is called plasticity. Since the 1970s, patterns of skeletal changes under various loading regimes have been illustrated by experimental research and studies of athletes (professional or not), and the body of research that supports the concept of “bone functional adaptation” is considerable (for a review, see Ruff, 2018). Though the processes are much less well-documented, the skeleton can also adapt to stresses by increasing the surfaces of muscular attachment sites, or by the formation of new articular surfaces covered with cartilage, for example.

Cross-Sectional Bone Geometry

Since the origin of the discipline, biological anthropologists have sought quantitative variables that may be considered as direct measures of bone strength, bone rigidity, or muscular activity. Originally, external linear measurements were analyzed, but they were largely replaced by cross-sectional geometric properties. Inspired by beam model theory used by engineers to analyze buildings, this approach consists of analyzing the distribution and quantity of cortical bone at a specific transverse section of a diaphysis in order to characterize long bone diaphysis adaptations to mechanical loading (Ruff, 2018). Many cross-sectional geometric properties were defined (such as the total area or the cortical area) but the polar second moment of area (J_p), considered as an overall measure of robusticity is the main variable analyzed nowadays. The image of a section made perpendicular to the longitudinal axis of the bone can be obtained through several means, the most common one being non-invasive imaging.

Cross-sectional geometric properties of the lower limb bones, especially the tibio-fibular complex, appear highly relevant to address mobility patterns, including the nature of the terrain covered (e.g., Sparacello et al., 2018). Data from the upper limbs, especially the humerus, permit inferences to be made about past workload (by comparing the

robusticity of the lower and the upper limbs, for instance, see [Macintosh et al., 2017](#)), and the preferential use of a single upper limb in activities (by studying asymmetry, see for instance [Sparacello et al., 2017](#)).

The potential ability to reconstruct behaviors in past human groups based on the analysis of cross-sectional geometric properties is undeniable. The methods are standardized and thus ensure repeatable and reproducible measurements, and the quantitative nature of the variables studied permits use of a large set of statistical tools that considerably facilitate data analyses. However, some limitations need to be mentioned. First of all, diaphyseal adaptations mainly occur during growth (see references in [Pearson and Lieberman, 2004](#)). In non-human mammals, growing bone responds to low or moderate exercise through significant additions of new bone, whereas this adaptive response is modest in mature bone. In humans, bone sensitivity to mechanical loading in adults is also lower than in juveniles, though a relatively great sensitivity seems to persist into young adulthood. What is "recorded" in bioarchaeological material is thus likely informative about what the individuals did during adolescence and maybe early adulthood but not necessarily at their time of death. Cross-sectional geometric properties correlate strongly with the size and shape of the whole body, and their standardization is thus required ([Ruff, 2018](#)). Ways of standardizing cross-sectional parameters have a significant impact on the results and need to be considered carefully. Finally, plastic effects do not fully mask neutral information (e.g., ancestry), and this may have an important effect when comparing temporally or geographically dispersed samples.

Kneeling Facets

Skeletal remains sometimes display extended surfaces at synovial joints, or supernumerary articular surfaces (e.g., "squatting facets" at the ankle) close to them. These features are usually considered as markers of habitual positions. Facets on the superior surface of the distal end of the metatarsals have been occasionally described, sometimes in association with distal extension of the proximal articular surface on the superior surface of the proximal phalanges, especially for the hallux. These modifications have been considered to be an indicator of skeletal plasticity to repeated kneeling (e.g., [Ubelaker, 1979](#); [Molleson, 2009](#)). There is no medical or experimental data to confirm this hypothesis, but these changes seem clearly related to the hyperextension of the toes. Unfortunately, this ARSC can take many forms on the metatarsals ([Fig. 1](#)), from a proximal extension of the distal articular surface to a ridge on the superior surface ([Ubelaker, 1979](#)). This variation in expression, and the fact that these changes have received relatively little attention until now, may explain why there is currently no standardized method to score this ARSC. As for the other markers of skeletal plasticity at synovial joints, further methodological research is required for this - potentially very pertinent ARSC.

Fig. 1



Skeletal Plasticity at **E**ntheses: The **E**xample of the **H**and

Several authors have looked for a relationship between muscular activity and the size of muscle attachment sites (e.g., [Zumwalt, 2006](#); [Nolte and Wilczak, 2013](#); [Karakostis and Harvati, 2021](#)), the underlying hypothesis being that surface area and surface complexity should increase through osteogenic activity stimulated by muscular contraction. Most of these studies focused on one or only a few entheses, and they found no clear relation between enthesal size and endurance exercise, muscle mass, or muscle-tendon length. Instead, the size of enthesal surfaces correlates strongly with body size, and moderately with age and birth year ([Nolte and Wilczak, 2013](#)).

Recently, Karakostis and colleagues proposed an original multivariate approach in order to reconstruct muscle synergies (for a review, see [Karakostis and Harvati, 2021](#)). This approach, strongly supported by several animal experimental studies, focuses on the proportions among different enthesal areas of the same skeleton. Their analyses of human remains, which mainly focuses on the entheses of the hand, provided promising results with potential discrimination of individuals with occupations involving high grip force from individuals involved in precise or less strenuous occupational tasks.

The main methodological issue regarding this approach concerns the identification of attachment site boundaries (and thus delineation of enthesal areas) for some individuals and/or some specific attachment sites ([Nolte and Wilczak, 2013](#); [Karakostis and Harvati, 2021](#)). Regarding the interpretation, more data on the physiological processes involved are required, especially in order to better understand when in the lifespan these skeletal adaptations occur. Based on data from non-human mammals this likely happens mostly during skeletal growth, though structures may respond to loads beyond that period (e.g., [Gao and Messner, 1996](#)).

Skeletal Alterations

Sometimes the tissues cannot adapt to the stresses they have undergone and become altered. When the alteration corresponds to trauma (e.g., bone, articular or dental fracture), the cause is likely a single event and is therefore less relevant for discussing daily life in the past. Microtrauma, produced by repetitive activity over time, is thus considered as more informative ([Merbs, 1983](#); [Dutour, 1992](#)). Such skeletal alterations are mainly described in the medical literature at synovial joints and fibrocartilaginous entheses.

Osteoarthritis and Degenerative **E**nthesopathies

A synovial joint is characterized by a capsule that delimits a space between the bones and which is filled with synovial fluid, and the presence of cartilage (hyaline and calcified) covering the bones. Synovial joints permit free bone movement and greater mobility, with articular cartilage absorbing shock and reducing friction during movement. Osteoarthritis (OA) is a degenerative condition and the most common joint disease, affecting millions of people worldwide ([Glyn-Jones et al., 2015](#)).

Fibrocartilaginous entheses are, in many ways, very similar to synovial joints. They are mostly found at long bone extremities and are characterized by two mediating layers (uncalcified and calcified fibrocartilage) between tendon/ligament fibers and bone. These two fibrocartilaginous layers are avascular and separated from each other by a regular calcification front, which represents the surface observed on dry bones ([Benjamin et al., 2002](#)). Age-related degenerative enthesopathies are quite common in healthy individuals (e.g., [Bakirci et al., 2020](#)).

The main factors evoked for the appearance of OA and degenerative enthesopathy are: (1) aging - that can be defined as the progressive incapacity of the individual to adapt to the variable environmental conditions, and (2) the repetition of minor trauma. The relationship between these factors (and many others, such as hormonal levels or body mass) is not well understood. For a long time the mechanism behind the appearance of such lesions has been ascribed to a “wear and tear” hypothesis: skeletal alterations gradually appear through life and become more and more extreme due to the accumulation of wear and tear produced by physical activity. This hypothesis has now been largely abandoned in biomedical science. Heavy work activities and high-impact sports are recognized as risk factors, but many other factors (such as obesity, previous injury, genetic background, etc.) have been identified, age being the most evident. More and more biomedical studies identify at least two phases during adulthood: an early phase where overuse can induce

microtrauma (and minor skeletal changes), and a second phase in adulthood when mechanical factors play only (if any) a secondary role and are marked by a generalized disruption of the soft and hard tissues and the appearance of major changes (Glyn-Jones et al., 2015; Bakirci et al., 2020).

There is a plethora of studies of OA and degenerative enthesopathies in the biological anthropological literature, but there is still no clear consensus regarding their reliability as ARSC. One obvious limitation comes from the relationship between this type of ARSC and age, considering the difficulty of assessing accurately (not to mention precisely) age-at-death in adult skeletal remains. Moreover, these skeletal alterations are generally recorded using qualitative, non-standardized, methods, that limit the reproducibility of the studies.

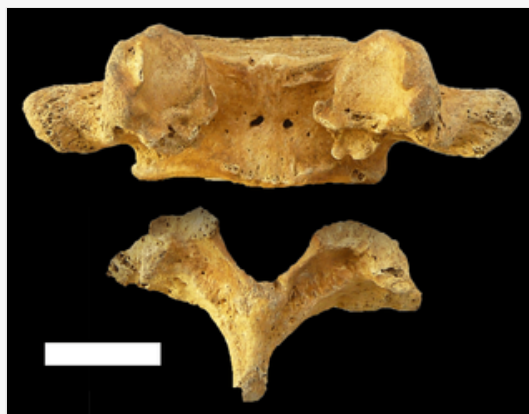
Most studies of identified skeletal collections found little evidence that enthesopathies and/or OA occurrences are related to physical activities (e.g., Winburn and Stock, 2019; Alves-Cardoso and Assis, 2021). This is likely due to several factors, the main one being that most studies are based on the assumption that major skeletal changes correlate with high biomechanical stresses, whereas these exuberant skeletal alterations are likely “only” indicators of an older age (or of a systemic pathological condition, see Villotte and Knüsel, 2013). Another possible limitation may come from the assumption that the presence of OA and degenerative enthesopathies is related to “normal” levels of biomechanical stress. This seems improbable and minor changes, in young adult individuals, are more likely indicators of very high strains.

Taking into account these (and many other) limitations, OA and degenerative enthesopathies may nevertheless have the potential to be a good indicator of heavy workload, but more research is required in order to identify the best skeletal locations. Theoretically, skeletal alterations at these sites should follow a pattern (e.g., right side dominance for the upper limb, influence of age) in identified skeletal collections compatible with biomedical data (e.g., Villotte et al., 2010; Villotte and Knüsel, 2014; Alves-Cardoso and Assis, 2021). For the study of archaeological material, it will also be necessary to find alternatives (such as ratios, see Villotte and Knüsel, 2014) to eliminate the influence of age without having to rely on the estimation of age-at-death.

Stress Fractures: The Example of Spondylolysis

Stress fractures due to accumulated injuries from repetitive, sub-maximal loads are common overuse injuries in athletes. Among the many locations where stress fractures can occur, very few are routinely studied in bioarchaeology, the *pars interarticularis* of vertebral arches being one of them (Fig. 2). Spondylolysis is an osseous defect in this area and typically affects the fourth and fifth lumbar vertebrae (Merbs, 1996). The general prevalence in the adult population is estimated between 3% and 6% (Fredrickson et al., 1984) and, in most cases, a stress fracture etiology seems most likely. Some sports participants (including throwing sports, gymnastics, and rowing) are clearly at risk, with frequencies above 10% in symptomatic and asymptomatic athletes (e.g., Soler and Calderón, 2000).

Fig. 2



Spondylolysis at a fifth lumbar vertebra. Scale bar: 2 cm.

In biological anthropology, high prevalence of spondylolysis has been linked to specific activity patterns and general heavy labor (e.g., [Merbs, 1983](#)). The main limit to determining causation comes from the influence of genetic factors, as inheritance is an identified factor in the development of a *pars interarticularis* defect ([Fredrickson et al., 1984](#)). Some family members may have a higher susceptibility to the lesion than others ([Fredrickson et al., 1984](#)), and spondylolysis may occur in association with other similar skeletal conditions (i.e., detached pieces of bone), suggesting that those individuals were genetically predisposed ([Verna and Villotte, 2016](#)). One way to avoid this problem would be to compare the frequency of spondylolysis among several sub-samples (according to biological or social factors) from the same population.

Irritation of the Periosteum and Aquatic Activities: External Auditory Exostoses

External auditory exostosis (EAE) is a progressive pathological condition caused by an irritation of the periosteum in the external auditory canal ([Di Bartolomeo, 1979](#)). Many conditions (e.g., *otitis externa*, eczema, trauma, infection) can be responsible for this irritation, but contact with cold water is the chief cause. A considerable number of clinical studies demonstrate that individuals regularly exposed to cold water are most predisposed to develop EAE (for a review, see [Villotte and Knüsel, 2016](#)). Induced reflex vasodilatation occurring in the bony meatus during cold-water activities produces an increase in tension in the periosteum, and repeated stimulation of the periosteum may induce new bone formation ([Harrison, 1962](#)). Wind chill appears to be an important factor, mainly on the severity of exostoses.

In biological anthropology EAE are considered to be a reliable marker of aquatic activities ([Kennedy, 1986](#); [Villotte and Knüsel, 2016](#)). Some limitations should be mentioned though. First of all, as for many other ARSC, individual differential susceptibility to stress exists for EAE ([Harrison, 1962](#)), and the influence of the genetic background has been strongly suggested for some past human groups (namely Neandertals, cf. [Trinkaus et al., 2019](#)). Between-group comparisons thus should be carried out with caution. Secondly, even if the process behind the appearance of EAE is extremely well-documented, the relative influence of several environmental factors is not fully understood. It has been shown, for instance, that EAE may occur in individuals frequently involved in aquatic activities in relatively warm water, and that exposure to the evaporation of sea mist, without immersion of the head in cold water, may be sufficient to promote EAE (for a review, see [Trinkaus et al., 2019](#)). Finally, early changes of EAE are sometimes difficult to grade in skeletal remains ([Villotte and Knüsel, 2016](#)).

Alteration or Adaptation? Diffuse Cortical Irregularity at Fibrous Entheses

In fibrous muscular attachment sites, which occur typically on the diaphysis of long bones, collagen fibers from tendons or ligaments attach to bone directly or via a mediating layer of periosteum ([Benjamin et al., 2002](#)). The surface of such entheses is usually irregular and poorly delimited on adult skeletal remains. Lesions at fibrous attachment sites are barely mentioned in the medical literature ([Henderson, 2013](#)), justifying avoidance of the term “enthesopathy” for the enthesal changes frequently seen at these sites.

Diffuse cortical irregularity (sometimes called “robusticity”) at fibrous entheses has long been considered as the product of bone remodeling stimulated by repeated - normal or vigorous - muscle contractions during adulthood. Even if this hypothetical relationship seems reasonable, it is based on almost no medical or experimental data (see [Villotte and Knüsel, 2013](#)). The correlations between scores of skeletal changes at fibrous entheses and parameters such as age-at-death and body size appear stronger than for fibrocartilaginous attachment sites ([Weiss, 2015](#); [Milella et al., 2020](#)). There are, however, empirical data suggesting that physical activities may participate in the occurrence of such diffuse cortical irregularity (e.g., [Lieverse et al., 2013](#); [Milella et al., 2015](#)). The “wear and tear” hypothesis may be useful for such type of changes, but more histological and experimental analyses are required before considering diffuse cortical irregularity at fibrous entheses as reliable ARSC.

4 Summary and Future Directions

It seems undeniable that some skeletal morphologies are related to the practice of physical activities. However, the study of these morphologies in past human groups raises many difficulties, in terms of methods, data analysis and interpretation of the results. Moreover, biomechanical stresses are never the unique cause of a given skeletal morphology. They induce changes in interaction with many other factors such as growth and aging processes, hormonal levels, diet, body proportions, and genetic background.

Several avenues of research are nevertheless open. Animal models, dissection of human cadavers and human identified skeletal collections are fundamental sources to establish solid methodological and interpretative bases. Basic anatomical and histological data, too often neglected, must be used wisely to discuss the results obtained. Thus, for instance, the concept of “bone functional adaptation” very often evoked for skeletal areas covered with calcified (fibro)cartilage (i.e., synovial articular surfaces and fibrocartilaginous entheses) has to be replaced by new theoretical frameworks, specific to these tissues. As the identification of a precise activity seems particularly difficult (if not impossible) for most ARSC, other approaches should be explored, notably the statistical identification of subgroups of individuals, without seeking to specify which activities were practiced.

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Keywords: Activity; Auditory exostoses; Bone functional adaptation; Cross-sectional bone geometry; Enthesis; Enthesopathy; Osteoarthritis; Skeletal plasticity; Stress fracture; Supernumerary facet; Synovial joint

Queries and Answers

Q1

Query: Please confirm that given names and surnames have been identified correctly and are presented in the desired order and please carefully verify the spelling of all authors' names.

Answer: Yes