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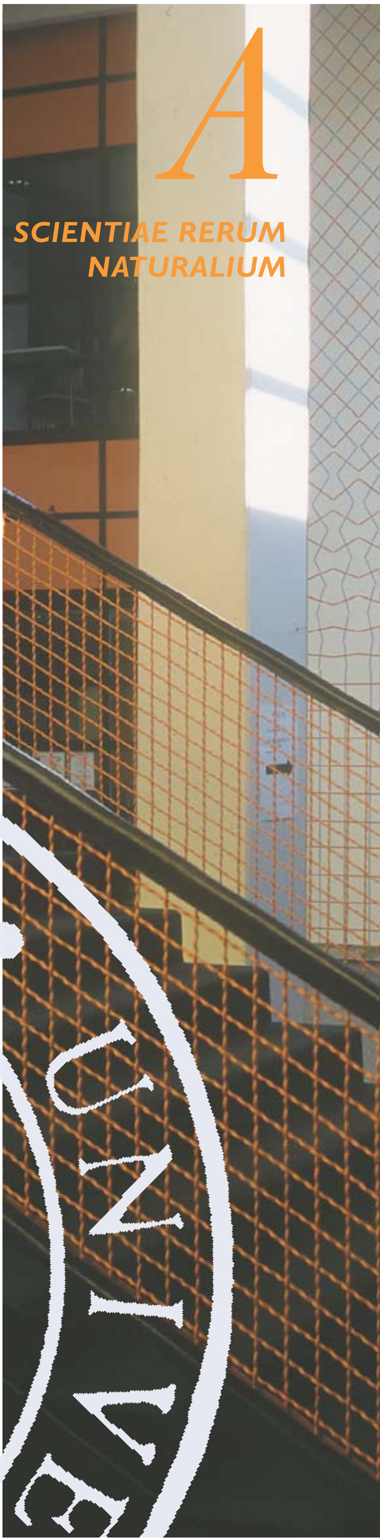

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Sirpa Niinimäki

RECONSTRUCTING PHYSICAL ACTIVITY FROM HUMAN SKELETAL REMAINS

POTENTIALS AND RESTRICTIONS IN THE USE OF MUSCULOSKELETAL STRESS MARKERS

UNIVERSITY OF OULU GRADUATE SCHOOL;
UNIVERSITY OF OULU,
FACULTY OF SCIENCE, DEPARTMENT OF BIOLOGY;
FACULTY OF HUMANITIES, ARCHAEOLOGY;
UNIVERSITY OF SHEFFIELD,
FACULTY OF ARTS AND HUMANITIES, DEPARTMENT OF ARCHAEOLOGY

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SIRPA NIINIMÄKI

RECONSTRUCTING PHYSICAL ACTIVITY FROM HUMAN SKELETAL REMAINS

Potentials and restrictions in the use of musculoskeletal stress markers

Academic dissertation to be presented with the assent of the Doctoral Training Committee of Technology and Natural Sciences of the University of Oulu for public defence in Kuusamonsali (Auditorium YB210), Linnanmaa, on 13 October 2012, at 12 noon

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Abstract

The purpose of my thesis is to improve the reliability of physical activity reconstructions by gaining better understanding of the effects of physical activity on bone structural adaptations: musculoskeletal stress markers (MSM) at muscle attachment sites and bone biomechanical properties. Bone responds to changes in mechanical loading resulting from activity and body weight. Activity reconstructions are important as they are the only means with which activity patterns of historic humans can be studied. However, MSMs have recently increased the debate about their reliability as activity indicators due to many bias factors which affect their appearance: age, size, sex and pathological changes.

I studied the effects of physical activity on entheses from three perspectives. First, individuals performing heavy labour should have higher MSM scores compared to the light labour group due to elevated degree of mechanical loading at enthesis. This was studied on a population with known occupation and was among the first study designs of its kind. Second, a covariance between bone biomechanical properties and MSM was studied to infer etiology of MSM. The affects of activity and body weight on bone biomechanical properties are well known due to studies in sports medicine, whereas the causal mechanisms behind MSMs are not as clear. In theory, both should respond to stress with similar mechanisms. This is a novel approach to investigate the etiology behind MSMs. Third, if there is a possibility of site-specific adaptation of cortical bone, MSMs, which are local adaptations, can also result from site-specific stress.

I found that while individuals performing heavy labour had higher scores, age-related changes in MSM override activity effects after biological maturity around 40 to 50 years. Also, MSMs and bone biomechanical properties are likely to remodel under same causal mechanisms as where there is an increase in one there is likely to be an increase in the other. Furthermore, bone has a possibility of site-specific response, as cortical thickness was increased at muscle pull sites compared to sites of no muscle pull. I propose that while MSM can be used to study the intensity of physical activity in individuals before they reach biological maturity, it is important to design studies where biasing factors, such as age, are considered.

Keywords: aging, biological anthropology, bones, entheseal changes, enthesis, musculoskeletal stress markers, osteology, physical activity

Niinimäki, Sirpa, Lihasten kiinnittymiskohtien mahdollisuudet ja rajoitukset fyysisen aktiviteetin rekonstruktioissa.

Oulun yliopiston tutkijakoulu; Oulun yliopisto, Luonnontieteellinen tiedekunta, Biologian laitos, PL 3000, 90014 Oulun yliopisto; Humanistinen tiedekunta, Arkeologia, PL 1000, 90014 Oulun yliopisto; University of Sheffield, Faculty of Arts and Humanities, Department of Archaeology, Northgate House, West Street, Sheffield, S1 4ET, United Kingdom

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Tiivistelmä

Väitöskirjani tarkoitus on tutkia lihasten kiinnittymiskohtien mahdollisuuksia ja rajoituksia fyysisen aktiviteetin rekonstruktioissa ja näin parantaa rekonstruktioiden luotettavuutta. Aktiviteettihistoriaa voidaan tutkia lihasten kiinnittymiskohdista luun pinnalla tai luun poikkileikkauksen ominaisuuksista, koska luu reagoi muutoksiin mekaanisen rasituksen määrässä. Mekaaniseen rasitukseen vaikuttaa aktiviteetin lisäksi ruumiin koko. Aktiviteetin rekonstruktiot mahdollistavat ammatin ja harrastusten selvittämisen pelkän luustomorfologian perusteella. Ruumiin koon ja aktiviteetin lisäksi myös ikä, sukupuoli, patologiset muutokset sekä ruokavalio vaikuttavat lihasten kiinnittymiskohtiin. Tästä syystä tämän menetelmän rajoitusten selvittäminen on oleellista luotettavien rekonstruktioiden aikaansaamiseksi.

Jos aktiviteetti heijastuu lihasten kiinnittymiskohtiin, raskasta ja kevyttä työtä tekevillä ihmisillä tulee olla erilainen luustomorfologia. Lisäksi, lihasten kiinnittymiskohtien morfologian sekä luun poikkileikkausten ominaisuuksien tulee muunnella yhdessä koska molemmat heijastavat aktiviteettia. Luun poikkileikkausten ominaisuuksien aktiviteettisidonnaisuus tunnetaan paremmin liikuntalääketieteellisten tutkimusten ansiosta. Kolmanneksi, jos luu voi vastata rasitukseen paikallisesti kasvattamalla luun paksuutta lihaksen vetosuuntaan nähden, myös luun pinnassa paikallisesti tapahtuvat muutokset ovat mahdollisia. Nämä ovat uusia lähestymistapoja aktiviteettia heijastavien syntymekanismien selvittämisessä.

Tutkimustulosteni perusteella raskasta ja kevyttä työtä tekevillä ihmisillä on erilainen luustomorfologia lihaksen kiinnittymiskohdassa. Nämä muutokset ovat alttiita myös ikäsidonnaisille muutoksille, joten noin 40–50 ikävuoden jälkeen fyysisen aktiviteetin intensiteettiä ei voida enää luotettavasti rekonstruoida. Aktiviteetin aiheuttamien muutosten syntymekanismi lihaksen kiinnittymiskohdissa on todennäköisesti sama kuin luun poikkileikkausten ominaisuuksilla, koska molemmat muuntelevat yhdessä. Lisäksi huomasin, että luu voi reagoida rasitukseen myös paikallisesti, koska luun seinämät olivat paksumpia lihaksen vetosuunnassa verrattuna kohtaan, johon ei liittynyt suoraa lihaksen vetosuuntaa. Ehdotan, että lihasten kiinnittymiskohtia voidaan käyttää aktiviteetin rekonstruktioissa, kunhan tutkimuksessa otetaan huomioon muut vaikuttavat tekijät, kuten ikä.

Asiasanat: biologinen antropologia, fyysinen aktiviteetti, historia, ikä, ikämuutokset, osteologia

To Joska

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List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I Niinimäki S (2011) What do muscle marker ruggedness scores actually tell us? International Journal of Osteoarchaeology 21(3): 292–299, first published online 2009 DOI10.1002/oa.1134.

II Niinimäki S (2012) The relationship between musculoskeletal stress markers and biomechanical properties of the humeral diaphysis. American Journal of Physical Anthropology 147(4): 618–628.

III Niinimäki S, Söderling S, Junno J-A, Finnilä M & Niskanen M (2012) Age and activity related trends in cross-sectional distribution of bone in the humerus. Manuscript.

IV Junno J-A, Niinimäki S, Niskanen M, Nunez M & Tuukkanen J (2011) Cross sectional properties of the human radial tuberosity. HOMO – Journal of Comparative Human Biology 62: 659–465.

Contents

1 Introduction

Activity reconstructions based on human skeletal remains are important as they are the only means with which activity patterns and intensity of activity of historic human populations or extinct species can be studied. However, these reconstructions have recently been the focus of a debate about their reliability as activity indicators (*e.g.* Jurmain & Roberts 2008). In this thesis, I aim for a better understanding of the effects of physical activity on bone structural adaptations by studying the relationship between musculoskeletal stress markers[1] (MSM), bone biomechanical properties and physical activity in the upper limb with respect to possible bias factors, such as age, size, sex and pathological changes.

Activity reconstructions are based on bone biomechanical properties and MSMs[2] (Jurmain *et al.* 2012). Analyses of the biomechanical loading of skeletal elements have been used to study the history of bipedal locomotion and locomotion patterns (Ruff 2008), patterns of mobility in prehistoric and historic human populations, such as marine-based versus terrestrial-based mobility (Stock & Pfeiffer 2001, Weiss 2003a), effects of unilateral versus bilateral activity (Shaw & Stock 2009), or even combatant weapon preference (Rhodes & Knüsel 2005). In addition, biomechanical properties have been used to study sexual division of labour (Wescott & Cunningham 2006). It is important to study biomechanical loading with respect to past activity, as there may be unexpected patterns, such as less marked sexual division of labour during the Early Upper Paleolithic compared to present-day hunter-gatherer sexual division of labour, or changes in behavioural patterns to a more sedentary lifestyle occurring before the onset of agriculture during the Late Upper Paleolithic and Mesolithic (Holt 2003). Another method used to reconstruct physical activity is to use MSMs. This method has been applied in studies of sexual division of labour (Wilczak 1998, Molnar 2006, Weiss 2007) as well as differences between populations in subsistence strategies (Churchill & Morris 1998) or differences within populations over time (Lieverse *et al.* 2009) or between socio-economic groups (Havelková *et al.* 2011), before and after the onset of agriculture (Eshed *et al.* 2004) or, in case of the Pueblo people, differences in labour intensity and labour patterns during pre-colonial and colonial times (Spielmann *et al.* 2009).

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[1] Sometimes called entheseal changes (abbreviated EC) as some researchers want to set these changes apart more clearly from the aetiology originally associate with MSM formation (Jurmain *et al.* 2012).

[2] Occupational stress has also been studied using presence and location of specific pathologies, such as osteoarthritis (Jurmain *et al.* 2012).

Activity reconstructions are based on bone's ability to respond to stress. Bone reacts to its mechanical environment - lean body mass, physical activity, body size and muscle moment arm - by changing its shape and structure (Ruff *et al.* 1994, Trinkaus *et al.* 1994, Seeman *et al.* 1996, Ferretti *et al.* 1998, Schiessl *et al.* 1998, Schoenau *et al.* 2000, Ruff 2000b, Schoenau & Frost 2002, Ruff 2003, Parfitt 2004, Petit *et al.* 2004). Bone mass can be increased or decreased with mechanical stimulus according to mechanostat theory: bone is adapted to normal levels of stress, whereas a response occurs at higher or lower levels of stress than the equilibrium range (Frost 1987). Bone mass is increased if the stimulus is high enough while decreased loading leads to removal of bone in a process called modeling, and if bone mass stays constant after resorption and formation the process is called remodeling (Schoenau & Frost 2002, Martin 2007). Peak bone mass is achieved during the first thirty years of life based on individuals' loading history (Johnston & Slemenda 1993, Parfitt 2004). Loading history (Forwood & Burr 1993) and cumulative effects of activity are important for bone mass maintenance and distribution (Ruff *et al.* 2006), but exercise can add bone mass even post-menopause (Kannus *et al.* 1995). However, bone remains adaptive in adulthood (Forwood & Burr 1993, Kannus *et al.* 1995, Seeman *et al.* 1996, Ferretti *et al.* 1998, Anderson 2001). Bone is strengthened towards the direction of stress by changes in overall shape.

1.1 Bone cross-sectional geometry in activity reconstructions

The usual direction of stress can be deduced from the shape of the bone shafts and thus bone cross-sectional properties have been utilised in activity reconstructions (*e.g.* Stock & Pfeiffer 2001, Holt 2003, Weiss 2003a, Wescott & Cunningham 2006, Stock & Shaw 2007, Shaw & Stock 2009). Bone biomechanical properties, such as the overall shape of a cross-section and the distribution of bone mass with respect to bone bending and torsional strength and axial compression strength, can be calculated from bone cross-sectional geometry (O'Neill & Ruff 2004). While mechanostat theory explains how and why there are changes in bone mass, the theoretical principles of beam theory have been applied to study bone mechanics to understand changes in bone cross-sectional shape and structure (Lieberman *et al.* 2004, Ruff *et al.* 2006, Stock & Shaw 2007). According to beam theory, the periosteal contour of bone is most relevant for resisting bending and torsion forces as it is located furthest from the neutral bending axis (Lieberman *et al.* 2004, Ruff *et al.* 2006, Stock & Shaw 2007). Thus, the overall shape of a bone shaft contributes significantly to the bending and torsion resistance (Lieberman *et al.* 2004, Ruff *et al.* 2006). The endosteal contour has relatively minimal impact on bone strength, but external architecture is strongly correlated with internal architecture (Stock & Shaw 2007).

1.2 Musculoskeletal stress markers (MSM) in activity reconstructions

The principal function of an attachment site is to provide surface area for the attachment of a muscle or a tendon. Thus muscle attachment sites, also called entheses, are sites where stress from muscle contraction force takes effect. Entheses are divided into two categories according to the type of muscle-bone attachments: fibrous and fibrocartilaginous. Fibrous attachments are further divided into bony and periosteal attachments. Usually fibrous entheses are associated with diaphyses, whereas fibrocartilaginous entheses are associated with epiphyseal and apophyseal attachment sites (Benjamin *et al.* 1986, Benjamin *et al.* 2002).

Entheses exhibit MSM as localised modifications of the bone surface. Several methods have been developed to quantify these changes (Hawkey & Merbs 1995, Robb 1998, Mariotti *et al.* 2004, Zumwalt 2005, Galtés *et al.* 2006, Villotte 2006). Scoring methods record the development of osteophytes (also called tubercles or ruggedness) and osteolytic defects (also called pits or stress lesions). Formation of a pit and/or a tubercle at an enthesis has been explained theoretically by Hirschberg (2005) under the standard biomechanical principles of bone remodeling. Flat bone surfaces model in response to stress according to whether deposition or resorption thresholds are reached, and a tubercle or a pit is formed accordingly. Furthermore, the strain of a muscle pull directs the formed tubercle or pit along the primary axis of stress (Hirschberg 2005).

1.3 Sources of bias in activity reconstructions

Both cross-sectional properties and MSM have limitations in their use and there are a considerable number of bias factors when applying these methods for activity reconstructions. Not all scientists agree on the extent to which loading patterns can be reconstructed from dry bones (Lieberman *et al.* 2003, Lieberman *et al.* 2004, Pearson & Lieberman 2004). Also, some authors emphasise the role of pathological conditions in MSM which may seriously compromise the accuracy of physical activity reconstructions (Jurmain *et al.* 2012).

Recording MSM for activity reconstructions may be problematic. A multifactorial aetiology of MSMs has been acknowledged by several authors as, in addition to physical activity, also age, body size, sex, genes, obesity, diet and pathological conditions have been noted to affect their appearance (Zumwalt *et al.* 2000, Mariotti *et al.* 2004, Chen *et al.* 2007, Slobodin *et al.* 2007, Jurmain & Roberts 2008, Villotte *et al.* 2010, Weiss *et al.* 2010, Jurmain *et al.* 2012). Body size, age and sex also have profound effects on bone cross-sectional properties. As body size is the baseline for the bone mechanical environment it affects bone cross-sectional properties significantly (Ruff 2003, Ruff 2005). Thus, before any attempts are made to reconstruct physical activity, bone cross-sectional properties must be standardised to this baseline. Overall body size affects also MSMs (Churchill & Morris 1998, Wilczak 1998, Zumwalt *et al.* 2000, Weiss 2003a, Weiss 2003b, Weiss 2007). Large individuals produce slightly higher scores on average, which may result from greater required effort for movement compared to smaller individuals.

Internal factors, such as age and sex hormones, affect both cross-sectional properties and MSM. In general, bone is deposited at the periosteal envelope prior to mid-adolescence and at the endosteal envelope after that (Ruff *et al.* 1994, Trinkaus *et al.* 1994, Seeman 2001, Daly 2007). Age-related changes include expanded medullary cavities, thinner cortices, and the net loss of trabecular bone (Trinkaus *et al.* 1994, Schiessl *et al.* 1998, Schoenau *et al.* 2000, Martin 2007). Age affects also bending and torsion rigidity, which increases with age in young adults due to expansion of the cortical and medullary areas (Petit *et al.* 2004) and the increase may continue through middle age and well into old age (Ruff and Hayes 1983, Feik *et al.* 1996, Sigurdsson *et al.* 2006). With respect to MSM, older individuals are more likely to exhibit an elevated degree of modifications (Kennedy 1989, Churchill & Morris 1998, Nagy 1998, Robb 1998, Weiss 2003b; Mariotti *et al.* 2004, Galtés *et al.* 2006, Molnar 2006, Weiss 2007, Villotte *et al.* 2010). Possible reasons for elevated scores in elderly individuals have been related to cumulative long-term activity patterns. Repetitions of activities alter MSM appearance, and in old age cumulative effects of stress are more likely to appear (Nagy 1998, Wilczak 1998). Rougher external bone may result from reduced osteoblast activity in older individuals resulting in thinner cortical bone with greater diameter and rougher external bone surfaces (Weiss 2007). This likely applies mostly to MSMs at diaphyses, namely fibrous attachments. Age effects on fibrocartilaginous attachments are likely due to changes in tissue properties of tendons by increasing tendon stiffness and thus mechanical loading of entheses (Jurmain *et al*. 2012).

There are systematic differences between the sexes in the degree of modifications at entheses, but the causal factors behind this observation are not known. Sex differences in bone cross-sectional properties and MSM may be due to hormones (Seeman 2001, Daly 2007, Weiss *et al*. 2010) and size (Churchill & Morris 1998, Wilczak 1998, Zumwalt *et al*. 2000, Weiss 2003a, Weiss 2003b, Weiss 2007). Prior to puberty, exercise appears to increase periosteal apposition in both sexes, whereas, during or late in puberty, exercise appears to result in periosteal expansion in boys but endocortical contraction in girls (Seeman 2001, Daly 2007). Sex differences may also result from possible gender-specific patterns in habitual activities (Ruff *et al*. 2006) or differences in force production capability between males and females (Miller *et al*. 1993, Kanehisa *et al*. 1994). Male scores are usually higher than female scores, but also reverse sex differences have been documented (Weiss *et al*. 2012 and references therein). According to Weiss *et al*. (2010), reverse sex differences in the case of specific cultures or populations are likely to be activity related, but when the same reverse sex difference occurs in many different cultures or populations, it may be hormonal or methodological.

1.4 Objectives

The scope of my research is to aim for a better understanding of the effects of physical activity on bone adaptation to stress; in particular MSM and bone biomechanical properties. This scope is divided into three perspectives (for summary of research questions, hypotheses and results, see Table 1). First, I evaluate whether MSM can be used to infer intensity of activity while considering the effects of biasing factors (I). Second, I study the possible causal mechanisms behind MSM development (II). Third, I explore the possibility of site-specific versus overall structural adaptation of bone to stress (II, III, IV). These results will be applicable for understanding how, why and to what extent bone is able to respond to stress site-specifically as manifested in changes in MSM scores, cross-sectional shape and cortical thickness. Thus, my thesis is a contribution to the current discussion on the reliability of physical activity reconstructions.

My first objective is to test whether individuals performing heavy and light labour exhibit differences in MSMs (I). The scores should be higher among the heavy labour group compared to the light labour group, as individuals performing heavy labour should have an elevated degree of mechanical loading at entheses. To explore this, I use a population with recorded information about occupation, age and sex (I). If differences in activity intensity are not evident as differences in MSM, any inferences on type of activity are not possible either. Further, the biasing effects of age and size on interpretation of activity intensity will also be considered.

My second objective is to study the possible causal mechanisms behind MSM development (II). The effects of activity on bone cross-sectional properties are well documented (*e.g.* Trinkaus *et al.* 1994, Kannus *et al.* 1995, Shaw & Stock 2009, Shaw 2010). Mechanisms behind alterations of these properties are explained through mechanostat theory (Frost 1987) and beam theory (Lieberman *et al.* 2004, Ruff *et al.* 2006, Stock & Shaw 2007). Changes in MSM should be based on the same mechanisms of bone remodeling (Hirschberg 2005). And, as both bone torsion rigidity and MSM are considered to reflect physical activity, they should covary. I use multiple cross-sectional locations of the humeral shaft to explore site-specific as well as general trends in the relationship between MSMs and biomechanical properties. This includes both those cross-sectional locations housing the attachment of the muscles of interest as well as those that do not. Previously, only the 35% cross-section location has been utilised in studies on the relationship between MSM and bone cross-sectional properties (Bridges 1997, Weiss 2003b).

My third objective is to study the effects of bone adaptation to stress as site-specific and overall changes affecting the shape and distribution of cortical bone in the humeral shaft and at the radial tuberosity (II, III, IV). Bone adapts to stress by altering the distribution of bone mass as well as MSM development. Physical activity loads the bone mechanically, which should, according to mechanostat theory (Frost 1987), increase bone mass. There may be a possibility to increase or maintain bone at muscle attachment sites against age-related bone loss (Forwood & Burr 1993, Kannus *et al.* 1995, Nguyen *et al.* 1998, Sigurdsson *et al.* 2006). Response to activity also varies between the proximal and distal humeral shaft where the activity increases the width of the proximal shaft more than the distal shaft (Haapasalo *et al.* 1996). This indicates that cortical bone mass and distribution can vary between the proximal and distal shaft with age and activity. However, cortical thickness and torsional rigidity may be governed by the overall stress regime acting on the diaphysis, rather than localised stresses at attachment sites. Furthermore, adaptation with shape might be an adequate stress response

(Rhodes & Knüsel 2005). I use multiple cross-sectional locations of the humeral shaft to study site-specific versus overall structural adaptation of bone mass. For the radius, I examine the mid-radial tuberosity site. In previous studies the focus has usually been on the 35% or 50% cross-section of the humeral shaft (except Rhodes & Knüsel 2005), and no studies exist on the cross-sectional properties of the mid-radial tuberosity.

To sum up, in this research I aim for a better understanding of the possible causal factors behind MSM development to improve the reliability of physical activity reconstructions. Furthermore, studying site-specific versus overall bone functional adaptation to stress will aid in understanding the processes resulting in changes in bone mass distribution and shape and changes in MSM to physical activity.

Table 1. Summary of research questions, hypotheses and results.

Paper	Original work	Research questions	Hypotheses	Results
I	Niinimäki 2011	Can MSM be used to study intensity of physical activity? What are the effects of age on this relationship?	Entheses of individuals performing heavy labour are under greater mechanical loading than the attachment sites of those individuals performing light labour.	Greater mechanical loading in heavy labour group among young individuals was evident as higher MSM scores. After biological maturity (at 40 to 50 years) age bias activity effects.
II	Niinimäki 2012	Do MSM and J covary due to their common relationship to physical activity?	Same causal mechanisms should be responsible for changes in MSM and biomechanical properties and should thus covary.	MSM and J covary, but there are also other factors affecting their appearance.
III	Niinimäki *et al*. (manuscript)	Does cortical bone thickness vary between locations? What are the effects of muscle pull?	Muscle pull can maintain or even increase bone mass at entheses. Response to activity varies between proximal and distal humeral shaft.	Cortical thickness at muscle attachment sites is thicker than at sites of no muscle pull. Cortical thickness decreases from distal to proximal humeral shaft reflecting decreased bending stresses.
IV	Junno *et al*. 2011	Does the pull of biceps brachii affect cross-sectional properties of mid-radial tuberosity?	Radial tuberosity is oriented to the direction of muscle pull while the attachment site for the biceps brachii tendon is additional bone over radial shaft.	The direction of greatest bending rigidity is oriented towards the biceps brachii muscle pull. Cortical thickness is reduced at radial tuberosity site.

2 Materials

I had three main requirements for the skeletal materials. First, I needed a large number of relatively intact and well-preserved humeri available for pQCT (peripheral quantitative computed tomography) scanning (II, III, IV) and recording MSM at entheses (I, II, III). Second, material of known occupation was essential to study the effects of heavy and light physical labour as well as age on MSM (I). Third, radii of a population with known occupation were required to study the cross-sectional properties of mid-radial tuberosity (IV).

I chose three skeletal populations: Helsinki, York (Barbican) and Newcastle (Blackgate) as they are large, well preserved skeletal collections representing populations with similar climatic adaptations. The Helsinki material consists of skeletons obtained from cadavers and the material is housed in the Natural History Museum, Helsinki. The York and Blackgate collections are archaeological and are housed at the University of Sheffield. Only skeletons of adults (18 years or older) were included in the samples. Age was known for the Helsinki material. For the archaeological material, I assessed age from the changes in the pubic symphysis, endocranial suture closure, and dental wear and sex from morphological differences in the pelvis and cranium (Bass 1987).

My selection criteria for humeri were that maximum length for size control and biomechanical length for determining cross-sectional locations for pQCT scanning could be measured accurately. For radii selection the criterion was an intact radial tuberosity. The observed radii were in excellent condition, as I studied radii only from the Helsinki sample. I followed the criteria of Mariotti *et al.* (2004) for preservation of entheses, where at least 50% of an enthesis is required for accurate scoring of the attachment. I rejected any pathological radii and humeri. Relevant numbers of individuals available for analyses are stated case-specifically in papers.

2.1 Helsinki (I, II, III, IV)

The Helsinki sample represents modern urban Finns of Southern Finland and consists of approximately 300 adults. As this skeletal material was obtained from cadavers, they were mostly in excellent condition with minimal taphonomic interference, although not all bones of an individual were present. Age, sex and occupation were known for most of these individuals (Kivalo 1957, I). The stated occupations are, for example, workman, seaman, office worker and shoemaker for males and housemaid, servant, and seamstress for females (I). Some ambiguous titles such as prisoner, senior citizen and wife are also given (I). Heavy physical labour was defined as tasks requiring lifting, moving heavy loads or getting short of breath involved in the profession (Chaffin 1981). I evaluated the intensity of activity as heavy or light where it could be assessed from the stated occupation. There were very few indications of trauma and a relatively low prevalence of degenerative joint disease among this sample (T Heikkilä, personal communication July 11 2011).

2.2 Blackgate (II, III)

The Blackgate cemetery is located in Newcastle upon Tyne, adjacent to the site of a former Roman fort. Radiocarbon dating of the skeletons shows that the cemetery was in use from the late Anglo-Saxon to early Norman periods (late 7th to the early 12th centuries AD). The cemetery was excavated between 1978 and 1992 with skeletal remains from a total of over 800 individuals being recovered. There is no contemporary settlement evidence associated with the cemetery, thus the origins and affiliations of the individuals buried in the cemetery are unknown (Nolan *et al.* 2010). Approximately one-third of the individuals were immature at time of death, and amongst the adults there were approximately equal proportions of females and males. There is a relatively low prevalence of infection and trauma among the skeletal remains, but there is a high prevalence of degenerative joint disease (A Chamberlain, personal communication July 15 2011).

2.3 York (II, III)

The cemetery at the Barbican site in York, excavated between June 2007 and February 2008, belonged to the former medieval Church of All Saints, Fishergate, York. Of the number of excavated articulated human skeletons, 547 individuals dated to the medieval period, and 113 individuals to the post-medieval period buried in mass graves. Two radiocarbon dates on the skeletal remains show that the medieval phase of burials at All Saints, Fishergate continued until about AD 1500. The post-medieval burials are likely to date to the time of the Siege of York in AD 1644 (McIntyre & Bruce 2010, McIntyre *et al.* in preparation). The medieval burials are from a population with normal attritional mortality with approximately one quarter of the individuals being immature at time of death. There is a high prevalence of degenerative joint disease in the sample (McIntyre & Bruce 2010, McIntyre *et al.* in preparation).

3 Methods

Humeri and radii were scanned with pQCT and scored for MSM. Maximum humeral length (Martin & Saller 1957, measurement M-1) was measured with an osteometric board with 1mm accuracy to be used as a size-standard. Humeral biomechanical length (Ruff 2000b) was measured with large sliding callipers with 1mm accuracy to determine cross-sectional locations defined as percentage of length measured from the distal end of the humeral shaft. Radial tuberosity (length and width) was measured with small sliding callipers with 0.1mm accuracy for determining cross-sectional location on mid-radial tuberosity.

3.1 Anatomical basis for biomechanical investigations

The shape of a whole humeral cross-section as well as the direction of muscle attachment sites at an enthesis should be oriented to the principal axis of stress, directed by muscle pull (Ruff 2003, Ruff 2005, see also Table 2). The cross-section at 80% from the distal humeral shaft houses the attachments for pectoralis major, teres major, latissimus dorsi, and triceps brachii (Table 2). Pectoralis major attaches on the proximal third of the anterolateral humeral shaft, teres major attaches on the proximal third of the anteromedial humeral shaft, latissimus dorsi attaches on the proximal third of the anterior humeral shaft, and triceps brachii on the posterior aspect of the humeral shaft (Table 2). The cross-section at 65% houses the attachments for deltoid and medial and lateral heads of triceps brachii. Deltoid attaches on the lateral aspect of the mid-shaft of the humerus. While the humeral flexion results in anterior and lateral deltoid pull, pectoralis major and latissimus dorsi pull anteriorly. Humeral extension results in medial teres major pull, but the overall resultant is an anteriorly directed force vector at the 80% and 65% cross-sectional locations. However, the pull of pectoralis major, teres major and deltoid is no longer discernible at 65% (see III: Fig. 1). Triceps brachii pulls posteriorly at 80% and 65%, and medially at 65%. The cross-section at 50% houses the attachments for deltoid, brachialis, coracobrachialis and triceps brachii where deltoid pulls laterally, brachialis pulls anteriorly, coracobrachialis pulls medially and triceps brachii pulls posteriorly (Table 2, see also III: Fig. 1). The shape of the 35% cross-section of the humeral shaft is affected by brachialis, brachioradialis and triceps brachii where brachialis pulls anteriorly, brachioradialis pulls laterally, and triceps brachii pulls posteriorly (Table 2, see also III: Fig. 1).

Table 2. List of muscles attaching on the humerus and their effects on the studied cross-sections.

Muscle	Site of attachment	Direction of pull	Cross-section	Action	Effect on shape*
Pectoralis major	Proximal third of the anterolateral humeral shaft	Anterior	80, 65	Adducts and medially rotates arm; extends flexed humerus	80: AP 65: AP
Teres major	Proximal third of the anteromedial humeral shaft	Medial	80, 65	Adducts and medially rotates arm; aids in extension of flexed humerus	80: AP 65: AP
Latissimus dorsi	Proximal third of the anterior humeral shaft	Anterior	80, 65	Adducts and medially rotates arm; extends flexed humerus	80: AP 65: AP
Deltoid	Lateral aspect of mid-shaft humerus	Lateral and anterior	65, 50	Anterior fibres flex and medially rotate arm, middle fibres abduct, posterior fibres extend and laterally rotate arm	65: anterior & posterior fibres AP 50: lateral fibres ML
Coracobrachialis	Distal third of the anteromedial humeral shaft	Medial	50	Adducts arm, weak flexor of arm	50: ML
Triceps brachii	Medial head: distal half of posterior humeral shaft; Lateral head: proximal half of posterior humeral shaft	Medial head: medially; Lateral head: posteriorly	80, 65, 50, 35	Extends arm and forearm	35: AP 50: medial head ML 65: lateral head AP 80: lateral head AP
Brachialis	Distal half of anterior humeral shaft	Anterior	50, 35	Main flexor of forearm	35: AP 50: AP
Brachioradialis	Distal third of lateral humeral shaft	Lateral	35	Flexion, pronation and supination of forearm	35: ML

AP=anteroposterior, ML=mediolateral

3.2 Bone cross-sectional properties (II, III, IV)

Information on cortical bone distribution and shape was required to study the possibility of a site-specific versus an overall structural response of the humerus and radius to stress. Information on bone biomechanical properties is best obtained from CT scans (O'Neill & Ruff 2004, Stock & Shaw 2007). Thus, humeri from the Helsinki, York and Blackgate materials and radii from the Helsinki material were scanned using a pQCT scanner (XCT-960A with software version 5.20, Norland Stratec Medizintechnik GmbH, Birkenfeld, Germany). Humeri were aligned for pQCT scanning according to the protocol presented in Ruff (2000b). Four cross-sectional locations at 80%, 65%, 50%, and 35% of biomechanical length from the distal humeral end were scanned (II, III). Radii were placed orthogonally and vertically to the axis of slice, where the radial tuberosity was upwards and orienting the radial tuberosity surface horizontally (IV). Radii were scanned at mid-radial tuberosity measured from the length of the tuberosity (IV). Bones were attached securely to a rigid plastic platform with steel wires 50 mm apart representing a parallel surface and to provide a control scale for the pQCT measurements. The slice thickness was 1.25 mm and the voxel size was 0.69*0.69 mm^2. A default threshold of 560 mg/mm^3 was used to separate bone from air.

I obtained information on cortical area, total area, and second moments of area and bone torsion rigidity. Cortical area (CA) represents the bone's resistance to axial tension or compression loads. Total area (TA) represents the total size of a cross-section including medullary and cortical areas. Second moment of area (I), also called moment of inertia represents bending rigidity around the mediolateral axis in the anteroposterior plane (I_x) and around the anteroposterior axis in the mediolateral plane (I_y). Torsional rigidity is described by J which measures torsional and average (twice) bending strength (Ruff 2003, O'Neill & Ruff 2004). It is derived from summing two perpendicular Is. Therefore $J= I_x+I_y$ or $I_{max}+I_{min}$ (Ruff 2003, O'Neill & Ruff 2004).

The effects of muscle pull were studied by measuring cortical bone thickness at the middle of sites of muscle pull, as well as at sites with no evident direction of muscle pull at the mid-lateral wall of the humeral shaft using Dataviewer. Measurements were taken perpendicular to the periosteal surface at each site. Mid-sites of muscle pull were measured for pectoralis major, teres major, and triceps brachii at 80% cross-section; deltoid and triceps brachii medial and lateral heads at 65% cross-section; deltoid, brachialis, coracobrachialis, and triceps brachii at 50% cross-section; and brachialis, brachioradialis and triceps brachii at 35% cross-section (see III: Fig. 1). In addition, from each cross-section a site of no muscle pull was measured.

3.3 Controlling for bias factors

I analysed males and females separately to account for hormonal influences on bone modeling after puberty (Ruff *et al.* 1994, Trinkaus *et al.* 1994, Seeman 2001, Daly 2007). For studies of activity intensity using the Helsinki material (I, IV) the sexes were pooled because of the relatively modest sample size of females with known activity (I, IV). I performed analyses both sex-specifically as well as for pooled-sex samples to compare trends. As there was no significant effect of including females in the data (I, IV; Niinimäki *et al.* 2012), only pooled sample data are shown. I analysed left and right sides separately as handedness can alter loads applied side-specifically.

The Helsinki sample was accompanied with reliable information about age and thus I could use the material to study the effects of age on activity markers (I, IV). However, because age in archaeological material can only be estimated as age ranges, I divided my material into two age categories using a section-point of 40 years. This section-point was chosen as bone loss and osteoporotic changes increase after biological maturity at 40 to 50 years (Forbes 1987, Johnston & Slemenda 1993). Due to the large number of individuals in the old age category in the Helsinki sample, the section-point was readjusted to 50 years to have more equal numbers of individuals across the age groups in the study of radial tuberosity cross-sectional properties (IV). Results remained similar regardless of the section-point used; thus I presented only those results using a section-point of 50 years (IV).

Bone cross-sectional properties must be standardised for baseline mechanical environment in order to study relative rather than absolute variation. Baseline environment is represented by a product of body weight and moment arm length (Ruff 2003, Ruff 2005). However, bones required to reconstruct body mass, such as the femur head (Ruff *et al.* 1991) or pelvic breadth and the bones required to reconstruct stature (Ruff 2000a), were present in only a few individuals. Thus, the use of reconstructed body mass as a size variable would have decreased the sample size. Adjusted humeral length can be used to reflect the baseline mechanical environment (Ruff *et al.* 1993, Trinkaus *et al.* 1994). I used humeral length raised to the power of 3 as a scaling factor for CA and cortical thickness measurements, and the bone length raised to a power of 5.33 for J measurement (Ruff *et al.* 1993, Trinkaus *et al.* 1994, see also Ruff 2000b, Stock & Pfeiffer 2001). These scaling factors describe the power relationship of J (torsional strength resists beam length and volume) and CA (axial compression resists volume) relative to humeral length. The scaling factor for J was theoretically derived and empirically tested for femoral and humeral cross-sections (Ruff *et al.* 1993, Trinkaus *et al.* 1994). It should be borne in mind that this size scaling method is problematic. The difficulty comes in terms of finding the appropriate scaling factor to describe the power relationship between bone length and cross-sectional properties (Ruff 2000b). Further, there are differences in the relationship between body proportions and body size between individuals and populations (Ruff 2000a, Ruff 2000b).

3.4 MSM scoring (I, II, III)

There are several available enthesis scoring systems (Hawkey & Merbs 1995, Robb 1998, Mariotti *et al.* 2004, Galtés *et al.* 2006, Villotte 2006) but only Galtés *et al.* (2006) and Villotte (2006) have considered the current anatomical understanding of entheses, namely division of entheses according to their muscle-bone –attachment: fibrous and fibrocartilaginous. In Villotte *et al.* (2010) this method was further modified, where observed variance in fibrocartilaginous attachments was reduced into a binary variable for statistical analyses. However, although scoring fibrocartilaginous entheses is fairly accurate using the Villotte (2006) guidelines, it is less accurate for fibrous entheses (Havelková & Villotte 2007). Therefore, I chose the Hawkey and Merbs (1995) method for recording MSMs. Three fibrous (pectoralis major, teres major, deltoid) attachments (I, II, III) and one fibrocartilaginous (biceps brachii) attachment (I) were used in the analyses. An enthesis was scored for ruggedness and stress lesions (pits) on a 0–3 ordinal scale. Ossification was not included as it is considered to result from trauma (Hawkey & Merbs 1995, Molnar 2006). I summed individual MSM scores for ruggedness and stress lesions to represent overall muscle use. Some researchers have used a continuum from ruggedness to stress lesions (*e.g.* Weiss 2003b; Eshed *et al.* 2004, Molnar 2006, Weiss 2007), but this over-emphasises the relevance of stress lesions and pre-supposes that they only develop from a pre-existing rugged lesion. For the teres major, insertion stress lesions are the most prominent feature; for the pectoralis major insertion, stress lesions rarely form as distinctive fossae, but severe pitting may exist; for the deltoid insertion, stress lesions are rarely present.

4 Results and discussion

My main goal was to understand the relationship between physical activity and bone structural adaptations to stress in order to explore the reliability of MSM as an indicator of physical activity. I found that MSM and bone torsion rigidity covaried, thus they are likely to remodel under the same casual mechanisms (II). Changes in MSM were accompanied by changes in cross-sectional shape (II, III) but not in the distribution of bone mass (III). However, cortical bone thicknesses at muscle attachment sites were different compared to sites where there was no evident direction of muscle pull (III, IV). Further, according to my results MSM can be used to represent intensity of physical activity (I). However, this should be applied with caution as there are also bias factors affecting their appearance, of which the most prominent is age (I, II, III, IV).

4.1 Interpreting activity from skeletal remains (I, III, IV)

If MSMs reflect physical activity, individuals performing heavier tasks should have higher degree of modifications at entheses than individuals performing lighter tasks. My results on individuals with known occupation and age indicated that the intensity of physical activity cannot be separated after biological maturity at 40–50 years using fibrous muscle attachments in the humeral shaft (I)[3]. After this age any interpretations of intensity of activity are biased by age-related changes. Subsequently also Villotte *et al.* (2010) and Alves-Cardoso and Henderson (2010) have studied individuals with documented occupation. Villotte *et al.* (2010) found that fibrocartilaginous muscle attachments of the upper limb can separate young individuals performing manual and non-manual labour. Similar to my results, they also noted that old age biased interpretations of physical activity (Villotte *et al.* 2010). Alves-Cardoso and Henderson (2010) found that individuals performing manual labour tended to have higher scores than non-manual labour individuals, but their results were significant only after controlling for age.

The direction of greatest bending strength can be used to ascertain habitual differences in muscle use. According to my results, the direction of greatest bending strength was most variable at the 50% humeral cross-sectional location

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[3] Also biceps brachii attachment at radius, which is a fibrocartilaginous attachment, was included in the analysis for this paper. However, in a subsequent analysis where this attachment was dropped the results on age-related trends remained similar (Niinimäki *et al.* 2012).

(III). This cross-sectional location can be used to study differences in activity patterns between groups on the preference of the elbow (AP) compared to the shoulder (ML). The direction of greatest bending strength was constant at the 80% and 35% cross-sections. Bending strength at the 35% cross-section was oriented towards the AP axis and bending strength at the 80% cross-section was oriented towards the ML axis (III). These trends likely reflect flexion of the elbow at 35% and fixing of the humerus close to the torso in the ML direction at 80%. The direction of greatest bending strength was different between the sexes at the 65% cross-section, which in males was more directed towards the AP direction, while in females there was mostly no preferential direction (III). These shape differences between males and females may result from greater loading of the shoulder among males or from muscle lever differences between sexes, as males have broader shoulders compared to females (Holliday 1997). At the radial tuberosity, the pull of the biceps brachii tendon provides the principal direction of stress (IV).

4.2 Possible causal mechanisms behind MSM development (I, II, III)

As both bone biomechanical properties and MSM are considered to reflect physical activity, both are considered to remodel under the same mechanisms and thus they should covary. There was a covariance between bone biomechanical properties and MSM, where higher MSM scores occurred with higher values of J (II). Thus the same mechanisms of bone remodeling are likely responsible for both the appearance of MSMs and the altering of diaphyseal dimensions as predicted by mechanostat theory and beam theory, and as theoretically explained by Hirschberg (2005). Hirschberg (2005) studied entheseal modifications in the light of bone remodeling theory where remodeling thresholds explain whether bone deposition is evident as ruggedness or whether bone resorption is evident as pits develop. Furthermore, age seems to have a similar effect on both MSM and J, where both increase with age (I, II; Ruff & Hayes 1983, Feik *et al*. 1996, Galtés *et al*. 2006, Sigurdsson *et al*. 2006, Villotte *et al*. 2010).

My interest in the relationship between biomechanical properties and MSM was to study the overall versus the site-specific relationships, as I included both those cross-sectional locations housing the attachment for the muscles of interest as well as those that do not (II). The relationship between MSM and bone biomechanical properties has been previously studied by Weiss (2003b) and Bridges (1997) but with a slightly different focus. I utilised a total of four cross-sectional locations along the humeral shaft to study site-specific as well as overall covariance between MSM and biomechanical properties whereas Weiss (2003b) and Bridges (1997) only included the 35% cross-section in their studies. I did not find a correlation between MSM and CA (III), but did find one between MSM and J (II). The correlation between MSM and J was mostly positive, with high MSM scores occurring with high J (II), a trend also found by Weiss (2003b). Some single muscle MSM and J correlated in my samples, but there was no such correlation between MSM and cross-sectional properties in Weiss' sample (2003b). It seems that the relationship between MSM and J reflects also the overall loads applied to the humeral shaft rather than a specific relationship. Bridges (1997) found only a weak inverse correlation between pectoralis major MSM and bone cross-sectional properties on the left side in males. She suggests that this may be due to her sample composition and possible pathological cases in her sample (Bridges 1997). To sum up, although a true causal relationship between MSM and J could not be studied, where there is an increase in one there is likely to be an increase in the other (II). This common increase is likely a result of bone response to physical activity at a young age, whereas in old age the increase can also be due to age-related changes in bone remodeling.

4.3 Bone response to stress: site-specific versus overall structural adaptation (II, III, IV)

My results on variation on cortical bone thickness indicate that there is a possibility of both site-specific as well as an overall structural adaptation to stress in the humeral shaft and radial tuberosity. As the main functions of MSM are to provide surface area for the attachment of a muscle or a tendon, they can be considered as site-specific adaptations to stress. In general, bone adapts to stress with changes in shape which are correlated with changes in MSM (II) rather than adaptation with bone mass, although there is some variation in cortical bone thickness between the proximal and distal humeral shaft and within cross-sectional locations between sites of muscle pull and no pull (III). This may be due to preservation of bone at muscle pull sites compared to sites of no muscle pull. Thus, muscle pull seems to have an effect on cortical bone thickness (III). However, muscle activity evident as MSM did not have a significant relationship with cortical bone mass (III).

The increase in cortical thickness found at muscle pull sites on the humeral shaft was reversed at the radial tuberosity, where cortical bone was thinner at muscle pull site than in sites of no muscle pull (IV). This difference is likely due to reduced bending stresses at epiphyses and apophyses where fibrocartilaginous attachments are found. Reduced bending stresses reduce the need for greater cortical thickness at these sites. Thus, it is likely that other locations of fibrocartilaginous attachments are associated with thinner cortical bone as well.

In addition to site-specific variation in cortical bone thickness, CA was reduced from the distal to the proximal humeral shaft (III). However, only CA at the 80% cross-section was statistically significantly smaller than in other cross-sectional locations (III). This is in agreement with results by Rhodes and Knüsel (2005) where CA was smallest at the 80% cross-section. Differences between the distal and proximal humeral shaft were also found by Haapasalo *et al.* (1996) where changes due to activity were greater in the proximal shaft than in the distal shaft. This is likely due to reduced bending stresses towards the ends of the diaphyses, which is evident as pit formation at MSM sites near the ends of the diaphysis.

Differences in CA between the proximal and distal humeral shaft may further illustrate the significance of adaptation with shape rather than bone mass. Thus, it seems that adaptation to stress occurs mostly by changes in shape (II, III, IV) and the geometrical properties of the bone are adapted to accommodate the principal directions of stress. Modeling towards the direction of stress occurs by increasing bone mass locally. Periosteal deposition is compensated by higher endosteal resorption rates as suggested by the results of papers III and IV. With this deposition-resorption mechanism as explained by mechanostat theory cross-sectional shafts can accommodate bone cross-sectional shape towards the direction of muscle pull without resulting in thick cortices at muscle attachment sites. This was most evident among older individuals where in some cases the original, more circular endosteal wall was still visible as denser trabecular bone (III, IV). Regardless of site-specific variation in cortical bone thickness where cortical thickness was thicker at muscle pull sites in the humeral shaft and thinner at the radial tuberosity, there was a very close approximation between the internal and external contours of cortical bone (III, IV). This is in agreement with Stock and Shaw (2007), who noted that external architecture is strongly correlated with internal architecture.

Although bone mass can be increased or at least preserved locally against age-related bone loss at sites of direct muscle pull it is not likely that cortical thickness and MSM reflect similar aspects of bone functional adaptation (III). While CA represents resistance to axial compression, MSM and J are functional responses to stress. Thus, there is no need to maintain or develop a thick cortical bone wall if stress can be accommodated with bone shape as also suggested by Rhodes and Knüsel (2005), and by surface structure as MSM. As MSMs are associated with J rather than CA, it suggests that the aetiology behind MSMs is related to muscle activity where surface development can aid in the orientation of cross-sections towards the direction of stress.

4.4 Effects of biasing factors on results (I, II, III, IV)

A variety of biasing factors affect MSM and bone biomechanical properties as well as interpretations of physical activity based on them. While a covariance between MSM and J was found, there were also other factors affecting their variance (II). Age and sex are known to affect the mechanisms involved in bone modelling, and these factors also affect the variance in activity markers: MSM and biomechanical properties.

Age effects are profound on MSM after biological maturity (Galtés *et al.* 2006), where age overrides activity effects in both fibrous and fibrocartilaginous muscle attachments (I; Villotte *et al.* 2010). Robb (1998) has suggested that after biological maturity, from 40–50 years onwards, the mechanisms affecting MSM formation may level off. Biological maturity also affects bone bending strength, where J increases and continues to increase through middle age and well into old age in both sexes (Ruff & Hayes 1983, Feik *et al.* 1996, Sigurdsson *et al.* 2006). In my data, cortical bone decreased with age, both as CA and as cortical thickness measured at sites where there was not direct muscle pull (III, IV). This is in accordance with earlier studies on aging effects on CA (Trinkaus *et al.* 1994, Schiessl *et al.* 1998, Schoenau *et al.* 2000, Russoa *et al.* 2006, Martin 2007). It may be that a bone's structural response to mechanical loading is similar to its aging response, thus affecting physical activity reconstructions based on MSM and J.

Differences in activity patterns between the sexes are mostly studied from the upper limb (Wilczak 1998, Lieverse *et al.* 2009, Spielmann *et al.* 2009, Villotte *et al.* 2010b, Weiss *et al.* 2010), but this is also where there is most sexual dimorphism due to hormones. Bone adaptation to stress differs between males and females due to sex hormones. It seems that among females bone response to stress may be under greater hormonal influence than activity influence: while there were significant trends in the male sample in the relationship between MSM and J (II), trends among females usually remained statistically insignificant.

Estrogen is responsible for greater endosteal apposition in females during puberty (Schiessl *et al.* 1998, Schoenau *et al.* 2000, Petit *et al.* 2004) and decrease during menopause (Schiessl *et al.* 1998, Schoenau *et al.* 2000). Also muscle mass is influenced by hormones (Gallagher *et al.* 1997, Ferretti *et al.* 1998, Janssen *et al.* 2000, Schoenau *et al.* 2000, Seeman 2001, Ruff 2003, Schoenau *et al.* 2002, Petit *et al.* 2004, Sumnik *et al.* 2006, Daly 2007). Hormonal influences are more marked in the upper limb where males have more muscle mass (Gallagher *et al.* 1997, Janssen *et al.* 2000, Ruff 2003, Sumnik *et al.* 2006) and as a result males develop relatively stronger humeri (Ruff 2003). Males have larger muscles both in absolute terms and relative to body mass starting from puberty, probably due to high testosterone levels (Schoenau *et al.* 2000, Ruff 2003) and greater force production capability (Miller *et al.* 1993, Kanehisa *et al.* 1994). As males usually have higher scores than females, reverse cross-cultural sex patterns are most likely to reflect hormonal influence or methodological problems (Weiss *et al.* 2010). Thus, hormonal influences on MSM and bone biomechanical properties in relation to physical activity should be considered.

Sexual dimorphism in size may also contribute to some sex differences. Males are on average larger than females and, as size is known to influence MSMs higher scores in males, may reflect their larger size (Weiss 2007). However, for a large body to affect MSM, some activity is needed. Sex differences may also result from more environmentally sensitive growth in males (Wilczak 1998).

4.5 Recommendations for application of MSM in activity reconstruction (I, II, III, IV)

My results indicate that MSM can be used to infer intensity of muscle activity among individuals before or after reaching biological maturity (I), as there is a possibility of site-specific response to stress (III, IV) and because the causal mechanisms behind MSM appearance are likely those which reflect physical activity and age (II). However, care should be taken when applying this method, as other factors also affect their appearance (I, II).

A distinction should be borne in mind between activity type and intensity of activity. When the interest is in intensity of activity, it is advisable to account for the total variation of the studied MSM sites (II), and in order to obtain a measure less sensitive to anomalies, to combine the MSM scores. A composite variable of several ordinal variables can be created if variables are measures of the same thing (in this case, intensity of activity affecting MSM sites) and then treated as a continuous variable (Rowe 2006). This enables considering the continuous nature of at least some fibrous MSMs in statistical analyses. Furthermore, Weiss (2003b; 2007) suggests using a composite variable (which she calls an aggregated MSM) as it is a measure less sensitive to anomalies. Havelková *et al.* (2011) combined information from one individual using percentage prevalence of enthesopathies. They argued for the use of parametric testing to detect significant differences between populations (Havelková *et al.* 2011).

Interpretations of type of activity may be more difficult. Discerning movements of the upper limb are difficult due to great mobility and instability of the shoulder joint. Many muscles around the shoulder joint are active during upper limb movement either as prime movers, antagonists or stabilisers (Gosling *et al.* 2002). Also, there are multiple muscles attaching to the same location - as seen with flexor and extensor origins, and on the linea aspera in the femur (Gosling *et al.* 2002).

Difficulties in interpreting activity type also arise from the variability in the degree of modifications in MSMs between different entheses. In addition to differences between fibrous and fibrocartilaginous muscle attachment sites (Villotte 2006), there is variance within fibrous muscle attachments. Most notable is the presence or absence of pits (II). Pits usually form towards the ends of the diaphyses, where bending stresses on the bone shaft are minimised. For the insertion of teres major, stress lesions are the most prominent feature; the pectoralis major insertion exhibits severe pitting, but pitting is rarely evident as distinctive fossae; for the insertion of deltoid, pits are rarely present (II). In addition, not all attachment sites exhibit similar scale of ruggedness. There have been some attempts to solve the problem of variation in MSM scores between muscle attachments. Standardisation of MSMs into z-scores has been used (Weiss 2003a, Weiss 2003b, Weiss 2007). However, as MSM are recorded as ordinal variables, the use of z-scores has been criticised (Stefanović & Porčić 2011). Havelková *et al.* (2011) used parametric testing on percentage prevalence of enthesopathies to compare differences between populations but non-parametric testing to compare differences in individual insertions. Robb (1998) and Mariotti *et al.* (2004) have suggested creating separate scales for each muscle attachment. This may be the best approach to consider the differences in the degree of surface development. However, large inter-population studies are needed for creating universal recording standards for each muscle attachment.

To sum up, due to differences in variation between attachment sites in MSM scores, difficulties interpreting specific tasks, the unknown effect of sex, and difficulties in methodology, I suggest that at the moment inferences concerning activity intensity or type should be made at a more general level, between populations or groups, within same sex- and age-groups (before or after biological maturity) and comparing between similar muscle attachment sites.

5 Conclusions

My main result was that bone has a possibility to respond to stress site-specifically, and, thus, MSM can be used to reconstruct physical activity if biasing factors are taken into account. For inferences about labour intensity, MSM is a useful method when young individuals are studied, as age-effects after biological maturity can override the effects of intense physical activity (I). A covariance between MSM and J suggests a possibility that they reflect similar properties, physical activity and age, under similar causal mechanisms (II). However, there was a considerable amount of variation not explained by their common covariance (II). Thus, care should be taken when applying this method, as other factors are also likely to affect their appearance. According to my results bone can adapt to stress site-specifically as well as through overall adaptation with bone cross-sectional shape and distribution (II, III, IV). In the humeral shaft, cortical bone was thicker at muscle pull sites than at sites of no pull (III). At the radial tuberosity, cortical thickness at the muscle pull site of the biceps brachii tendon was thinner (IV). This difference between cortical thicknesses at muscle pull sites of fibrous attachments on the humeral shaft compared to the fibrocartilaginous attachment at the radial tuberosity may reflect differences in mechanical loading between the two types of muscle-bone -attachment. In both types of attachments, bone mass was increased at the periosteal envelope which results in cross-sectional shapes oriented towards the direction of stress. However, in the case of the radial tuberosity, even a substantial increase of bone mass at the stressed sites was compensated for by endosteal resorption (IV). There was also a reduction in CA from the distal to the proximal shaft which was likely due to reduced bending stress towards the proximal humeral shaft (III). Both CA and cortical thickness at sites of no muscle pull decreased with age (III). This suggests that bone mass is maintained at muscle attachment sites against age related bone loss. Finally, MSM was associated with J rather than CA, where the former represents bone adaptation to torsional stress resulting in shape changes towards the direction of stress and the latter represents the withstanding of axial stress, where overall changes in CA in adulthood are related to aging. To conclude, I propose that MSM can be used to study the intensity of physical activity in individuals before they reach biological maturity. However, it is important to design studies where age, sex, population and muscle attachment type are considered.

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