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Biomechanics of the human hand during suspensory locomotion: a combined pressure and kinematic approach.

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Abstract

The human hand is a key anatomical area for understanding behavioural transitions in fossil hominins, particularly in relation to the evolution of human locomotion. Previous studies have examined the pressure distribution in non-human primate arboreal and terrestrial locomotion although pressure in relation to human arboreal locomotion remains unstudied. A novel combined pressure and kinematic approach is used to quantify for the first time pressure and the location of peak pressure experienced by the human hand across a range of diameters and hand postures during static and dynamic suspension activities. Significant differences were found in normalised peak pressure between the 45mm and 105mm diameters when all activity categories were combined (thumb adducted, thumb abducted, and dynamic suspension). Further analysis showed that for separate activity categories there were significant differences in normalised peak pressure between the 45mm and 105mm diameters for both the thumb adducted and abducted activities. In all cases the 45mm diameter had a greater normalised peak pressure value. The location of peak pressure has been shown to be significantly affected by diameter on the third digit and fourth proximal phalanx when the thumb is abducted. The mode locations for all activities and diameters were on the fourth-to-second digits and moved distally as the diameter increased from 45mm to 105mm. These results suggest that increasing the diameter of a superstrate [support positioned above the body: Hunt K D, Cant J G H, Gebo D L, Rose M D, Walker S E, and Youlatos D (1996) Standardized descriptions of primate locomotor and postural modes. *Primates*. 37: 363-387] decreases the normalised peak pressure and that diameter size affects the location of peak pressure when the thumb is abducted during suspension. There was a significant preference for the 45mm diameter out of all three diameter sizes. These results are consistent with ergonomic studies of grasping by human hand during daily manipulative activities.

1. Introduction

The evolution of the human hand is of great interest to palaeoanthropologists as its morphology has the potential to reflect key evolutionary transitions, particularly as the hand is used for a range of purposes, such as feeding (Hunt, 1994; 1996), tool production and use (Key and Dunmore, 2015; Williams et al. 2012), and locomotion (Hunt, 1994; Isler, 2002a; Schmitt et al. 2016). The human hand has a greater manipulative ability compared to other non-human primates (hereafter primates) despite many similarities in their morphologies (Feix et al. 2015 ; Marzke and Marzke, 2000; Marzke and Shackley, 1986; Pouydebat et al. 2014). As the hand is not required for terrestrial locomotion in humans, comparison of human hand morphology to that of primates may allow some insight into the evolutionary trade-offs that have occurred during hominin evolutionary history. A key question in palaeoanthropology is the range of locomotion in which fossil hominins may have engaged, particularly in relation to the transition from arboreal locomotion to that of habitual bipedalism (Hunt, 1996; Kivell et al. 2011; 2015). This study aims to provide comparative data to previous primate arboreal pressure studies (Samuel et al. 2018), along with kinematic data, to examine the distribution of pressure and the relationships to morphological structures in human and primate hands during arboreal locomotion.

1.1. *Biomechanics*

Biomechanics are key for understanding the relationship between anatomical morphology and function. External forces, such as ground reaction force (GRF), can put a limb into compression, bending, or tension depending on its position in relation to the force (Patel, 2010). It has been suggested that the skeletal structures in a limb are likely to be adapted to tolerate habitual mechanical forces, as well as the potential for occasional extreme forces that would be detrimental to the limb, and therefore the overall fitness of an individual (Ruff et al.

2006). In order to prevent damage due to sudden extreme forces to a bone is able to withstand a greater amount of force than is generally habitually applied, this value is known as the safety factor (Blob et al. 2014; Kawano et al. 2016). It has been shown, however, that safety factors can vary between bones in an organism (Blob et al. 2014).

For example, in the tiger salamander the femur and humerus are about the same size but their safety factor values differ (Kawano et al. 2016). The humerus has a higher safety factor than the femur despite the femur having greater bone stresses (Kawano et al. 2016). On the other hand, the humerus and femur in alligators have similar general loading values but they differ in safety factor values (Blob et al. 2014). The alligator humerus has a larger safety factor despite its smaller size in comparison to the femur (Blob et al. 2014). Therefore, the safety factor value does not appear to follow a set relationship with the mechanical loading of the bone. This suggests that the bone may be strengthened to accommodate a habitual loading 'baseline' and then variation in other factors (e.g. size, Blob et al. 2014), not just potential extreme loading, contribute to the determination of the safety factor value. Therefore, limb morphology is likely to reflect the experienced forces, particularly for habitual activities such as locomotion. All potential forces and variables should be taken into account when drawing conclusions about the forces experienced by an anatomical element and the potential related behaviour.

1.1.1 Forces on the skeleton

The force experienced by an individual is known as stress, and the change in the shape of the anatomical structure induced by the stress is known as strain (Lucas et al. 1999). It is suggested that during postural positions an organism's body is supported predominantly by the skeleton and ligaments and so its anatomy is evolved to minimise ligament strain and decrease muscle activity, and therefore some of the stresses placed upon bone (Hunt, 1991). Therefore, when a particular organism uses a specific postural niche this should be reflected in the biomechanics of its skeleton. For example, the phalanges of a chimpanzee (*Pan troglodytes*) curve ventrally and thus allow the strain caused by gripping the cylindrical object, or branch, to be more equally spread out compared to the straight phalanges of a human (Hunt, 1991; Richmond, 2007; Nguyen et al. 2014). The straight phalanges of a human also decrease the size of the area affected by radial torsion, which may lead to an increased risk of tissue damage due to the decreased area over which the strain is applied (Hunt, 1991). In comparison to four limbed terrestrial animals the prehensile hands and feet of primates allow them to firmly hold the substrate they are locomoting on and produce a range of tensile and compressive forces alongside friction, which is beneficial when using highly inclined substrates (Preuschoft and Günther, 1994; Preuschoft, 2004). Long digits are advantageous in arboreal environments for increasing the diameter of objects that can be grasped, although this causes issues in regard to pressure (Preuschoft, 2004). For example, longer digits result in a larger surface area for the force to be spread across which reduces the pressure, but this can be counteracted by decreasing the overall width of the hand, foot, and digits (Preuschoft, 2004).

The positional behaviours of arm hanging from a single arm and vertical climbing are suggested to distinguish chimpanzees from Old World monkeys, which do not engage in these behaviours (Hunt, 1992). Since arm hanging requires greater shoulder mobility compared to vertical climbing, it is hypothesised that this positional behaviour will have a greater influence on the chimpanzee forelimb skeleton (Hunt, 1991). This is evidenced via the cranially orientated glenohumeral cavity that allows full abduction of the humerus in chimpanzees and in conjunction with the cone shaped thorax, allows the arm to be positioned closer to the centre of gravity (Hunt, 1991). However, it has been shown that hominoids have less shoulder mobility in the craniodorsal region compared to quadrupedal monkeys (Chan, 2008). It has been demonstrated that the relationship between scapula position and locomotion category is not consistent across all species of primates (Chan, 2007). For example, the scapulae of anthropoids that engaged in quadrupedal arboreal locomotion were significantly more dorsally positioned than those of their terrestrial counterparts (Chan, 2007). In contrast, no significant difference was found in the scapula position of arboreal and terrestrial strepsirrhines (Chan, 2007). Therefore, the ranges of motion permitted by different upper limb morphologies warrants further research.

When force is applied in one direction, an equal reaction force will be generated in the opposite direction; this is known as Newton's third law of motion (Newton, 1687). Whilst Newton's third law is applied in static conditions, where no acceleration occurs, small changes in the shape of the object may occur, such as flesh deformation when a hand or foot is put on the ground during locomotion (Lucas et al. 1999). In dynamic conditions, such as locomotion on a horizontal surface, the force of the limb being applied to the substrate generates a reaction force, in the opposite direction, known as GRF (Lucas et al. 1999; Patel, 2010; Patel and Wunderlich, 2010).

The moment arm is the shortest distance between the rotational axis and the force vector (Lucas et al. 1999). The moment's magnitude is the result of the multiplication of the length of the moment arm and the applied force (Lucas et al. 1999). Therefore, during digitigrade locomotion when the GRF is perfectly vertical the horizontal distance between the GRF vector and the centre of the wrist joint, as the proximal joint to the metacarpophalangeal (MCP) joint, is known as the external moment arm around the wrist (Patel, 2010). The shorter moment arm, the more in line the forelimb with the GRF vector and therefore the forelimb is subject to increased compression opposed to bending (Patel, 2010) (see Figure 1).

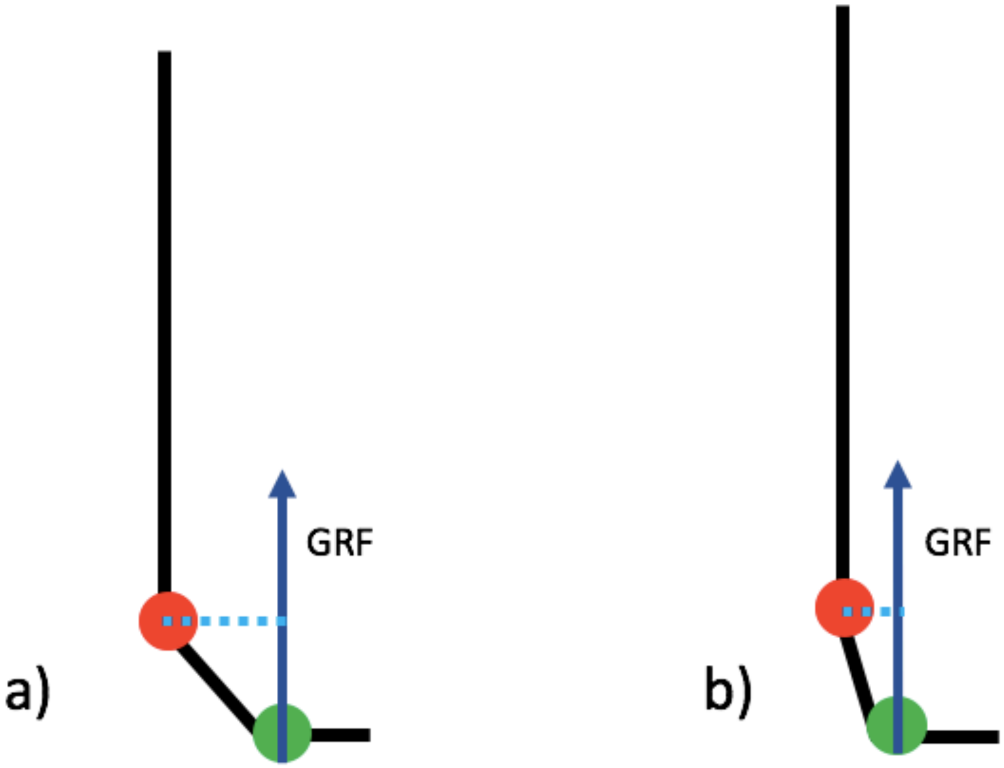

Figure 1: Schematic of the forelimb showing differences in moment arm length at different hand postures with the same GRF. Adapted from Patel (2010).

a) Palmigrade-like posture, b) digitigrade posture.

Red circle – wrist joint, green circle – MCP joint, dark blue arrow – GRF vector, light blue dotted line – moment arm. The GRF is depicted as vertical, however, this is not always the case and this will affect the positioning of the moment arm.

Bone, in particular cortical bone, is stronger under compressive stresses compared to tensile stresses and during bending one side of the bone is in tension and the other in compression (Keaveny and Hayes, 1993). Therefore, it would be beneficial to decrease the moment arm in order to put the skeletal element in its strongest plane during terrestrial locomotion. It should be noted that the effects of limb positioning during arboreal locomotion have not been fully investigated. My study will aim to address how superstrate size affects the positioning of the human hand and the wrist, and how this affects peak pressure values and the location of peak pressure in relation to the substrate reaction force generated during arboreal suspensory locomotion.

1.1.2. Limb angles and joint reaction forces

The ground reaction force experienced by the limb can also change with speed. For example, it has been shown that GRF increases with increases in the speed of quadrupedal locomotion (Patel, 2010). During bipedal locomotion the amount of time that a limb is in contact with the substrate decreases as the speed of locomotion increases (Lee and Farley, 1998). Other variables, such as limb angles, also change with the speed of locomotion. The angle of a limb during locomotion affects the joint reaction forces (JRFs) that it experiences. Comparison of bare foot and high heeled bipedal walking in human females showed that the angle of the first metatarsal to the substrate at "peak resultant force" significantly increased when high heels were worn, and that there was also a significant two-fold increase in the JRFs when heels were worn compared to barefoot walking (McBride et al. 1991: 285). The JRFs on the first metatarsal were applied more dorsally when high heels were worn as opposed to bare feet (McBride et al. 1991). Therefore, as GRF increases with speed, and the limb angles (in some species) alter with speed, it is likely that GRF also influences the JRFs. Further study in this area is required before definite conclusions can be drawn.

Within primates, some locomotion studies have shown a change in limb angle in relation to the speed of locomotion. For example, as the speed of quadrupedal locomotion increases, the limb angle of olive baboons (*Papio anubis*) alters from a digitigrade position to an increasingly palmigrade position (Patel, 2010; Patel and Wunderlich, 2010). In contrast, no effect of speed on the angle of the limbs during quadrupedal galloping locomotion was observed in vervet monkeys (*Chlorocebus pygerythrus*) and a squirrel monkey (*Saimiri*) (Vilensky et al. 1990). It should be noted that they did not investigate the limb angles during normal walking gait, and therefore it is difficult to make inter-gait comparisons on intra-gait data. In bipedal animals, the limb angles are also altered with increasing speed (Lee and Farley, 1998).

1.1.3. Centre of gravity

During unimanual forelimb-suspension the body mass is directly below the hand (see Figure 11a in Hunt et al. 1996), whereas during forelimb swing (dynamic locomotion) the body mass moves beneath the hand and in a series of arches below the superstrate[1] (similar to Figure 25 in Hunt et al. 1996). The position of the body mass in relation to the substrate will affect the position of the centre of gravity (CoG), as illustrated by the lowering of the CoG on relatively smaller substrates by increased elbow flexion and decreased shoulder height measured in the support phase during arboreal quadrupedal primate locomotion (Schmitt, 2003). Primates of different sizes were used, thus making direct kinematic comparison on the same substrate size difficult (Schmitt, 2003). To control for this the general substrate size category ("small, medium, and large") was calculated relative to the body mass of the

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[1] In accordance with Hunt et al. (1996) superstrate is solely used to refer to a support where the organism's body mass is positioned below, i.e. suspensory locomotion, and substrate refers to supports where the body mass is located above or next to the support. Standardised locomotion and postural definitions are used in this study as described by Hunt et al. (1996), to aid comparability with other studies.

primate (Schmitt, 2003: 1027). The pliability of each support was not noted by Schmitt (2003). The CoG during locomotion affects the forces acting on the body, and each individual anatomical region (Preuschoft et al. 1998). Over the course of a gait cycle the CoG changes position and these changes require work, which is the product of force and distance travelled, unless it is a 100% pendulum (Lucas et al. 1999; Preuschoft et al. 1998). Work equals energy, which manifests itself in a variety of ways, such as kinetic, potential, strain and thermal energy (Lucas et al. 1998). As a limb ascends during the gait cycle it gains potential energy, as it is going against the direction of gravity, and the quantity of potential energy depends on the weight of the limb and the height it rises (Lucas et al. 1999). The potential energy is then converted into kinetic energy as the limb descends (Lucas et al. 1999). The kinetic energy of an object can be calculated by multiplying mass with the travelling velocity squared and dividing by two (Lucas et al. 1999). Therefore, the larger the mass of an object, and the greater the ascent and descent, the greater the amount of potential energy and kinetic energy (Lucas et al. 1999). Once the object, or limb, touches the floor at the end of the descent the kinetic energy is transformed into strain energy which acts on the floor (Lucas et al. 1999). Therefore, the body mass of an individual is likely to affect the amount of work required to move the forelimb and body during suspensory locomotion, and thus the amount of mechanical stress experienced by the individual.

The positioning of the hand during locomotion is influenced by the position of the CoG. For example, in a Japanese macaque (*Macaca fuscata*) and white-handed gibbon (*Hylobates lar*) as the incline increased and the CoG moved away from the position of the foot, the hand positioning moved further towards the back of the substrate (Nakano, 2002). The change in position and the degree of incline at which the change occurred were different for each species, and thus suggests that the intermembral index [(humerus+radius)x100/(femur+tibia)] may play a role in determining hand position, and positional changes, during arboreal locomotion (Nakano, 2002). Changes in the incline of a substrate were also shown to affect the hand positions in bonobos (*Pan paniscus*), in contrast to the consistent foot positioning (Schoonaert et al. 2016). The bonobo hand position became increasingly lateral on the pole between the inclinations of 30-60°, compared to the use of knuckle-walking when the pole was at a 0° incline (Schoonaert et al. 2016). This suggests that the incline of a substrate plays a role in determining how forces are experienced by the hand during quadrupedal arboreal locomotion in bonobos (Schoonaert et al. 2016).

1.1.4. Wrist

The support used by chimpanzees was within 30 degrees of being completely vertical in more than 19% of arm hanging cases and 88% of vertical climbing cases (Hunt,1991). A high degree of ulnar deviation in the wrist of chimpanzees allows the hand to span greater circumferences when the forearm and support are both near vertical (Hunt, 1991). This is due to positioning the hand perpendicular to the vertical or near vertical support (Hunt, 1991). Orangutans (*Pongo*) have the greatest degree of ulnar deviation followed by gibbons (*Hylobates*), chimpanzees, and then gorillas (*Gorilla*), which may reflect the amount of arboreal locomotion in which each species engages (Tuttle, 1969).

In human piano playing, ulnar deviation was the only biomechanical variable to be significantly (and positively) correlated with tempo, although it had weak non-significant negative correlations with the other variables (Lee, 2010). Among the anatomical variables analysed, hand width and length significantly positively correlated with each other as well as finger length and finger span (Lee, 2010). Whilst these results show the importance of a flexible wrist in piano playing (Lee, 2010), it also suggests that the relationship between wrist mobility and other anatomical aspects of the hand is more complex than previously thought. As previously mentioned, high levels of ulnar deviation are beneficial to arboreal postures (see Hunt, 1991; 1992) and it has been noted that the amount of flexion experienced by the wrist increases with diameter size during unimanual forelimb-suspension in hylobatids (Sarmiento, 1988). It should be noted that human wrist movement is predominantly linked to tool manufacture and use (e.g. Williams et al. 2010). Assessing what role wrist mobility plays in arboreal locomotion in humans, particularly in relation to the size of the substrate or superstrate used and the pressure experienced, will provide further information on the potential selection pressures that may have acted upon the anatomical components of the human hand during its evolution by offering a comparison to tool manufacture and use studies.

1.1.5. Tool use

The positioning of the hand during a particular activity, such as stone tool production, will affect the forces experienced by the hand. In the three-jaw chuck grip position an object is held by the first three digits with the second and third digits slightly spread apart and opposed to the thumb (see Figure 1D in Marzke, 1997). When using the three-jaw chuck grip with the dominant hand on a hammer-stone during the production of Oldowan bifacial choppers, the second and third digits were orientated so that they were opposite the striking platform (Williams et al. 2012). The second and third digits thus experienced significantly greater normal force, pressure-time integral (PTI; pressure kPa multiplied by time), and pressure values than the thumb (Williams et al. 2012). This differs to the results of Key and Dunmore (2015) who found that the thumb of the non-dominant hand experienced significantly greater forces during core repositioning and securing than the second and third digits. Whilst no specific hand grip was noted, as participants used a variety of grips (Key and Dunmore, 2015), these findings suggest that the effect of hand placement in relation to the application of force during specific activities should be studied further. In contrast to Williams et al. (2012), Rolian et al. (2011) also examined the biomechanical effects of stone tool production and use on the human hand, by using load cells inside a metal ‘hammerstone’ and ‘flake’ on a vulcanised rubber ‘core’ and a cardboard substrate respectively. An increase in digit length required a slightly decreased amount of force from the muscles of the hand in order to ensure the digit is stable during the simulated production and use of stone tools (Rolian et al. 2011). Average joint stress in pooled males and females were generally not found to differ statistically between the simulated tool production and use (Rolian et al. 2011). The methodological differences between Rolian et al. (2011) and that of Williams et al. (2012) makes direct comparison between the two studies difficult. The use of metal tool substitutes by Rolian et al. (2011), instead of actual stone, makes it difficult to directly apply their results to the effects of stone tool production and use on the hand during human evolution. Further quantification of the biomechanics of other materials, such as rubber, compared to stone are needed before comparisons can be made.

1.1.6. Hand grips

Hand grips can be divided into two broad categories, precision grips and power grips (Napier, 1956). Precision grips involve the distal phalanges of the fingers and thumb, or the distal phalanx of the thumb and the intermediate phalanx of the index finger (Napier, 1956). The power grip involves the fingers and thumb securing an object against the palm (Napier, 1956). Therefore, the surface areas available for force distribution are different between precision and power grips, which suggest that this may result in different pressure distribution patterns for each type of grip, as pressure is the application of force over an area (Seo and Armstrong, 2008). Many previous locomotion studies have collected both pressure and force data to examine how the GRF and distribution of pressure interact (e.g. D'Août et al. 2001; Patel and Wunderlich, 2010). It should be noted that they have predominantly examined terrestrial locomotion and have focused on the foot rather than the hand, and therefore analysis of the interaction between pressure and kinematic data in arboreal locomotion is needed. This is particularly relevant in relation to the arboreal hypotheses on the origin of bipedalism, for example the assisted bipedalism hypothesis (Thorpe et al. 2007).

This project is important because it will build upon the current literature on human arboreal locomotion, as well as providing comparative data to allow investigation of the effects of different anatomical adaptations on the forces experienced by the body during locomotion. There are many studies that have examined the biomechanics of the human hand during stone tool manufacture and use (e.g. Key and Dunmore, 2015; Rolian et al. 2011; Williams et al. 2012), however, there is very little literature on the hand biomechanics of humans during arboreal suspensory locomotion (see Alexander, 1994 for human and ape joint comparisons; Samuel et al. 2018 for bonobo hand pressure during arboreal locomotion; Schoonaert et al. 2016 for bonobo gaits on different arboreal inclines). This study aims to investigate the biomechanics of arboreal suspension in humans with the body mass located below the superstrate, and will also provide a contrast to the previous biomechanical studies of arboreal (e.g. Hunt, 1991; Nakano, 2002), and terrestrial (e.g. Patel, 2010; Patel and Wunderlich, 2010) locomotion in primates.

The use of kinematic and pressure methods will allow the location of peak pressure to be assessed in relation to the diameter of the superstrate, the value of normalised (by body mass and hand area) peak pressure, the position of the thumb in relation to the rest of the hand, and the differences between static (postural-like) activities and dynamic (locomotion-like) activities. Many of the previous locomotor studies have focused on terrestrial locomotion (D'Août et al. 2001; Demes et al. 1994; Hatala et al. 2013; Patel, 2010; Patel and Wunderlich, 2010). The combination of arboreal and bipedal morphological features seen in fossil hominins, such as *Australopithecus afarensis* (Bush et al. 1982; Kimbel and Delezene, 2009), arboreal hypotheses for the origin of bipedalism (Hunt, 1996; Thorpe et al. 2007; Thorpe et al. 2014), and the arboreal locomotor tendencies of many species of primate (Doran, 1993; Isler 2002a, b, 2004; Remis, 1995; Thorpe and Crompton, 2006), and of a number of modern human generally non-industrialised populations in relation to the acquisition of honey and other resources (Kraft et al. 2014; Venkataraman et al. 2013), means that the biomechanics of arboreal locomotion in humans warrants further research.

1.2. *Kinematics*

The study of kinematics allows the analysis of the specificities, and differences between, different locomotor categories in a variety of primate species. There are numerous studies of primate terrestrial locomotion (e.g. D'Août et al. 2001; Demes et al. 1994; Patel, 2010; Patel and Wunderlich, 2010), whereas there are comparatively few for arboreal locomotion, of which most have examined vertical climbing (e.g. Isler, 2002a). For example, a range of anatomical elements on the fore- and hindlimbs, head, and body of gorillas (*Gorilla gorilla gorilla*) and bonobos (*Pan paniscus*) engaging in vertical climbing were manually digitised, as the reflective markers could not be directly attached to them (Isler, 2002a). Bonobos were found to have a greater variability in gait parameters, such as cycle duration and stride length, compared to gorillas, and the flexion-extension joint angles of both species generally exhibited a similar range for the fore- and hindlimb joints (Isler, 2002a). The difference in leg length and body mass between the two species may explain some of the variation observed (Isler, 2002a). It is important to note that the gorillas climbed a rope that was secured at both ends, whereas the bonobos climbed on a rope that were not secured at the bottom (Isler, 2002a). Therefore, any interspecific variation in the biomechanics of climbing may be, at least in part, due to coping with differences in compliancy of the substrate. This highlights the importance of the similarity of the equipment set up used for each species in order to make valid comparisons between species and with other studies.

A large variation in vertical climbing gait patterns has also been observed in gibbons (*Hylobates lar*, *H. leucogenys*, and *H. gabriellae*) when compared to gorillas (*Gorilla*), spider monkeys (*Ateles*), and macaques (*Macaca*) (Isler, 2002b). The large intermembral index of gibbons, 130 compared to a slightly smaller 116 for gorillas (Payne et al. 2006), suggests that the intermembral index of a primate may affect the kinematics of arboreal locomotion. Therefore, in order to examine the potential arboreal locomotor capabilities of extinct hominins, who have a mixture of more primitive and more derived traits (e.g. *Australopithecus sediba*, Kivell et al. 2011; and *Australopithecus afarensis*, Bush et al. 1982; Kimbel and Delezene, 2009), the kinematics of human arboreal locomotion as well as limb proportions should be examined to provide a comparison to primate data.

Substrate size has been shown to affect limb positions, particularly the extent of elbow flexion-extension during vertical climbing. Chimpanzees use an extended-elbow posture on larger diameters, and a more flexed elbow posture on smaller diameters (as described in Hunt et al. 1996) which aids momentum for vertical ascent (Hunt, 1992). This dichotomy has also been observed in the vertical climbing of spider monkeys (*Ateles fusciceps robustus*) and woolly monkeys (*Lagothrix lagotricha*) on large and small diameter substrates (Isler, 2004). Exact elbow angles were not measured, but two distinct categories (flexed and extended) were instead used for a broad kinematic comparison (Isler, 2004). On the small diameter substrate, significant differences were only found in female woolly monkeys, with duty factor and stride length increasing and speed and relative stride length decreasing on the vertically orientated rope compared to the small diameter tree substrates (Isler, 2004). In spider monkeys on the large compared to the small diameter, relative length of stride and mean duration of cycle significantly decreased, and duty factor significantly increased (Isler, 2004). Interspecies comparison of Isler's (2004) results is only possible on the small diameter substrates and the variation in the effects of substrate type on gait parameters suggests that there are species specific differences within locomotor categories.

While the body mass is positioned below the superstrate during suspension, compared to somewhat parallel to the substrate during vertical climbing (see descriptions in Hunt et al. 1996), the superstrate diameter may also affect the kinematics of the hand during suspension. My study will examine the effect of superstrate size on suspensory locomotion in humans, with particular attention to the relationship between how the hand is positioned on a specific diameter and the resulting pressure experienced.

Kinematic and force data have been combined to investigate the role of the hand in terrestrial locomotion in a male and female olive baboon (*Papio anubis*) a male and female patas monkey (*Erythrocebus patas*), and two rhesus macaques (*Macaca mulatta*) (Patel, 2010). Kinematic markers applied to the forelimb under anesthetised conditions allowed a more accurate interpretation of joint movement compared to previous studies using manual digitisation of anatomical segments in video footage (Isler, 2002a; Patel, 2010). Increases in speed of gait were associated with increased GRF, and at peak force there was a negative correlation between wrist joint angle and GRF (Patel, 2010). This resulted in a more palmigrade posture (Patel, 2010) and illustrates that the primate hand is flexible in its response to external forces. Further study, with a larger and more varied sample, would provide additional insight into the role of the hand in locomotion.

The difficulties with applying retroreflective markers to primates means that the majority of kinematic studies have used human participants. It has been found that the range of joint motion in the thumb is limited by the anatomical position of the joint (Lin et al. 2011). For example, the interphalangeal (IP) joint experienced a significantly greater degree of flexion compared to the MCP and carpometacarpal (CMC) joints, and the CMC joint experienced significantly less abduction but significantly more internal rotation than the MCP joint (Lin et al. 2011). The position of one joint can affect the expected position of other joint regions. For example, there is a synergistic relationship between wrist movement and the distal interphalangeal (DIP), proximal interphalangeal (PIP), and MCP joints during active wrist flexion and extension, whilst the finger movement remained passive (Su et al. 2011). An increase in wrist extension resulted in an increase in finger flexion, and as wrist flexion increased so too did finger extension, the correlation was strongest for the PIP and MCP joints, and weaker for the DIP joint (Su et al. 2005). The second and third digits had a significantly greater range of motion compared to the fourth and fifth digits (Su et al. 2005). This contrasts with the results of El-Shennawy et al. (2001) and Buffi et al. (2013) that demonstrated that the CMC joints of the fourth and fifth digits have a greater range of motion compared to the second and third digits. However, Su et al. (2005) did not take into account soft tissue thickness which may affect the range of passive finger movement due to passive deformation of the volar surface of the fingers. Overall, this illustrates that wrist position should be considered when examining the position of the fingers.

From a kinematic perspective of joint loading in the human hand it has been noted that the majority of the hand joints examined were significantly more flexed during the power grip, opposed to the precision grip (Goislard de Monsabert et al. 2014). The hook grip used by primates during suspension (see Alexander, 1994) bears some kinematic similarities to the power grip as defined by Napier (1965), as the fingers are opposing the palm. Therefore, investigation of the relationship between wrist and finger position in relation to pressure in an arboreal suspensory context would be beneficial for further understanding the biomechanics of the human hand from an evolutionary perspective. Furthermore, comparison of human kinematic data to primate kinematic data for the same activities would be highly beneficial in examining the range of motion that certain anatomical morphologies use during tasks.

It has been demonstrated that an increase in cylinder diameter above a certain threshold results in decreased hand contact area (Seo and Armstrong, 2008). This is further illustrated by the increasing pressure at the distal phalanges and decreased palmar pressure during inward torque as handle size increases (Seo et al. 2007). Inward torque when gripping a cylindrical object with finger and thumb opposed is defined as when the torque is in the direction of the fingertips compared to outward torque where the torque direction is towards the palm and opposing thumb (Seo et al. 2007). A potential explanation is that the increased force at the distal phalanges causes the intermediate and proximal phalanges to move away from the substrate (Seo and Armstrong, 2008). Whilst the general trend for decreasing contact area with increasing diameter has been noted, no study has used kinematic data to analyse hand position and joint angle variation in relation to differences in cylinder diameter. This study will address this issue by combining kinematic positional data with pressure data for a range of cylinder diameters.

There have been many previous kinematic studies of primate locomotion (e.g. D'Août et al. 2001; Demes et al. 1994; Isler 2002a, b, 2004; Patel, 2010; Patel and Wunderlich, 2010). Despite this, the kinematics of human arboreal locomotion has not been fully addressed. There have been previous kinematic studies of the human hand during non-arboreal activities (e.g. Lin et al. 2011; Su et al. 2005). In these studies the body mass has played a minimal role in the positioning of the hand, unlike arboreal suspensory locomotion where the body mass is below the hand and the superstrate (see Figures 11a-b and 25 in Hunt et al. 1996). The combined use of pressure and kinematic methodology in my study also allows a more accurate investigation of hand positioning, potential contact area, and the location of peak pressure, and therefore builds upon the previous studies of Seo et al. 2007 and Seo and Armstrong (2008).

1.3. *Primate pressure data*

Many of the previous pressure data studies, in relation to locomotion, have analysed the pressure distributions in the feet, particularly in relation to addressing the question of the origins of bipedalism (Hatala et al. 2013). It was found that although "regional standardised footprint depth" and "regional standardised maximum plantar pressure" showed a weak correlation, the correlation strengthened as the speed of locomotion increased (Hatala et al. 2013: 26). The heel and the hallux experienced the maximum pressures over the entire foot, as well as being the deepest footprint regions (Hatala et al. 2013). Whilst this relationship is not significant it bears some resemblance to the pressure tripod proposed by Marchi (2005), where the calcaneus, first metatarsophalangeal (MTP) joint, and fifth MTP joint are the main points for stress dissipation through the substrate during bipedal locomotion in humans. It should be noted that the experimental set up used by Hatala et al. (2013) had the pressure pad and sediment pit positioned separately. A separate study showed that there were differences in pressure distribution when a participant walked across a hard substrate and a sand substrate with a pressure plate underneath it (D'Août et al. 2010). This indicates that the type of substrate has an effect on pressure distribution (D'Août et al. 2010). This was acknowledged by Hatala et al. (2013) through the use of a substrate that had similar properties to the sediment in which the Laetoli footprints were formed to allow comparison to hominin locomotion. The distribution of pressure in human hands during arboreal locomotion has not previously been analysed. Therefore, the distribution of pressure in the hand during the gait cycle potentially may follow a similar pattern to that in the foot, with the first and fifth rays and the thenar and hypothenar regions being areas of high pressure during arboreal locomotion in humans.

The origins of bipedalism have further been analysed through the differences in pressure in primate feet during bipedal and quadrupedal locomotion. For example, differences in the movement of the CoP in the foot as the locomotor stance progressed were observed in quadrupedal and bipedal locomotion in bonobos (D'Août et al. 2001). During bipedal locomotion, the CoP progressed proximally along the lateral side of the foot and then moved distally followed by medially towards the hallux, whereas during quadrupedal locomotion the CoP travels distally along the lateral side of the foot but does not move medially (D'Août et al. 2001). Even though only a small number of individuals were analysed it highlights the initial differences in pressure and force distribution in bonobo locomotion (D'Août et al. 2001). As these results are preliminary, a larger sample size is needed to verify the conclusions of D'Août et al. (2001).

Pressure distribution is also related to ontogenetic differences in the foot contact area during bipedal locomotion. For example, the roll-off pattern, determined by tracking the centre of pressure (CoP) during the gait cycle, in newly walking toddlers was more variable and unstable than in those who had been walking for two weeks, and differed from the more stable CoP trajectory of the adult gait (Hallemans et al. 2003). It is suggested that the differences in stability of roll-off patterns led to newer walkers having a larger foot contact area, which results in a decrease in peak pressure compared to adult walkers (Hallemans et al. 2003). An increase in contact area in relation to a decrease in pressure values was also noted when comparing habitually shod, partially shod, and habitually unshod populations (D'Août et al. 2009). The habitually unshod population had significantly lower pressure values than the habitually shod population, this may be due to wider feet in the habitually unshod sample and thus a larger contact area for force to be distributed across (D'Août et al. 2009). This illustrates that whilst some differences in pressure distribution are related to ontogeny, habitual behaviour can also shape how pressure is experienced by the foot (D'Août et al. 2009). My study will use comparison between pressure and hand size data in bonobos (J. Neufuss unpublished; Samuel et al. 2018) and in a human sample to examine how locomotor differences affect theoretical contact area and pressure distribution in the hand during suspensory locomotion.

Other pressure studies have examined primate hands, either in relation to specialised phalanges (Kivell et al. 2010), gait changes (Patel and Wunderlich, 2010), and knuckle-walking (Matarazzo, 2013; Wunderlich and Jungers, 2009). For example, olive baboons change from a digitigrade posture to a more palmigrade posture as their speed of locomotion increases, although during both postures the fingers have decreased functional length (Patel and Wunderlich, 2010). GRF was shown to increase with speed (Patel and Wunderlich, 2010). Palmar contact also increases with speed and therefore there is a larger area for the force to dissipate across (Patel and Wunderlich, 2010). Even though the CoP remained at the metacarpal heads for both digitigrade and palmigrade locomotion the increased palmar contact area with speed is suggested to moderated the amount of pressure experienced by the metacarpals during locomotion at increased speeds (Patel and Wunderlich, 2010). This also illustrates the importance of the substrate-hand interaction in determining the distribution of pressure during a particular activity.

Specialist morphology, such as extremely long fingers, can also affect the pressure distribution of the primate hand. For example, it has been found that during head first descent the fingers of aye-aye's (*Daubentonia madagascariensis*) were curled up off the substrate which prevented the fingers experiencing increased amounts of pressure during descent compared to ascent (Kivell et al. 2010). This is in contrast to the palms, where a statistically significant increase in peak pressure was experienced during descent compared to ascent (Kivell et al. 2010). The hindlimbs experienced a greater percentage of the PTI during descent, which was unexpected compared to the hindlimb focused ascent and more even horizontal locomotion PTI results (Kivell et al. 2010). This is suggested to be a mechanism to reduce the load on the hands with their specialised digits (Kivell et al. 2010). It should be noted that whilst Kivell et al. (2010) focus on vertical climbing-like locomotion (ascent and descent), as the slope is below the 45 to 90 degrees defined by Hunt et al. (1996) as vertical climbing, their study illustrates that hand morphology affects how pressure is experienced by the hand in primates.

Differences in hand morphologies have also been shown to affect how pressure is experienced by the hand in chimpanzees and gorillas during knuckle-walking (Matarazzo, 2013). Chimpanzees have more variable ray lengths than gorillas which results in the third digit having a more forward position, and therefore being the touch off digit, during knuckle-walking when the palm is facing backwards in chimpanzees compared to the more in line phalangeal arrangement of the gorilla hand during palm back knuckle-walking (Matarazzo, 2013). The digit experiencing peak pressure for each step was found to be significantly correlated with the touch off digit used for both species (Matarazzo, 2013). The chimpanzee results of Matarazzo (2013) are consistent with the results of Wunderlich and Jungers (2009), who also examined the distribution of pressure during knuckle-walking in chimpanzees. In young chimpanzees, it was found that knuckle-walking on an arboreal substrate produced higher pressures on the third and fourth digits, compared to a terrestrial surface, where the second to fourth digits experienced similarly high pressures (Wunderlich and Jungers, 2009). This illustrates that the positioning of the hand during knuckle-walking affects how pressure is experienced by the hand and that this is particularly relevant in relation to digit positioning. The results of Wunderlich and Jungers (2009) also suggest that the type of substrate used for locomotion (arboreal or terrestrial) may also affect how pressure is distributed in the hand. The relationship between hand positioning and peak pressure location should therefore be investigated further in an arboreal context in order to provide a comparison to studies of terrestrial locomotion.

There are a limited number of pressure studies examining arboreal locomotion in primates (e.g. Samuel et al. 2018), and none that examine arboreal locomotion in humans. Some human pressure data has been collected in relation to static grips and applied torque (Seo et al. 2007), and whilst this is not directly comparable to studies of dynamic locomotion it does provide an initial insight into the effects of the size of the substrate being grasped on the distribution of pressure in the hand. The decrease in grip force as the diameter increases is suggested to potentially be due to the position of the hand on the diameter (Seo et al. 2007). In the study by Seo et al. (2007), the participant's hand was supinated and the diameter grasped with the thumb abducted and opposing the fingers. This suggests that the smaller diameter allowed the thumb and fingertips to be positioned opposite the palm, and thus exert greater force onto the palm, whereas the distance between the fingertips and the tip of the thumb increased as the diameter increased (Seo et al. 2007). Therefore, the positioning of the anatomical components of the hand on different sized diameters may affect the grip force, and ultimately pressure, experienced by the hand. It should also be noted that the participant's body mass was not suspended directly below the diameter (Seo et al. 2007). In my study, whilst there will be a range of diameter sizes the body mass of the participants will be suspended below the diameter during each activity, and therefore the results may differ from those of Seo et al. (2007).

Pressure distribution in the bonobo hand during a range of arboreal locomotion, including vertical climbing, suspension, and arboreal knuckle-walking, on a 120mm diameter was examined by Samuel et al. (2018). It was noted that whilst the thumb was observed to make contact with the substrate and superstrate during vertical climbing and suspension it registered very little, if any, pressure (Samuel et al. 2018). This then brings into question how the relative size of the digits affects the pressures experienced during locomotion, as bonobos have a short thumb compared to humans (Feix et al. 2015). The thumb was generally positioned in an adducted position during suspension (Samuel et al. 2018). It was also noted that the second-fourth digits were held together during arboreal locomotion, which meant that analysis of separate digits was not possible (Samuel et al. 2018). The suspensory hand positions of the human participants in my study also consistently had the second-fourth digits positioned together, however, the use of kinematic markers allows the positions of the third and first digits to be mapped to the corresponding pressure data. The results of my study will therefore provide a comparative sample to the bonobo suspension results of Samuel et al. (2018).

Suspension on both transverse and longitudinal axes of the horizontal pole was used by the bonobos, however, no differences were observed between the different types of suspension (Samuel et al. 2018). This means that suspension along the longitudinal axis of the pole by the human participants in my sample is comparable to the suspensory behaviours of the bonobos in the study by Samuel et al. (2018).

The regions of bonobo hands that experienced peak pressure most often during both suspension and vertical climbing were the distal phalanges and the proximal region of the palm (Samuel et al. 2018). This is in contrast to Patel's and Wunderlich's (2010) study of pressure distribution during terrestrial locomotion in olive baboons where during palmigrade locomotion the CoP remained at the metacarpal heads in the distal region of the palm even though the area that the force was applied to had proximally increased. The distal and proximal phalanges were loaded during suspension, whereas the intermediate phalanges often were not loaded to the threshold which was detectable by the pressure mat (Samuel et al. 2018). This then brings into question the position of the phalanges relative to each other and the palm during suspension, and how this affects the pressure experienced by the hand. The pressure results of Samuel et al. (2018) were masked into the regions of the palm and the digits, and as previously noted it was not possible to distinguish individual digits. Despite this, during suspension peak pressure in the digits often occurred in the region approximated to be on or near the distal phalanx of the third digit (Samuel et al. 2018). This suggests that the third digit may play a key role in suspensory locomotion in bonobos.

The combination of video and pressure data used allowed the timings of the gait cycle to be analysed in relation to the pressure experienced by the hand (Samuel et al. 2018). Their results show that initial contact with the pressure mat did not always result in that particular anatomical area reaching the pressure threshold of 15 kPa on the pressure mat first (Samuel et al. 2018). For both suspension and vertical climbing peak pressure occurred around the middle of the stance phase, compared to arboreal knuckle-walking where peak pressure occurred in the latter half of the stance phase (Samuel et al. 2018). The third digit was generally the touch off digit during arboreal knuckle-walking in bonobos (Samuel et al. 2018). This appears to follow a similar pattern to the relationship between peak pressure and touch off digit in knuckle-walking chimpanzees (Matarazzo, 2013). This suggests that the timing and distribution of peak pressure during arboreal locomotion may be similar across primate species. However, further research within each of the arboreal locomotion categories with a wider range of comparative samples is needed before conclusions can be drawn. My study aims to provide comparable human suspensory pressure data to the bonobo pressure data in the study by Samuel et al. (2018) in order to further elucidate the function of the hand in fossil hominin locomotor behavior.

Pressure studies can be used to examine the relationship between the forces experienced during arboreal locomotion and the skeletal morphology of a species. The results of Congdon's and Ravosa's (2016) study examining the effect of different types of arboreal locomotion on hand and foot pressure in three species of strepsirrhines (ringtailed lemurs, *Lemur catta*; Coquerel's sifakas, *Propithecus coquereli*; and red-ruffed lemurs, *Varecia rubra*) concluded that phalangeal curvature does not accurately reflect the amount of suspensory locomotion in which an individual engages. This differs from previous biomechanical analysis of primate hands which suggests that phalangeal curvature reduces the strain experienced by the hand during unimanual forelimb-suspension (Hunt, 1991). For all the of the strepsirrhine species analysed, the third digit of the hand had significantly higher peak pressure than the other digits during quadrupedal below branch locomotion compared to vertical climbing and quadrupedal locomotion above branch (Congdon and Ravosa, 2016).

When examining homologous digits, the mean pressure values across all of the locomotor categories, and for all of the species, supported the hypothesis that the differences in pressure experienced by homologous digits in the hands and feet are non-significant (Congdon and Ravosa, 2016). On the other hand, when peak pressure values for homologous digits were investigated significant differences were found in vertical locomotion for the first digit for all three species, as well as in the third and fourth digits for *V. rubra* (Congdon and Ravosa, 2016). In below branch quadrupedal suspension in *V. rubra* and *P. coquereli* the fifth digit of the foot was not utilized, whereas the fifth digit of the hand was, so no analysis for homologous digits could be made for those species for that particular locomotor category (Congdon and Ravosa, 2016). Therefore, it was stated that above branch quadrupedal locomotion is the only locomotion category that has no significant differences in peak pressure between homologous digits (Congdon and Ravosa, 2016). It should also be noted that whilst Congdon and Ravosa (2016) provide both mean pressure and peak pressure results, they do not specify which is the most reliable method of measurement when looking at variations in pressure experienced during arboreal locomotion.

The interspecies variability of their other findings suggests that other factors that influence the forces experienced during arboreal locomotion, such as body mass, should be investigated. Only arboreal locomotion involving all four limbs was investigated by Congdon and Ravosa (2016). It should be noted some forms of suspension do not involve both the hands and feet and thus may affect the forces experienced. For example, it has been suggested that chimpanzees are biomechanically adapted to engage in efficient arm hanging behavior and that the phalangeal curvature allows more even distribution of pressure and reduces the radial torsion experienced by the palmar tissues, even though the entire body mass is below the single hand gripping the branch (Hunt, 1991).

Congdon and Ravosa (2016) also did not take into account the hand and foot size of the species examined. The hand and foot pressures were found to be similar during arboreal locomotion (Congdon and Ravosa, 2016) but a smaller hand size or a larger foot size would change the area that the force was acting on. A greater substrate reaction force may be experienced by the hindlimb, as suggested by Demes et al. (1994), but dependent on the surface area of the hands and feet in contact with the substrate the pressure distribution may vary to the differences in force experienced by the fore- and hindlimbs. This may also be affected by substrate size, as Seo et al. (2007) found that in humans as substrate diameter increased above 57mm the contact area of the palm decreased. It should also be noted that the pressure pad used by Congdon and Ravosa (2016) had sensors with an area of 1.82cm^2. The exact hand and foot size of the species analysed, ring-tailed lemurs (*Lemur catta*), Coquerel's sifakas (*Propithecus coquereli*), and red-ruffed lemurs (*Varecia rubra*), were not stated in connection with the sensor size. Therefore, whilst Congdon and Ravosa (2016) claim that the width of the digits was smaller or the same as the sensor area it is difficult to completely separate finger pressure from palm pressure for analysis. This is because the length of the fingers for each species was not mentioned and the large sensor area may make it difficult to accurately separate the two anatomical areas, especially around the MCP joint. It should also be noted that Congdon and Ravosa (2016) suggest that the effect of different diameters of substrate on the pressure experienced by the hands and feet should be investigated in future research. My study will address this by investigating the effect of diameter on the peak pressure and location of peak pressure in the human hand during arboreal suspensory activities (unimanual forelimb-suspension and forelimb swing as defined in Hunt et al. 1996).

There have been many pressure studies of primate locomotion (e.g. D'Août et al. 2001; Kivell et al. 2010; Patel and Wunderlich, 2010; Samuel et al. 2018), as well as many examining human locomotion (e.g. Bosch et al. 2009; Eils et al. 2002; Nurse and Nigg, 1999; 2001). The studies that have analysed human locomotion have tended to examine the foot in a terrestrial setting (e.g. D'Août et al. 2009; Hallemans et al. 2003; Hatala et al. 2013). Therefore, more pressure studies of human arboreal locomotion are needed in order to provide a comparative data set to the arboreal pressure studies of primates. Pressure studies in the ergonomic literature have examined the effects of diameter size on pressure in the human hand (e.g. Seo et al. 2007). Despite this, they have done so in a static context with the body mass perpendicular to the handle being gripped. My study will build upon the ergonomic literature by examining the effects of diameter size on the pressure experienced by the hand in an arboreal setting, with the body mass below the superstrate, as well as providing a comparative sample to the suspensory bonobo data of Samuel et al. (2018). Therefore, this study will be comparable to pressure studies of primate locomotion and ergonomic studies of the effects of diameter size on the pressure experienced by the human hand.

1.4. *Clinical studies*

Clinical studies provide an insight into the effects of biological degradation or maladaptation on the functions of the human hand. These studies can help highlight the anatomical regions of the hand that play important roles in grip function, and ultimately arboreal locomotion. For example, in a study of the interaction between grip (measured via a power grip) and pinch (measured via a precision grip) strength and osteoarthritis in the hands of postmenopausal women, it was found that the presence of osteoarthritis in the hand had a negative effect on pinch and grip strength, particularly at the DIP joints (Bagis et al. 2003). The combination of the DIP, PIP, and CMC joints being affected by osteoarthritis and producing the lowest pinch strength suggests that forceful precision grips require a greater amount of joint mobility than forceful power grips, which were most reduced when only two joints (DIP and PIP) were affected. Whilst the Bagis et al. (2003) looked only at postmenopausal women, these results suggest that there are differences in joint combinations required for 'normal' movements. Power grips, as used by primates during arboreal locomotion (see Alexander, 1994), will be used during the arboreal suspensory locomotion in my study, and based on the findings of Bagis et al. (2003) it would then be expected that the joints of the fingers, and therefore positioning of the digits, would play a greater role in grasping compared to the wrist joint.

The study of joint loadings during particular hand grips can provide information on the types of activities that pose higher risk factors to developing degenerative joint diseases, such as osteoarthritis (Bagis et al. 2003), in the hand. For example, Goislard de Monsabert et al. (2014) estimated joint pressure and joint forces from estimated muscle tensions based on a musculoskeletal model that incorporated grip force and kinematic data from precision and power grips performed by subjects. They found that whilst grip force is greater in the power grip than in the precision grip, the joint pressures are higher and increase proximally in the precision grip (Goislard de Monsabert et al. 2014). The most proximal thumb joint, the trapeziometacarpal (TMC) joint, experiences the greatest joint pressures and has a high frequency of osteoarthritis (Goislard de Monsabert et al. 2014). In the index finger the DIP and PIP joints are most likely to be affected by osteoarthritis, while the highest joint pressure was experienced by the MCP joint (Goislard de Monsabert et al. 2014). This suggests that whilst joint pressure increase may be a risk factor in the development of hand osteoarthritis, this is not always the case and other factors may also contribute. Investigation of the location of peak pressure in the human hand whist grasping would be beneficial alongside examining joint pressures, as understanding hand loading from both joint and palmar or finger perspectives would provide a more holistic understanding of how to hand experiences mechanical forces during different activities. My study will provide an examination of the location of peak pressure from the palmar and finger perspective in the human hand during grasping in an arboreal suspensory context.

The thumb, particularly the TMC joint, has been a key area of clinical research (e.g. D'Agostino et al. 2014; 2016; 2017). The mechanisms of joint stability have been of interest from a clinical perspective in relation to surgical decisions, especially for the highly mobile TMC joint (D'Agostino et al. 2014). It has been shown that the dorsoradial ligament at the TMC joint has a greater role in TMC stabilisation than the anterior oblique ligament due to its greater stiffness (D'Agostino et al. 2014). The skeletal morphology of the TMC joint in humans compared to other catarrhines and fossil hominins suggests that the human thumb is highly mobile thumb and has the ability to firmly grip objects (Marzke et al. 2010). It is noted that the stabilisation of the joint is reliant on the ligaments in combination with the skeletal morphology (Marzke et al. 2010), therefore both hard and soft tissues should be considered when investigating the evolutionary pathways of anatomical regions. Examining how pressure is experienced by the human hand, particularly in relation to the location of peak pressure, in comparison to other primate species can provide an insight into the roles of anatomical structures during particular activities. Combining the analysis of pressure with the study of the variation in internal hand morphology between humans and primates may allow inferences to be made in relation to particular structures and their roles, or lack of, in certain behavioural situations. It should be noted that peak pressure cannot be considered a proxy for the loading of the local tissues and bones, as its location is specific. Therefore, further study is needed on how pressure varies around the location of peak pressure.

Understanding the full ranges of motion for a joint will provide an insight into the potential selection pressures for that anatomical region when the extent of the motions used for a particular activity are examined. The joint anatomy of the hand, in particular the CMC joints, affects the range of movement possible. For example, it has been illustrated that the fourth and fifth CMC joints have a greater range of movement than the second and third CMC joints (El-Shennawy et al. 2001). This is partly due to the morphology of the metacarpal bases and the distal carpal row; a styloid on the base of the third metacarpal is dorsoradially positioned and assists in locking the concave base of the third metacarpal and the convex surface of the capitate, compared to the saddle-like joints of the fourth and fifth metacarpals and the hamate (El-Shennawy et al. 2001). It was also found that the fourth and fifth CMC joints had a high degree of mobility (Buffi et al. 2013), but that it was less than that found in the study by El-Shennawy et al. (2001). This may be due to the use of cadaveric specimens with manipulation via external forces by El-Shennawy et al. (2001) and *in vivo* methods by Buffi et al. (2013). These results highlight the need to study joint motion in living individuals in order to gain a more accurate representation of joint motion for biomechanical models. Whilst my study will not be investigating the exact angles of the hand joints, comparison of peak pressure and location of peak pressure will be carried out between thumb adducted and thumb abducted hand positions, and the anatomical constraints of the hand will be taken into account when discussing the results.

The pressure distribution in the hand has been examined from a clinical perspective in relation to falls and the potential resulting injury (see Choi and Robinovitch, 2011). The effect of fall angle, soft tissue thickness with and without additional foam buffering, and body mass index (BMI) were investigated by Choi and Robinovitch (2011) in falls of a short distance (5cm) onto a force plate. An increase in BMI was found to be associated with an increase in peak pressure and force, but not related to the thickness of the soft tissue, particularly at the wrist (Choi and Robinovitch, 2011). The use of a 5mm foam layer on the palm reduced the peak pressure, but it did not affect the peak force (Choi and Robinovitch, 2011). It should be noted that the sample is small (N = 13) and only consists of female individuals (Choi and Robinovitch, 2011). Therefore, potential sex specific differences cannot be tested and thus the results are only applicable to part of the general population. Anthropometric variables, such as arm length and hand size, were also not examined. As the body mass in the study by Choi and Robinovitch (2011) was located above the hand, their results will provide a contrast to my study where the body mass is located below the hand. This will provide an insight into whether the position of the body mass in relation to the hand affects the location of peak pressure.

Many of the clinical studies illustrate that hand anatomy affects the range of motion possible for each anatomical region of the hand (El-Shennawy et al. 2001; Buffi et al. 2013), as well as highlighting that some specific activities require different joint combinations compared to other activities, such as power grips compared to pinch grips (Bagis et al. 2003). This suggests that different regions of the human hand may play different roles in grasping during arboreal locomotion.

1.5. *Ergonomic studies*

Ergonomic studies have often been overlooked in anthropological studies relating to hand morphology and use. Ergonomics examines the most efficient way of carrying out an activity, and therefore it is interesting to look at the results of such studies from an evolutionary perspective with a particular focus on major transitions within human evolutionary history. Key (2016) provides an overview of how ergonomic studies can be applied to lithic analysis, in particular stating that there is need for further interdisciplinary research. The majority of grip force studies analyse the effects of varying cylindrical handle size (Edgren et al. 2004; Eksioglu 2004; Kong and Lowe, 2005; Seo et al. 2007). Whilst this allows the examination of hand postures similar to those used by primates during arboreal locomotion, such as power grips (Alexander, 1994), it does so in a static context and without the effects of body mass. My study will build upon the understanding of the relationship between grip pressure of the human hand and cylindrical diameter of the gripped object in both static suspensory and dynamic suspensory contexts.

Based on multiple ergonomic studies, the optimum cylindrical handle diameter for the average human hand is between 30-40mm (Edgren et al. 2004; Hall, 1997; Kong and Lowe, 2005; Seo and Armstrong 2008). Strain gauges were used by Edgren et al. (2004) to measure perpendicular grip force in cylindrical handles with a range of diameters. The resulting vectors were then summed to determine the magnitude of the total force and the vector angle was calculated (Edgren et al. 2004). Of the handle diameters used, it was found that the greatest grip force was generated with the 38.1mm diameter cylindrical handle, and that grip force increased up to this diameter and then decreased as the diameter continued to increase (Edgren et al. 2004). Both dominant and non-dominant hands were tested and a statistically significant difference was found between the grip force generated for each of them (Edgren et al. 2004). The vector angle was found to increase with hand size, but this was only applicable in the largest diameter handle (76.2mm) (Edgren et al. 2004). The male sample produced statistically significantly greater grip forces than the female sample. Age was also found to have a significant effect of grip force and the age distributions for each sample differed (Edgren et al. 2004). Therefore, as noted by Edgren et al. (2004), it is difficult to state that there is a definite statistically significant difference between male and female grip forces.

The optimal diameter of 30-40mm was also found by Hall (1997: 191) using “small capacitive pressure sensors” and Kong and Lowe (2005) using a modified pressure glove. Kong and Lowe (2005) only examined the second to fifth digits and did not include the thumb. Of the four digits examined they were divided up into the distal, intermediate, and proximal phalanges, and the associated metacarpal heads, so when total finger force is used it refers to the whole finger and metacarpal head (Kong and Lowe, 2005). This causes some issue for comparison to other studies which do not include the metacarpal head when examining finger force. When each finger segment was analysed, the distal phalanges were found to produce the greatest force, with the amount of force generated decreasing proximally to the associated metacarpal head (Kong and Lowe, 2005). When the second to fifth digits, including the metacarpal heads, were examined the third digit had the greatest contribution to total force (Kong and Lowe, 2005). This was followed by the second and fourth digits (Kong and Lowe, 2005). Mid-range cylindrical handles, between 30-40mm, were considered the optimal diameter because they allowed for the greatest grip force and highest perceived comfort rating (Kong and Lowe, 2005). It should be noted that this is a subjective method for obtaining diameter preference and I therefore suggest that ranking the diameters from most preferred to least preferred may be a more easily comparable method of obtaining diameter preference.

The anatomical measurements of the human hand can also affect the amount of grip force that can be exerted. For example, hand dimensions were shown to relate to maximum grip force and perceived comfort when the span between two handles is varied (Eksioglu, 2004). A modified thumb-crotch length (TCLm) measure was used and nine handle spans covering TLCm to 40mm less than TCLm were analysed (Eksioglu, 2004). The TCLm is calculated by positioning the thumb at a 45° angle to the third digit and measuring the horizontal distance between the PIP joint of the third digit and where the index finger and thumb meet (Eksioglu, 2004). A handle span 20mm smaller than an individual's TCLm was found to facilitate the maximum voluntary grip force and had the highest perceived comfort rating, while spans 20-25mm smaller than TCLm showed the least muscle activity (Eksioglu, 2004). Span sizes greater and smaller than 15mm to 25mm less than TCLm had significantly lower maximum grip force (Eksioglu, 2004). A dynamometer with varying grip spans, opposed to a cylindrical handle, was used to measure grip force, this highlights the need to take anthropometric measurements into account when comparing hand grip results from a varied sample.

The shape of the handle can also affect the distribution of grip force. For example, Rossi et al. (2014) examined the interaction between handle shape, hand position, and grip force within a human sample (although the male-female spread of participants is not stated). For both the circular and elliptically shaped handles the third digit and the thumb were shown to significantly contribute to the exhibited grip force, and the thumb also significantly contributed to the grip force for the double frustum handle shape (Rossi et al. 2014), which indicates that the thumb and third digit play a key role in grip force. Kinematic analysis demonstrated that when gripping the double frustum shaped handle the wrist extension increased significantly compared to the other two handle shapes (Rossi et al. 2014). Whilst no information is provided by Rossi et al. (2014) to determine the direction of the relationship, it is stated that the interplay between fingers and the shape of the handle was significant at the PIP joint angles, compared to the other finger joints. The hand position for each handle was not standardised, as the participants were able to choose whichever position suited them for each handle (Rossi et al. 2014). Therefore, it is not possible to assess exactly how hand position affected force distribution for each handle shape. Further study into the effect of handle shape on force distribution is therefore needed.

Cylinder diameters have also been shown to have an effect on the contact area of the hand. Seo and Armstrong (2008) found that as cylinder diameter increases, contact area decreases. They suggest that this may be due to two reasons: (1) reduced grip force resulting in a decrease in the amount of deformation, and therefore surface area, of the palmar tissue, and/or (2) the concentration of force at the distal phalanges altering the DIP and PIP joint angles and causing the intermediate and proximal phalanges to move away from the substrate (Seo and Armstrong, 2008). Pressure data from the study by Seo et al. (2007) on the effect of cylinder diameter and torque on grip force show a decreased contact area of the palm with a large (83.2mm) diameter cylinder compared to a medium (57.8mm) diameter cylinder under inward (in the direction of the fingertips) and outward (in the direction of the palm and opposing thumb) torque and no torque conditions. When maximal grip strength with no torque was applied, in both the medium and large diameters, the greatest areas of pressure were at the first distal phalanx and the third distal phalanx (Seo et al. 2007). A similar area of high pressure was also observed on the proximal phalanx of the third digit at the medium diameter (Seo et al. 2007).

When outward torque was applied, the pressure in the distal and proximal phalanges of the third digit decreased but the pressure remained highest in the first distal phalanx at both the medium and large diameters (Seo et al. 2007). The application of inward torque once again resulted in the greatest areas of pressure at the distal phalanges; the first, second, and third distal phalanges were consistent between both diameters but the fourth distal phalanx was at least 124.82 kPa higher in the larger of the two diameters (Seo et al. 2007). Using the equation created by Seo and Armstrong (2008), the optimum handle diameter is 40mm, which is about 18mm smaller than the diameter at which hand contact area begins to decrease. Whilst pressure and contact area were noted in Seo et al. (2007) and Seo and Armstrong (2008) respectively, joint angles and the position of the digits in relation to each other were not. Therefore, combining kinematic data with pressure analysis would allow a more rounded understanding of the effect of diameter on grip force and hand anatomy.

Whilst the majority of ergonomic studies have examined static grip postures (e.g. Edgren et al. 2004; Kong and Lowe, 2005; Seo et al. 2007) no previous study has investigated how the position of body mass in relation to the hand affects the pressure experienced by the hand. My study will examine the effects of static and dynamic suspension on hand pressure, when the body mass is suspended below the hand. When compared to the results of previous ergonomic studies, this will allow an insight into whether other factors, such as body mass, may affect the relationship between the human hand and the object being gripped. Further investigation of the optimal diameter in a suspensory context will be particularly useful, when compared to comparative primate data, for assessing the relationship between morphology and function. Especially when using human and primate data to make inferences about the locomotor and behavioural capabilities of fossil hominins.

1.6. *Hand evolution*

The morphology of the human hand bears some similarities to primate hands; however, the manipulative abilities differ (Feix et al. 2015; Marzke and Marzke, 2000; Marzke and Shackley, 1986; Pouydebat et al. 2014). How this morphology evolved is of much interest to palaeoanthropology, particularly in the areas of locomotion and tool use (Schmitt et al. 2016; Williams-Hatala, 2016). Within primates the hand plays a key role in many activities, such as locomotion, grooming, and feeding, all of which are important parts of primate daily life (Feix et al. 2015; Patel and Wunderlich, 2010; Pouydebat et al. 2014). Therefore, trade-offs between the different functions of the hand may be apparent in the hand anatomy of some species.

Only skeletal remains are present in the fossil record it is therefore difficult to infer the exact muscle anatomy of fossil hominin hands. For example, Richmond et al. (2016) outline that a flexor pollicis longus (FPL) muscle that is mostly, or fully, separated from the flexor digitorum profundus (FDP) muscle is characteristic of modern humans, as the FPL is not always present or completely detached from the FDP in primates. It is therefore suggested that it is likely that the last common ancestor of chimpanzees and modern humans would not have had a FPL, but the attachment site for the FPL is found on the majority of fossil hominin hands (Richmond et al. 2016). Whilst this identifies that the FPL muscle was present it does not, as noted by Richmond et al. (2016), offer any clue as to the degree of separation between the FPL and FDP, and therefore independent thumb movement range, in any of the fossil hominin hands due to lack of soft tissue preservation.

Despite the difficulties with the lack of soft tissue in the hominin fossil record, the hand is implicit in answering many of the overarching questions within palaeoanthropology. There is debate surrounding the multiple theories of the origin of bipedalism, such as the knuckle-walking hypothesis, various arboreal hypotheses, and the postural feeding hypothesis (Hunt, 1996; Kivell and Schmitt, 2009; Richmond et al. 2001; Thorpe et al. 2007), however, these analyses are further complicated by the lack of soft tissue preservation in the fossil record. The oldest most complete hand in the hominin fossil record belongs to *Ardipithecus ramidus*, a potential hominin dating to 4.4mya (Lovejoy et al. 2009a, b). It is suggested that *Ar. ramidus* did not engage in the range of arboreal locomotion seen in extant apes, such as vertical climbing and suspension, but instead climbed carefully and bridged gaps in arboreal substrates using palimgrady hand positions (Lovejoy et al. 2009a). This is facilitated by a highly mobile wrist (Lovejoy et al. 2009a). It should be noted that whilst Lovejoy et al. (2009a) state that the phalanges of *Ar. ramidius* are between *Pan* and *Gorilla* in length, they do not mention the degree of phalangeal curvature. As previously mentioned, greater phalangeal curvature is suggested by Hunt (1991) to reduce strain and radial torsion experienced by the digits during suspensory grasping. It is therefore difficult to fully assess the range of arboreal locomotion that *Ar. ramidus* engaged in without considering the degree of phalangeal curvature.

1.6.1. Mosaic morphology

Within the hominin fossil record many fossils exhibit a combination of primitive and derived morphological traits. This has caused some debate as how to interpret the morphology in relation to behaviour, particularly as to whether they are significant functional adaptations or primitive retentions (Ward, 2002). Hands in both humans and primates have a range of functions in locomotion, object manipulation, and social relationships (Feix et al. 2015; Patel and Wunderlich, 2010; Pouydebat et al. 2014). It should be noted that hands, particularly nearly complete hands, are rare in the hominin fossil record. The recent fossil discoveries of

Homo naledi and *Australopithecus sediba* are therefore of great interest in the analysis of hominin hand evolution (Berger et al. 2015; Kivell et al. 2011; 2015).

The *Australopithecus sediba* (1.977 mya) MH2 hand has a selection of primitive traits, such as prominent flexor sheaths on the phalanges and a moderate degree of phalangeal curvature (Kivell et al. 2011). Alongside this, MH2 also has some derived traits, such as a relatively long thumb compared to the length of the fingers and expanded apical tufts on the distal phalanges (Kivell et al. 2011). The long thumb is outside of the range of variation seen in modern humans and this is suggested by Kivell et al. (2011) to show that *Au. sediba* had the potential to make stone tools but also engaged in some degree of arboreal locomotion. This is in contrast to the attribution of stone tool making to *Homo habilis*, via the OH 7 hand, which differs in morphology from that of *Au. sediba* (Kivell et al. 2011). It is also noted by Almécija et al. (2010) that the pollical distal phalanx digit of OH 7 shows little to no insertion for the FPL, which differs to that of *Orrorin tugenensis*, a potential hominin from around 6 mya that has an insertion for the FPL similar to modern humans. This difference in morphology between *Au. sediba* and *H. habilis* potentially suggests that there may have been multiple hand morphologies in existence within the same time range (Kivell et al. 2011).

The hand of *Homo naledi*, dating to between 236 kya and 335 kya (Dirks et al. 2017), provides an insight into the morphological characteristics of a member of the most recent genus of hominins. The wrist is morphologically similar to modern humans and *Homo neanderthalensis* (Kivell et al. 2015). In contrast to this, the phalanges exhibit curvature within the ranges of the OH 7 *H. habilis* specimen and *Australopithecus afarensis* (Kivell et al. 2015). The thumb length of *H. naledi* is at the uppermost edge of the modern human range (Kivell et al. 2015). Whilst the proximal and intermediate phalanges have a high degree of curvature, the flexor sheaths ridge morphology is within the modern human range, and this is suggested to potentially be due to the increased curvature acting as a strain mediator and decreasing the muscle forces required for strong grasping (Kivell et al. 2015). This differs to what is seen in *Au. sediba* (Kivell et al. 2011), where the prominent flexor sheaths indicate that high muscle forces may have counteracted the constraints on grasping of shorter and less curved phalanges. The first metacarpal of *H. naledi* is particularly unique in having a conspicuous ridge on the palmar surface, which is suggestive of high thenar muscle forces (Kivell et al. 2015). *Au. sediba* predates *H. naledi*, and therefore comparison of the hands of both species suggests that there are potentially multiple ways in which the hand can adapt to the loadings imposed by some degree of potential arboreal locomotion.

1.6.2. Tool use or arboreality?

The Laetoli footprints, which have been attributed to *Australopithecus afarensis*, indicate that by 3.6 mya hominins engaged in some degree of bipedal locomotion (Raichlen et al. 2010; White and Suwa, 1987). This is concurrent with the valgus knee, the adducted hallux, and the longitudinal arch on the medial aspect of the foot, amongst other features associated with bipedalism, seen in *Au. afarensis* (Kimbel and Delezene, 2009). *Au. afarensis* also exhibits some primitive characteristics in the upper limb associated with arboreal locomotion, such as curved phalanges with robust ridges for the flexor muscles (Bush et al. 1982; Kimbel and Delezene, 2009). This questions whether *Au. afarensis* did engage in arboreal locomotion as well as bipedalism, and if so, brings into consideration the degree of arboreal locomotion that they engaged in.

The length of anatomical regions of the hand, in addition to the degree of phalangeal curvature, can also be used to investigate the potential behavioural capabilities of hominins.

A range of thumb and finger proportions, as well as variation in digit segment lengths, are seen across extant primate species, fossil hominins, and modern humans (Feix et al. 2015). This is of particular interest in fossil hominins, whose behavioural capabilities have to be inferred from the remaining skeletal material. Based on the kinematic model used by Feix et al. (2015) modern humans generally have a greater manipulative ability with small objects compared to other extant primates. It was also found that some extant primate species had manipulative abilities that approached those of modern humans but had a wide range of variation in their thumb and index finger segment lengths (Feix et al. 2015). Analysis of a composite *Au. afarensis* hand and an *Au. sediba* hand using both *Pan* and modern human ranges of motion in the TMC joint found that both species had a manipulative range similar to modern humans (Feix et al. 2015). This is in line with research which suggests that *Au. africanus* had the ability to produce human-like grips (Skinner et al. 2015). It should be noted that, as mentioned by Feix et al. (2015), this study only investigated precision grips using the tip of the index finger and thumb and therefore further research is needed to examine precision grips using the pads of the digits.

Tool use requires a high degree of manipulation and is therefore of particular interest in the evolution of the human hand (Key and Dunmore, 2015; Williams-Hatala, 2016). The earliest currently known stone tools date from 3.3 mya (Harmand et al. 2015), and they increase in complexity as the hominin fossil record becomes more recent (Harmand et al. 2015; Toth and Schick, 2007). Oldowan tools, dating from 2.6 mya, require a range of grips during their manufacture and use (Key and Dunmore, 2015; Williams et al. 2012). This suggests that the ability to produce these grips was present by 2.6 mya, although with the observations of primate tool use using organic materials and the lack of preservation of organic materials, it may be possible that the ability to produce these grips was present earlier than currently thought (Humle and Matsuzawa, 2009; Sanz et al. 2004). As the origins of stone tool manufacture and use are pushed back further, they become closer to the earliest definite evidence for bipedalism in hominins which have a mixture of bipedal and arboreal traits. This highlights the need for further investigation into whether how the hand is loaded during particular behaviours is reflected in the anatomical morphology and therefore, if it is possible to clearly distinguish between arboreal and non-arboreal hand use.

As the hominin fossil record seldom preserves soft tissue, with the exception of rare cases such as the Taung child endocast (Dart, 1925), inferences about how morphology related to function must be made from skeletal evidence. Therefore, understanding how morphological form relates to function in extant primates and humans is beneficial for providing insight into the behavioural and locomotor capabilities of fossil hominins. Many different methods have been used to investigate hand evolution, such as comparative morphology between humans and primates, patterns of joint diseases, primate observations, electromyography (EMG), pressure data, and experimental archaeology (Key and Dunmore, 2015; Marzke and Marzke, 2000). In recent years, medical advances have allowed the internal structure of the hand to be analysed in greater detail (Orr, 2016; Vereecke and Wunderlich, 2016). This furthers the understanding of how form relates to function in the musculoskeletal system. My study will combine kinematic and pressure analysis to gain a greater insight into how hand positioning, in relation to the superstrate, relates to how the hand is loaded during arboreal suspensory locomotion in humans. It will also provide comparative data to previous studies of primate arboreal suspension (see Samuel et al. 2018) to further examine the evolution of the human hand from a functional morphology perspective.

1.7. *Primate locomotion*

Among primates, humans are the only species that is habitually bipedal. All other primate species use a wide range of locomotor behaviours (Payne et al. 2006). For example, orangutans (*Pongo pygmaeus and P. abelii*) engage in suspensory, quadrumanous climbing, assisted bipedal walking, and quadrupedal locomotion (Thorpe and Crompton, 2006). The orangutans are the most arboreal of the great apes, with chimpanzees and gorillas tending to spend large quantities of time using terrestrial knuckle-walking, as well as some arboreal positions (Doran, 1993; Remis, 1995; Thorpe and Crompton, 2006). Bonobos also engage in a combination of terrestrial and arboreal locomotion, and when male bonobos are compared to male chimpanzees they use an increased amount of suspensory locomotion (Doran, 1993). It is also noted that bonobos are more likely to travel between feeding sites using arboreal locomotion, compared to chimpanzees (Doran, 1993).

Body mass has an effect on the frequency of climbing and supports chosen. For example, after controlling for the relationship between body mass and social rank, in the context of feeding larger male chimpanzees engaged in vertical climbing less frequently than smaller males and used thinner branches in the lower sections of the canopy (Hunt, 1994). This seems initially to be unusual but suggests that in relation to feeding behaviour there may be some trade-offs between the energy required for vertical climbing and the optimisation of support size (Hunt, 1994).

Another large bodied ape, the Sumatran orangutan (*Pongo abelii*), has been shown to also use small diameter supports whilst arboreal (Thorpe et al. 2007). The Sumatran orangutan engages in assisted arboreal bipedalism, where the hindlimbs are bipedal and one forelimb is used to support or balance the body whilst arboreal and was found to most often involve multiple branch supports with the smallest diameters available, less than 4cm (Thorpe et al. 2007). This is comparable to the optimal diameter size for human hands suggested by the ergonomic literature (Edgren et al. 2004; Hall, 1997; Kong and Lowe, 2005; Seo and Armstrong 2008). This suggests that there is a complex relationship between body mass, type of arboreal locomotion, hand dimensions, and chosen diameter of substrate for the locomotion.

Whilst orangutans spend the majority of their time in the canopy, unlike chimpanzees, their assisted arboreal bipedalism is similar to that seen in chimpanzees when feeding (Hunt, 1996; Thorpe et al. 2007). The postural feeding hypothesis suggests that arboreal bipedal postures assisted by the hand on an overhead branch and terrestrial bipedal standing to access the lower branches of small trees observed in feeding chimpanzees, alongside the arboreal-bipedal mosaic morphology of australopithecines, implies both arboreal and terrestrial components to the origin of modern human bipedalism (Hunt, 1996). It is also noted that the hindlimb joint extension during assisted arboreal bipedal locomotion in orangutans is more similar to human bipedalism than the flexed hindlimb assisted arboreal bipedalism of other great apes (Thorpe et al. 2007). Thus, it is implied by Thorpe et al. (2007) that the origins of human bipedalism may not only be arboreal but are older, and more arboreal, than previously thought. This therefore warrants further investigation of the biomechanics of arboreal locomotion, with particular focus on the hand, and diameter preference in humans and a wider sample of primates.

Primate locomotion can be divided into two categories based on the biomechanical effects on the limbs. These categories are: compression, where the centre of mass (CoM) is above the substrate and generates force onto the substrate, and tension, where the CoM is below the superstrate, and thus ‘pulls’ on the limbs (Thorpe and Crompton, 2006). A combination of compression and tension may be used in a locomotor category or posture depending on the number of limbs involved and their positioning (see Hunt et al. 1996, and appendices A and B in Thorpe and Crompton, 2006). The position of the limb relative to the body therefore affects the forces that it experiences, and in my study the participant’s body mass will be positioned below the grasping hand which will put the majority of the forelimb in tension. In this study, postural and locomotor modes will be used as standardised by Hunt et al. (1996) in order to allow greater comparability to other studies.

Different types of locomotion result in different distributions of body weight, and therefore pressure distributions. For example, bipedal locomotion in Japanese macaques (*Macaca fuscata*) resulted in a more proximal CoP in the foot whereas in quadrupedal locomotion there was a swift movement of the CoP towards the distal part of the foot (Hirasaki et al. 2010). This is potentially due to the more anterior CoM placement in quadrupedal locomotion compared to the posterior CoM position during bipedalism (Hirasaki et al. 2010). The flexion or extension of the elbow, depending on substrate diameter, during vertical climbing (Hunt et al. 1996; Hunt, 1992) influences the CoM of the primate (Isler, 2004). This can influence the pressure distribution in the hands and feet contacting the substrate, as illustrated by the CoM shift in the study by Hirasaki et al. (2010). My study will provide data on the effect on pressure distribution when the body’s CoM is below the superstrate in suspensory locomotion.

The effect of substrate size on limb positioning during arboreal quadrupedal locomotion was investigated by Schmitt (2003). Their findings show that as substrate size decreased elbow flexion increased and shoulder height decreased (Schmitt, 2003). The increased elbow flexion brings the primate’s body mass closer to the substrate, and thus lowers the CoG (Schmitt, 2003). The body mass being kept close to the substrate during vertical climbing in strepsirrhines would aid stability and decrease the energy needed for locomotion (Preuschoft et al. 1998). Chan (2007) states that the scapula position plays a large role in determining the potential positions of the forearm in primates. Therefore, it is logical that the change in elbow angle is consistent with a change in scapula height across all species analysed in Schmitt’s (2003) study. It should be noted that the horizontal poles were classified as small, medium, or large in relation to the mass of the primate under study (Schmitt, 2003). Despite this, the exact calculation in relation to how the size categories were allocated was not noted by Schmitt (2003). Therefore, whilst elements of the limb position change as the substrate size decreases, it is difficult to make exact comparisons between species and apply the findings to other studies.

The main locomotor mode of a primate also affects the force distribution through the forelimbs and hindlimbs. This is illustrated in the study by Demes et al. (1994) on force analysis of quadrupedal primate locomotion. Predominantly quadrupedal primates had a more even distribution of peak vertical force between the fore- and hindlimbs, although the hindlimbs were still slightly higher, compared to primates that engaged in suspensory locomotion, which had high peak vertical forces on the hindlimbs (Demes et al. 1994). It was found that within the primate order there was a general trend for the hindlimbs to produce a greater propulsion force and the forelimbs to produce a greater braking force (Demes et al. 1994). There is, however, a degree of variation between species and limb position during locomotion. For example, during quadrupedal gallop, the fore- and hindlimb pairs of vervet monkeys include a trailing and leading limb, with the trailing limbs having the greatest net propulsion force and the leading limbs having the greatest net braking force (Demes et al.

1994). The reduction in limb protraction of the trailing limb at touchdown and an increase in limb retraction when the limb leaves the substrate, compared to the leading limb has been suggested as a possible explanation (Demes et al. 1994). This is in line with the results of the study by Vilensky et al. (1990), where it is also noted that the body positioning and support provided from other limbs influenced the amount of protraction or retraction exhibited by a limb during a galloping gait.

It was also found that GRF increases continuously as speed increases (Demes et al. 1994), which is in line with the subsequent findings of Patel and Wunderlich (2010). The joint and limb angles of vervet and squirrel monkey trailing and leading fore- and hindlimbs were not found to consistently change when the speed of terrestrial locomotion increased (Vilensky et al. 1990). In contrast to this, the results of Patel and Wunderlich (2010) and Patel (2010) show that as speed increases in an olive baboon, a terrestrial quadruped, the hand position became more palmigrade-like. It is therefore suggested that locomotor flexibility between degrees of terrestrial and arboreal locomotion may affect the musculoskeletal limb morphology of primates and subsequently how it responds to an increase in external stresses.

There are a variety of potential hand postures that can be used by primates during locomotion. The hand can be in either a vertical or horizontal orientation, this is assessed based on the position of the palm in relation to the substrate or superstrate (Schmitt et al. 2016). Suspension is classed as a vertical hand posture as the digits are loaded but the palm is not, and may not be in contact with the superstrate, which contrasts the horizontal hand position used in vertical climbing (Schmitt et al. 2016). The hook grip (as illustrated in Alexander, 1994), where the thumb is in line with the rest of the digits, is generally used during arboreal suspension (Schmitt et al. 2016). Combining kinematic analysis with pressure data in my study will allow the examination of hand position in relation to loading during arboreal suspensory locomotion in humans.

Arboreal human locomotion, in particular suspensory locomotion, has not been studied as extensively as that of primates. The majority of studies focus on rock climbing (MacLeod et al. 2007; Mermier et al. 1997; Quaine et al. 2003), although there are a few more recent studies that examine human tree climbing (Kraft et al. 2014; Venkataraman et al. 2013). Much of the rock climbing literature focuses on energy expended by the body in relation to climbing difficulty (Mermier et al. 1997; Sheel et al. 2003; Watts and Drobish, 1998). Some studies examine grip force and finger strength but do so in a non-climbing environment and often do not take into account factors such as body mass (MacLeod et al. 2007; Quaine et al. 2003). Whilst for the most part rock climbing is near vertical, the hand and foot positions in relation to the climbing substrate generally differ from those observed in primate arboreal locomotion (see Figure 1 in Sylvester et al. 2006, and Figures 1-3 in Isler, 2004). Therefore, rock climbing can provide some information on non-terrestrial human locomotion, it cannot be considered a proxy for true arboreal locomotion. Analysis of tree climbing in modern human populations questions the locomotor assumptions that can be drawn from comparative skeletal analysis only, as distal tibia morphology in the human range was found to allow ankle flexion to a similar degree to chimpanzees (Kraft et al. 2014; Venkataraman et al. 2013). Therefore, further studies examining human soft tissue, as well as bone, and the forces it is subjected to during arboreal locomotion is needed to provide further insight into the relationship between human anatomy and locomotion category.

As arboreal locomotion, in particular suspension, on a specific built apparatus has not been previously investigated in humans it is difficult to directly compare some of the primate studies to the studies of human arboreal locomotion. In order to make inferences about the locomotor capabilities of fossil hominins, comparison is needed between humans and primates. Therefore, data on human suspension in conditions that are more similar, or identical, to those of the primate studies (e.g. Samuel et al. 2018) is needed to allow conclusions to be drawn on how hand morphology is related to function. My study replicates the equipment set up of Samuel et al. (2018), and the largest diameter used (105mm) is comparable to the diameter size (120mm) that the bonobos were suspending on in Samuel et al's. (2018) study. Substrate size has been shown to affect joint and body positioning in primate locomotion, although only above substrate quadrupedal locomotion was investigated (Schmitt, 2003), and previous ergonomic literature has also highlighted the effects of diameter size on hand pressure (e.g. Seo and Armstrong, 2008; Seo et al. 2007). This indicates that the effects of diameter size on human suspension warrant further research. My study will also allow investigation of the effects on normalised peak pressure when the participant's body mass is either static below the hand or moves beneath the hand during suspension. Patel and Wunderlich (2010) and Patel (2010) suggest that the positioning of the hand can act to mediate the stresses experienced during locomotion. Using kinematic and pressure mapping methods I will examine how hand position, particularly in relation to thumb position, affects normalised peak pressure and the location of peak pressure in human hands across a range of diameters.

1.8. *Hypotheses*

Based on the reviewed literature, I hypothesise that, 1) there will be no difference in normalised peak pressure between the thumb adducted and thumb abducted positions, but thumb positioning may affect the location of peak pressure; 2) normalised peak pressure will be higher during dynamic compared to static suspension across all diameter superstrates; 3) there will be a significant difference in normalised peak pressure between the three diameters; 4) there will be a significant difference in the location of peak pressure across all diameter superstrates, with the peak pressure occurring more often at the distal phalanges as the diameter increases (based on Seo and Armstrong, 2008); 5) the location of peak pressure in the human hand will be comparable to that of bonobos when engaging in suspension using the same relative diameter (i.e. 105mm compared to 120mm).

2. Methods

2.1. *Participants*

Participants were adult male and female volunteers (age range: 24-42 years) from the School of Sports and Exercise Sciences and the School of Anthropology and Conservation at the University of Kent. The sample used in the current analysis consists of six healthy adult individuals (three males and three females) with no known hand injuries or orthopedic impairments within the last year. Data on eight additional individuals was also collected (five males and three females). Only the data on their diameter preference is presented here. Ethics and risk assessment approval was obtained from the University of Kent before data collection took place. Each participant signed an informed consent form before participating.

2.2. *Climbing equipment*

A custom built climbing apparatus was designed in conjunction with, and built by, Sports Equip (http://www.sportsequip.co.uk). It consisted of a vertical climbing pole with footrests, and a suspension pole which was attached perpendicular to the support for the vertical climbing pole (see Figure 2). The suspension pole was set at a height of 2.1m above the ground. This height allowed the participant's entire body to be off the ground by only 5-10cm during the suspensory activities, thus minimizing the risk of injury if a participant was to fall off the suspension pole. Risk of injury was further minimized by using exercise padding underneath each pole. The vertical climbing section of the apparatus was not used for this study.

The equipment was made of metal to provide the required stability and coated in a matt finish to minimize reflections from the metal which could interfere with the motion capture cameras. Sandbags were then placed on top of the base plates and against each of the upright poles in order to further secure the apparatus when in use. The horizontal suspension pole was square with a 2.5 x 2.5cm box section to prevent the diameters rotating when they were grasped during the suspension activities. Three different-diameter sleeves were made of plywood by the University of Kent's School of Architecture with a square-centre that would allow the sleeve to slide onto the horizontal pole box section. Each sleeve was 300mm in length and was coated with a layer of matt grey paint to minimize any reflections that may interfere with the motion capture cameras.

Figure 2: Suspension apparatus set up. Red rectangle: horizontal suspension pole where the suspension activities took place.

Review of the ergonomic literature highlighted that the interaction between the human hand and the substrate varies with different diameters (Seo and Armstrong, 2008; Seo et al. 2007). Therefore, three cylindrical sleeves with diameters of 45mm, 80mm, and 105mm were created from plywood. The sleeves were fitted onto the horizontal bar (see red box in Figure 2) which had a square cross-section with sides of 2.5cm. This was the smallest possible bar that could be used whilst supporting human body mass. The smallest diameter of sleeve that could be used (45mm) was therefore limited by the cross sectional area of the horizontal pole. The 45mm diameter sleeve was close in size to the optimal handle diameter (30-40mm) for the human hand (Edgren et al. 2004; Hall, 1997; Kong and Lowe, 2005; Seo and Armstrong 2008), whilst still maintaining the structural stability of the apparatus. The 105mm diameter sleeve represented the equivalent diameter (120mm) that was used in the bonobo pressure experiments by Samuel et al. (2018), after accounting for variation in bonobo vs. human overall hand size (see Alba et al. 2003 for skeletal comparisons; soft tissue human data: this study; soft tissue bonobo data: J. Neufuss, unpublished). The 80mm diameter was chosen as an intermediate diameter size. Two shorter, 100mm, length sleeves with diameters of 45mm were also created and functioned as additional handholds, for the non-dominant hand, either end of the main diameter sleeve when on the suspension pole.

The equipment replicates the suspensory conditions of the bonobo experiment by Samuel et al. (2018). This is in order to facilitate comparison between humans and great apes, which will allow a more in depth understanding of how morphology is related to function. This is particularly important when making inferences about the locomotor behavioural capabilities of fossil hominins.

2.3. *Pressure*

A Novel ® S2119 pressure mat (Novel GmbH, Munich, Germany) was used to measure hand pressure on each of the diameters. The pressure mat had a rubber coating which allowed it to remain flexible enough to wrap around the different diameters, whilst also enhancing the durability of the pressure mat. The mat has a total of 512 sensors, each 1 x 1 cm, arranged in 16 rows and 32 columns. The pressure mat was connected to a Pliance ®-xf-32 analyser box

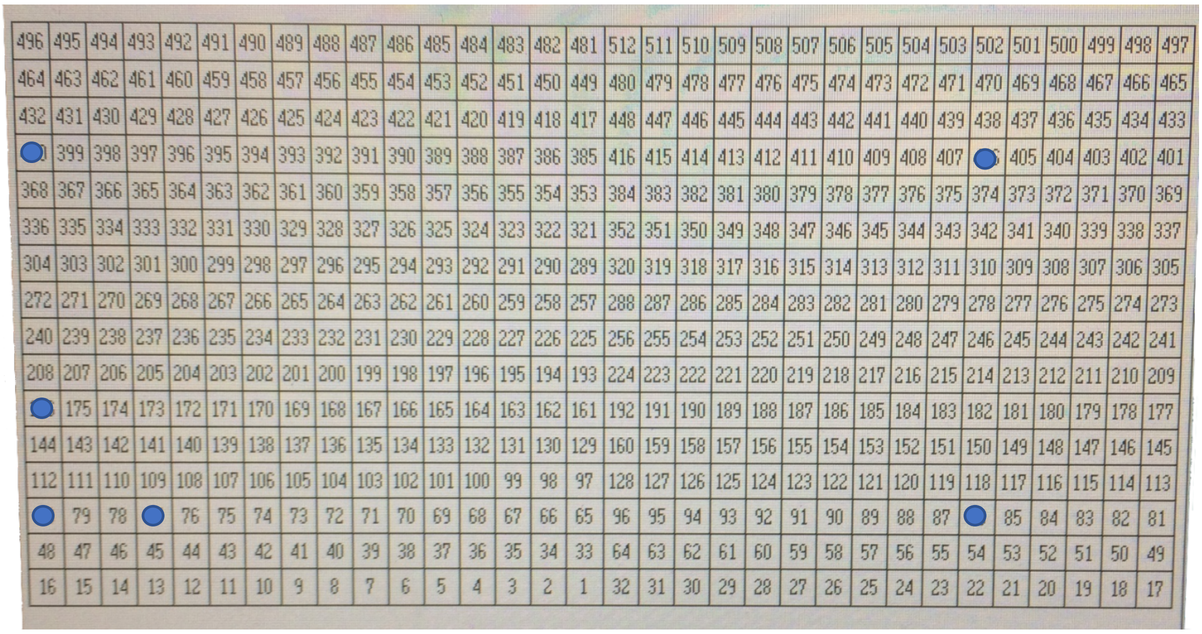
(Novel, GmbH, Munich, Germany), which was connected to a charged battery pack, and the data collection rate was set at 35Hz. The data collected were sent using the wireless sync boxes, via bluetooth, to a computer which ran the Pliance ®-xf-32 Recorder software (version 24.3.5; Novel, GmbH, Munich, Germany). The Pedar side wireless sync box was connected to the Pliance ®-xf-32 analyser box via a thin fiber optic cable. The Operator side wireless sync box was connected to the Qualisys (Qualisys AB, Goteburg, Sweden) motion capture system, which used Oqus cameras (Qualisys AB, Goteburg, Sweden), via a BCN adapted cable. The pressure mat calibration range was set at 15-600kPa. This setting was chosen, from the available calibration ranges, based on the body mass ranges for human adult males and females in relation to estimated hand size. Pilot data showed that the 15-600kPa calibration range encompassed the range of pressure values produced by humans in static and dynamic activities.

The width of the pressure mat (rows 1-16) was wrapped around the diameter of the 45mm diameter. It was wrapped lengthways (columns 1-32) for both the 80mm and 105mm diameters, to maximize the sensors surface available for grasping. There was some overlap in the pressure mat when it was wrapped lengthways around the 80mm diameter. This overlap started at column 27 and therefore any trials with pressure data in column 27 at peak pressure on the 80mm diameter were excluded from analysis. In some trials noise occurred alongside the pressure data. Noise is classified as low level activation of the pressure sensors that is not directly underneath the hand when the activity is being carried out. The pressure mat was zeroed before each trial to ensure that each trial had the same baseline, thus enabling the trials to be compared to each other.

The pressure mat was attached to the pole using Velcro ®. This allowed the pressure mat to be attached to the diameter without moving during the trials on one diameter, and then removed and replaced when the diameter was changed over.

It should be noted that the thickness of the pressure mat (4mm) and Velcro ® (5mm) added an additional 18mm to the diameter. However, the pressure mat was pliable and therefore deformed slightly underneath the hand when the participant engaged in suspension. It was not possible to measure the exact diameter under each region of the hand during each of the suspensory activities. Therefore, the known and non-deformable diameter measurements of 45mm, 80mm, and 105mm are used but it is acknowledged that the final diameter sizes are larger than this.

Six 4mm retroreflective markers were placed on the edges and corners of the mat to allow mapping of the markers on the hand to the location of the pressure mat and its sensors in subsequent analysis. The exact pressure sensor locations of the markers for each of the diameters were noted, for use during the mapping stage of the analysis. Each of the diameters had a specific pressure mat marker combination due to the different sizes of the diameters (see Figures 3a-c). For the 45mm diameter the markers were placed on the pressure mat sensors 80, 176, 400, 77, 86, and 406. For the 80mm diameter the markers were placed on the pressure mat sensors 489, 486, 506, 393, 9, and 26. For the 105mm diameter the markers were placed on the pressure mat sensors 487, 484, 499, 391, 7, and 19.



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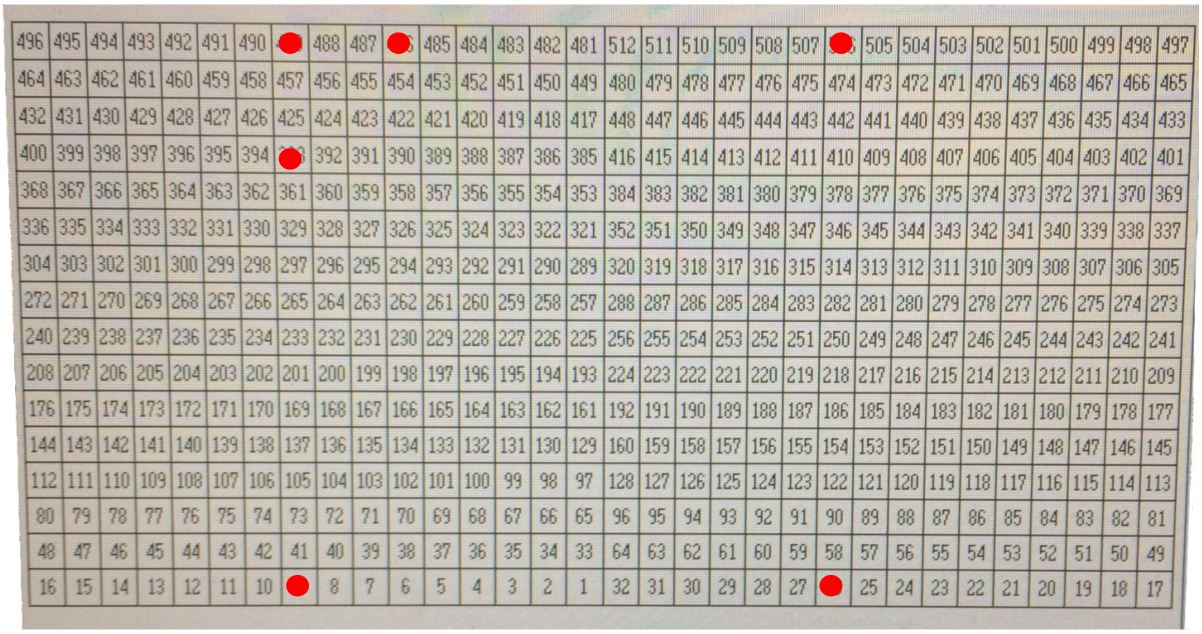
3a)



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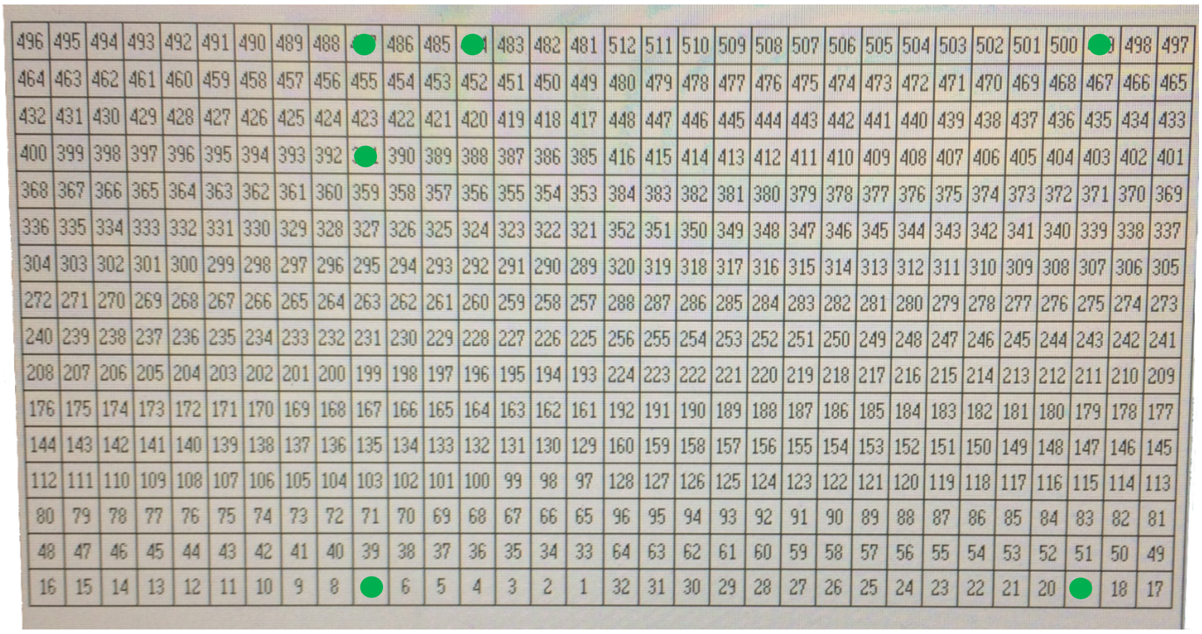
3b)



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3c)

Figure 3a: 45mm diameter pressure mat marker positions. 3b: 80mm diameter pressure mat marker positions. 3c: 105mm diameter pressure mat marker positions.

2.4. *Kinematic*

A Qualisys (Qualisys AB, Goteburg, Sweden) motion capture system consisting of eleven Oqus cameras (Qualisys AB, Goteburg, Sweden) was used to capture kinematic data on the hand position during each trial, and Qualisys Track Manager (version 2.15; Qualisys AB, Goteburg, Sweden) was used to label and automatically track the markers. All of the eleven cameras were placed in a circle around the suspension pole. Five of the cameras were attached to a runner on the ceiling and the six remaining cameras were put on tripods and set at different heights. The cameras were positioned so that at least three of the cameras could see each of the markers when the participant's hand was on the diameter (see Figure 4). All unwanted reflections were either masked in Qualisys Track Manager or were covered with non-retroreflective material. The cameras were then focused until the climbing apparatus could be clearly seen and the system was then calibrated to an acceptable level for the camera positions used (average residuals less than 1.25 and standard deviation less than 1.75mm). The calibration wand length used was 501.5mm. The calibration frame was placed on a raised platform so that it was visible to all eleven cameras and close to the area where the suspension activities would take place.

Figure 4: Qualisys motion capture system with Oqus cameras and suspension apparatus set up.

Twenty 4mm retroreflective markers were positioned on the hand to define the first and third digits, and the wrist (Figure 5). Single markers were used to define hand areas where the joints had only one degree of freedom, whereas triads of markers were used to define areas of the hand where the joints had more than one degree of freedom. The markers were attached to the participant's hand using small squares of double-sided tape.

The markers labelled t1-8 were used to define the thumb. Single markers were placed at the head and base of the distal first phalanx, whereas triads of markers were used to define the proximal first phalanx and the first metacarpal. Markers labelled m1-9 were used to define the third ray. Single markers were placed at the head and base of the distal, intermediate, and proximal phalanges of the third digit, the head and base of the third metacarpal, and the head of the fourth metacarpal. It was found that when placed directly on the metacarpal heads, the markers moved distally when the digits were fully flexed, so the markers for the head sections of the third and fourth metacarpals were placed just behind the metacarpal heads. This meant that when the participants flexed their digits fully that the markers did not move with skin as it moved over the metacarpal heads. Markers labelled f1-3 were used to define the wrist. Single markers were placed on the radial and ulnar heads, and just proximal to the ulnar styloid process. See Figure 5 for details. The participant’s hand was palpated in order to find the bony land marks. Previous studies of the thumb have found the effects of skin movement on marker position to be negligible (Kuo et al. 2002).

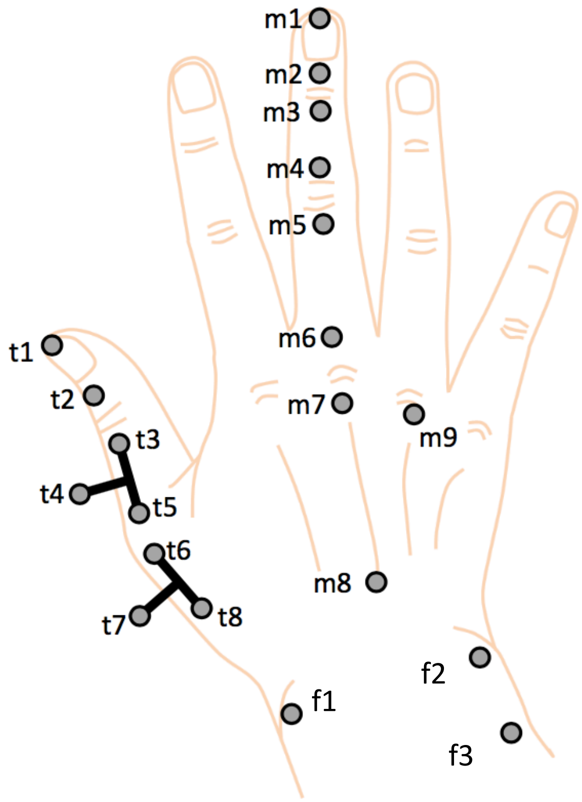


Figure 5: Marker placement on the first and third digits. Image courtesy of Dr Szu-Ching Lu.

Qualisys was set to automatically stop fifteen seconds after starting. This was deemed a suitable length of time as, once started, each activity lasted for approximately five seconds. Both the Novel Pliance and the Qualisys systems were synced together to allow the peak pressure frame to be matched to the correct corresponding Qualisys frame. Both programmes started at the same time, Qualisys automatically ran for fifteen seconds and Pliance was manually stopped as close to fifteen seconds as possible. This allowed the position of the hand to be determined in relation to the location of peak pressure. Qualisys ran at a frequency of 105Hz and Pliance ran at a frequency of 35Hz. Therefore, the frame ratio between Qualisys and Pliance was 3:1.

2.5. *Biometric data*

Participants provided age, sex, dominant hand, height, and body mass data. Body mass was taken from a set of scales whilst the participant was wearing shoes (because shoes were worn during the experiment). Height was measured without shoes. Hand length was measured using ImageJ (Version 2.0.0-rc-43/1.51o, Schindelin et al. 2015) on a digital scan (with a 10cm scale) of the palmar surface, from the tip of the third ray to the wrist crease. Palm width was also measured as the widest distance across the heads of the second to fifth metacarpals.

The circumference of each diameter was then calculated as a percentage of the participant's hand length using the "normalized handle size" equation in Kong and Lowe (2005: 499). This was also carried out for a separate sample of sixteen adult bonobo individuals (J. Neufuss, unpublished). An adult bonobo was defined as an individual that was fifteen or more years old, in accordance with the methodology of Enomoto (1990) and Idani (1990). As these were a separate sample to the bonobos in the study by Samuel et al. (2018), the mean hand length was calculated. The circumference of the 120mm diameter superstrate used in Samuel et al's. (2018) study was then compared to the mean bonobo hand length, and the results of which were compared to those calculated for my 105mm diameter human sample.

2.6. *Experiment*

Three activity categories were tested; static hanging with the thumb adducted, static hanging with thumb abducted, and dynamic suspension in which the individual could grasp the superstrate anyway they wanted from the previous two thumb position categories. Both thumb adducted and thumb abducted are classed as unimanual forelimb-suspension, and dynamic suspension is classed as forelimb-swing using the standardised postural and locomotor modes of Hunt et al. (1996). In order to maximise the potential for natural movement each participant was given the same instructions on how to position their hand, either with the thumb adducted or abducted but they were allowed to position their thumb comfortably within each scenario. Participants were all given the same instructions on how to perform the dynamic suspension activity but they were allowed to choose how to position their thumb from the previous categories (adducted or abducted) for the dynamic suspension trail. The participant's thumb position was recorded after each dynamic suspension trail. Each activity was tested on one diameter before the pressure mat was removed and the diameter changed over. The retroreflective markers on the pressure mat were then rearranged for the new diameter, the pressure mat was attached to the new diameter, and all three activity categories were tested again. This was repeated until all three of the diameters had been tested. The three diameters were tested in a randomised order for each participant.

2.6.1. Static thumb adducted and abducted suspension

In the static thumb adducted or abducted suspension (unimanual forelimb-suspension) the participant stood beneath the diameter on the suspension pole, facing along the pole, and positioned their dominant hand a distance from the diameter. The participant then placed their hand between the markers that defined the edges of the pressure mat, with their thumb either in adducted (next to the index finger, see Figure 6) or abducted (away from the index finger, but not in opposition to the fingers, see Figure 7) position. They then lifted their feet off the ground and suspended their body mass from their hand for around five seconds, or for less time if they felt their body rotating beneath the superstrate. For the thumb abducted posture, it was not always possible to fit the entire hand with the thumb abducted onto the pressure mat in participants with larger hands. In these cases, trials for the palm and thumb were taken separately. The differences in normalised peak pressure between the trials with the hand partially on the pressure mat and the hand fully on the pressure mat were later assessed via a Mann-Whitney U test to assess a significant difference between them.

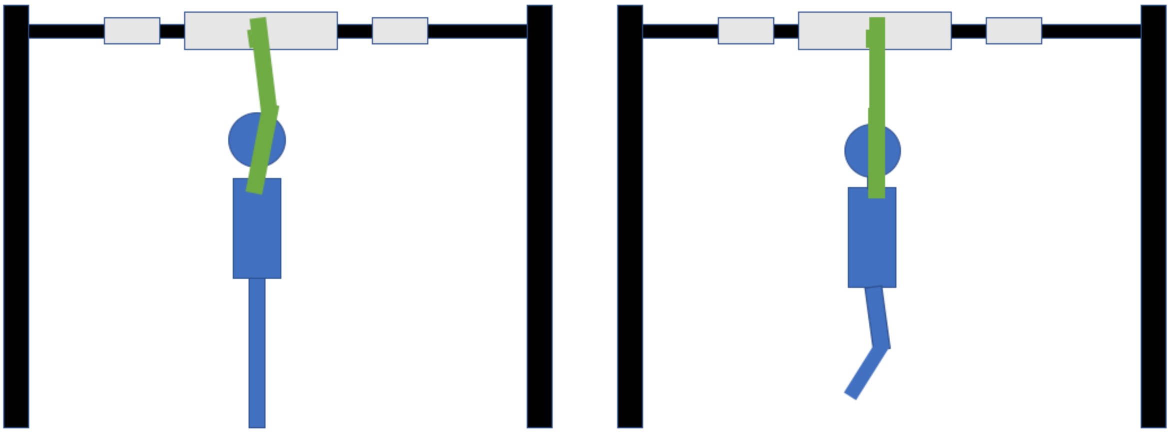


Figure 6: An approximation of the static thumb adducted experiment. Green arm: dominant arm.

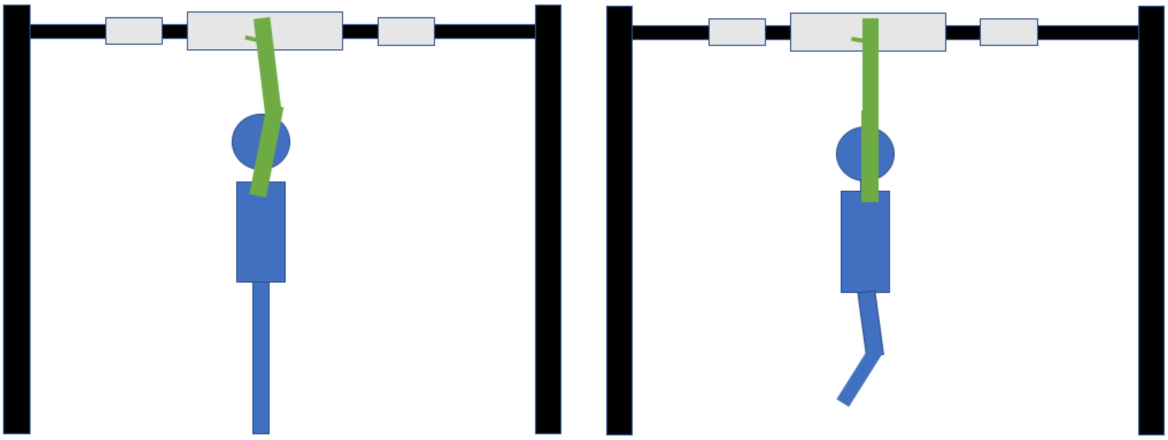


Figure 7: An approximation of the static thumb abducted experiment. Green arm: dominant arm.

2.6.2. Dynamic suspension

The dynamic suspension (forelimb swing) activity was carried out by the participant standing underneath the diameter and facing along the suspension pole, with their dominant hand held a distance from the diameter. Qualisys and Pliance were started together. The participant placed their dominant hand on the pressure mat, using any hand grip they preferred, lifted their feet off the floor. They then swung themselves longitudinally along the pole to grasp the end of the suspension pole with their non-dominant hand. They then released the diameter with the pressure mat and lowered their feet to the floor. (See Figure 8).

Multiple trials (at least N = 3) of each of the activities were taken to ensure at least one usable pressure and kinematic pairing for analysis for each of the activities on each of the diameters. All three activities were run on one diameter before the pressure mat was removed, the diameter taken off the suspension pole and replaced by the next diameter for testing, the pressure mat markers positioned for the new diameter, the pressure mat wrapped around the new diameter and the three activities run again. The activities were run in the order: static thumb adducted, static thumb abducted, and dynamic suspension. After all the trials for all three diameters had been run, the participant was then asked to state their preference of diameter from most preferred to least preferred.

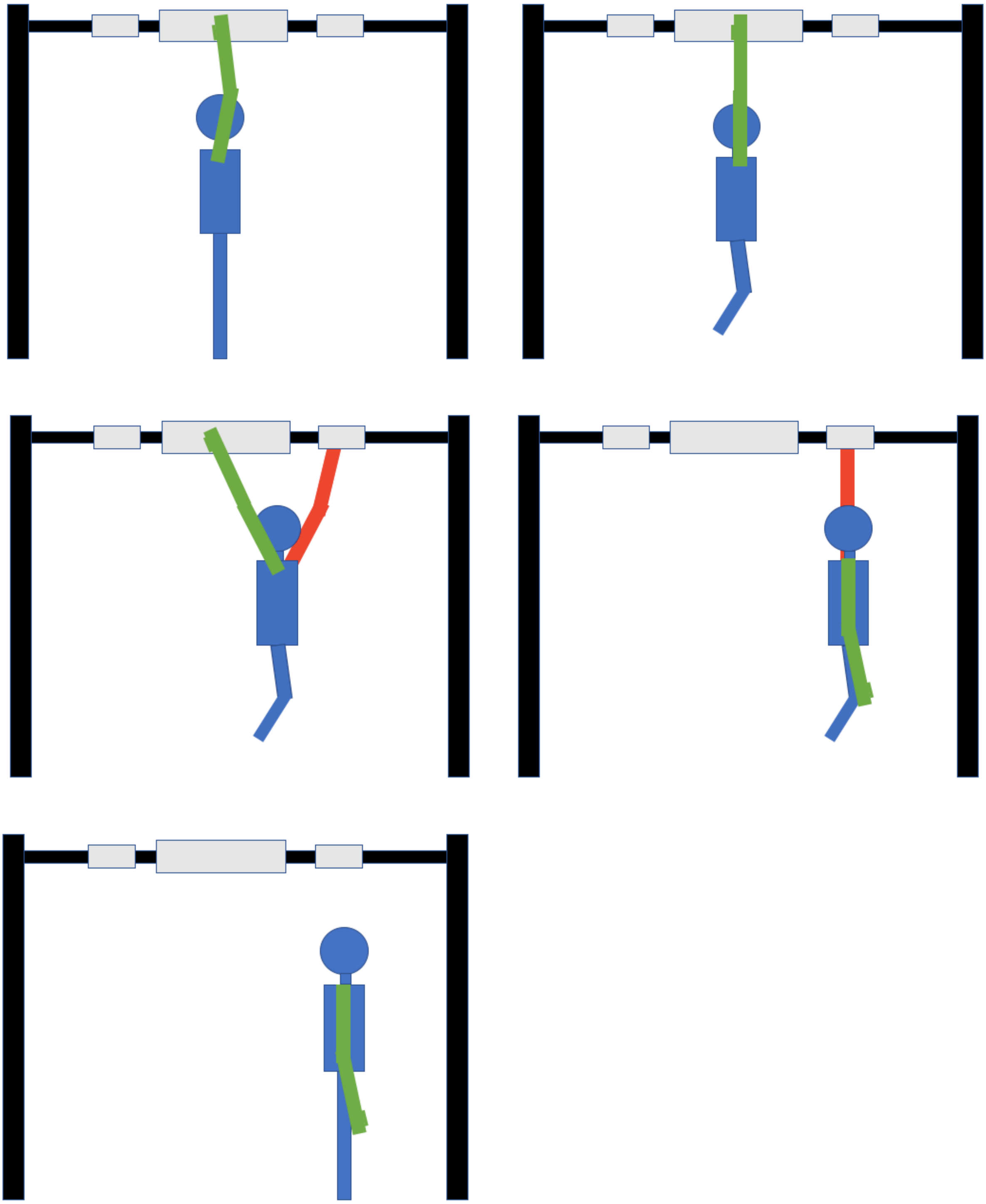


Figure 8: An approximation of the dynamic suspension experiment. Thumb here is shown in the adducted position. Green arm: dominant arm. Red arm: non-dominant arm.

2.7. *Data processing*

Kinematic data files were processed in Qualisys Track Manager. Gap filled trajectories that were automatically produced by Qualisys were removed and only measured trajectories were analysed. This was to prevent any assumptions about the path of the markers during each trial. Markers were processed for the section of the trial where the hand approached the pressure mat, the duration of the activity, and then just as the hand left the pressure mat. No filters were applied during the data collection and data processing for both the pressure and kinematic data files. No filters were used during the mapping section of the analysis using the 3D-to-2D mapping programme developed by Dr Szu-Ching Lu (see Figure 9).

A Qualisys file was classed as usable if a minimum of the markers used for the circle fitting component of the mapping process (see below), were present and markers t1-3, t5-6, t8, m1-9, and f1-3 were present at the Qualisys frames corresponding to the peak pressure frames in Pliance. Once a Qualisys file was completely processed it was exported to a .mat file for further analysis in MATLAB R2016a (Mathworks Inc, Natick MA).

Pressure data was assessed in Pliance-x-32 (Novel, GmbH, Munich, Germany). A pressure file was classed as usable in the cases of thumb adducted and dynamic suspension with thumb adducted if the whole area of registered pressure was clearly inside the edges of the mat, or it was just on the mat edge with predominantly low pressure values (around the 15-60kPa range) along the section that was on the mat edge. In the cases of thumb abducted and dynamic suspension with thumb abducted a pressure file was considered usable if the whole area of pressure was clearly inside the edges of the mat. In the cases where the participant's hand was too big to completely fit on the mat when the thumb was abducted, if the palm or thumb was clearly within the edges of the mat or if the palm or thumb were just on the edge of the mat and those sensors showed mainly low pressure values (around the 15-60kPa range), then the pressure file was considered usable. The usable pressure files were then exported to ASCII files for further analysis in MATLAB R2016a.

2.8. *Mapping kinematic data to pressure data*

MATLAB R2016a (Mathworks Inc, Natick MA) was used to run the 3D-to-2D mapping programme developed by Dr Szu-Ching Lu (see Figure 9). The .mat kinematic file and the corresponding ASCII pressure file were imported into the 3D-to-2D mapping programme. A circle fitting of the pressure mat to the kinematic markers allowed the spread of the sensors along the diameter to be calculated, as well as assessing the position of the first and third digits in relation to the edges of the pressure mat. The markers are then mapped to the closest corresponding sensor to their X, Y, Z coordinates. This produces a pressure-kinematic data map and allows the location of peak pressure to be assessed in relation to the position of the first and third digits and the wrist.

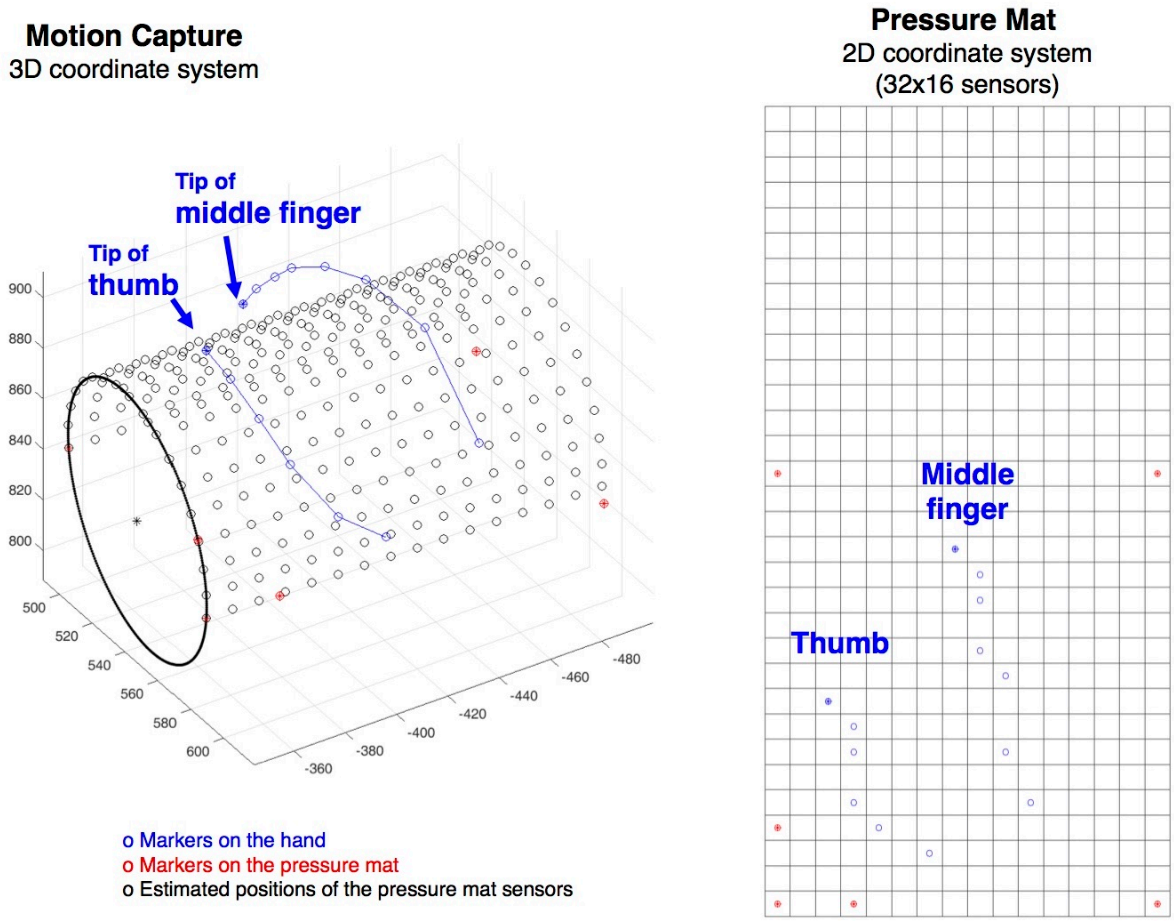


Figure 9: Mapping of 3D kinematic data to 2D pressure data using the 3D-to-2D mapping programme developed by Dr Szu-Ching Lu. Image courtesy of Dr Szu-Ching Lu.

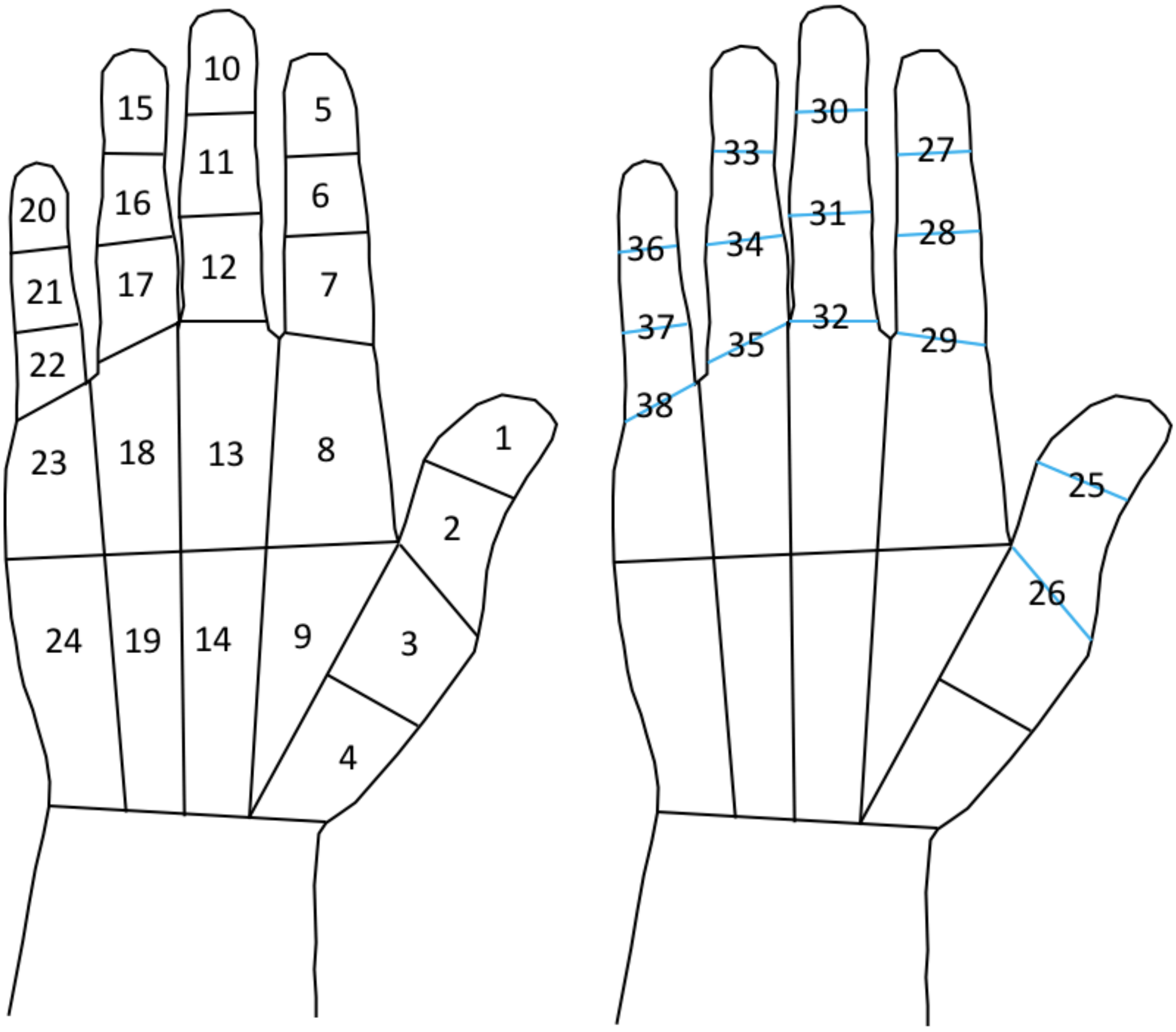
2.9. *Validation of 3D-to-2D mapping method*

The position of the retroreflective markers on the pressure mat may have also introduced some error into the mapping analysis, as the markers were required to be placed at the exact centre of the sensors on the pressure mat. The positioning of these markers was visually assessed. Due to the rubber coating on the pressure mat it was difficult to identify the exact centre of each sensor with certainty. The diameter of the makers was smaller than the width and length of the pressure sensors, therefore pressing down on a centrally or off-centre positioned marker had the same effect of activating the pressure sensor. The results of the circle fitting component of the 3D-to-2D mapping programme showed that higher levels of error were observed in the position of the markers on the pressure mat at the opposite end of the diameter to those used for the circle fitting. The greatest error was seen on the 45mm diameter, followed by the 80mm and then the 105mm diameters. In order to assess the level of accuracy of the 3D-to-2D mapping programme a validation test was carried out on each of the three diameters.

The full marker set was applied to the participant's hand. The participant then lightly placed their hand on the diameter, with their feet on the floor, and pressed down the distal phalanges of the first-fifth digits in sequential order. The resulting kinematic and pressure files were then mapped to each other. The results showed that for all of the diameters, the markers on the first and third digits on the hand corresponded to the relevant activated pressure sensors, and the activated pressure sensors for the remaining digits corresponded to logical positions in relation to the markers on the third and first digits of the hand. This demonstrated that the 3D-to-2D mapping programme worked to an acceptable level of accuracy.

2.10. *Location identification*

The methodology developed by Borel et al. (2016) was adapted to identify the location of peak pressure for each of the mapped trials. The hand was divided into anatomical segments and each segment was assigned a number (see Figures 7a-b, and Table 1). Digits were separated into distal, intermediate, and proximal phalanges, and the palm was divided into the heads and bases of the first-through-fifth metacarpals. The MCP, PIP, DIP, and IP joints for each ray were also assigned a number. In a few of the trials multiple locations of peak pressure were observed, as well as peak pressure occurring in the middle of the metacarpal. In these cases, a new number was assigned for each new combination and location.



10a) 10b)

Figure 10a: Anatomical hand segments used for mapping the location of peak pressure. Right hand, palmar side. 10b: Joints used for mapping the location of peak pressure. Right hand, palmar side.

Table 1: Numeric codes for the location of peak pressure.

Code number	Anatomical location
1	DP1
2	PP1
3	MC1 head
4	MC1 base
5	DP2
6	IP2
7	PP2
8	MC2 head
9	MC2 base
10	DP3
11	IP3
12	PP3
13	MC3 head
14	MC3 base
15	DP4
16	IP4
17	PP4
18	MC4 head
19	MC4 base
20	DP5
21	IP5
22	PP5
23	MC5 head
24	MC5 base
25	IP1 joint
26	MCP1 joint
27	DIP2 joint
28	PIP2 joint
29	MCP2 joint
30	DIP3 joint
31	PIP3 joint
32	MCP3 joint
33	DIP4 joint
34	PIP4 joint
35	MCP4 joint
36	DIP5 joint
37	PIP5 joint
38	MCP5 joint
Multiple locations and mid-metacarpal locations	
39	MC1 head and MC1 base (thenar region)
40	IP2 and PIP2 joint
41	PP3 and DP3
42	PP4 and MC3 head
43	Middle of MC2
44	PP4, PP3, and DP3

45	Middle of MC3
46	MC2 base and Middle of MC2
47	DP2 and IP3
48	PP5, IP4, and MC4 head

In the 3D-to-2D mapping programme output (see Figure 11) each marker that was directly attached to the hand (see Figure 5) was shown as a red circle with a line joining them to the next marker for that digit. Markers t4, t7, and f1-3 (see Figure 5) were not shown as they were not directly on the hand or were positioned on the wrist where no pressure was observed. If peak pressure occurred directly under a marker it was assigned to the number for the corresponding anatomical location. If peak pressure did not occur under a marker the anatomical location of peak pressure was estimated from the location of the markers and the area experiencing pressure for that frame. If the head and base markers for the third metacarpal spanned four sensors, then the top two sensors were assigned to the metacarpal head and the bottom two sensors assigned to the metacarpal base. If the head and base markers for the third metacarpal spanned five sensors then the top two sensors were assigned to the metacarpal head and the bottom two sensors assigned to the metacarpal base, but the middle (third from top and bottom) sensor was categorised as the middle of the third metacarpal. The length of the second, fourth, and fifth metacarpals was estimated in relation to the length of the third metacarpal and the same four square, or five square, rules were applied accordingly.

If peak pressure occurred on a sensor that did not have a marker but was between two separate anatomical segments with markers, it was classified as a joint and given the corresponding code. Joints of the digits without markers were estimated from the joint positions of the digits with markers. There were some slightly ambiguous cases, often around the MC1 head, MCP1 joint, and PP1 area, where it was unsure if the peak pressure sensor was at the metacarpal head, proximal phalanx, or respective joint. Where markers were present, if the line connecting the two separate anatomical segments (e.g. head of the first metacarpal and proximal phalanx of the first digit) crossed over the peak pressure sensor then it was classified as the relevant joint. If not, it was classified as the nearest anatomical segment (e.g. metacarpal head or proximal phalanx). See Figure 11 for an example of 3D-to-2D mapping programme output.

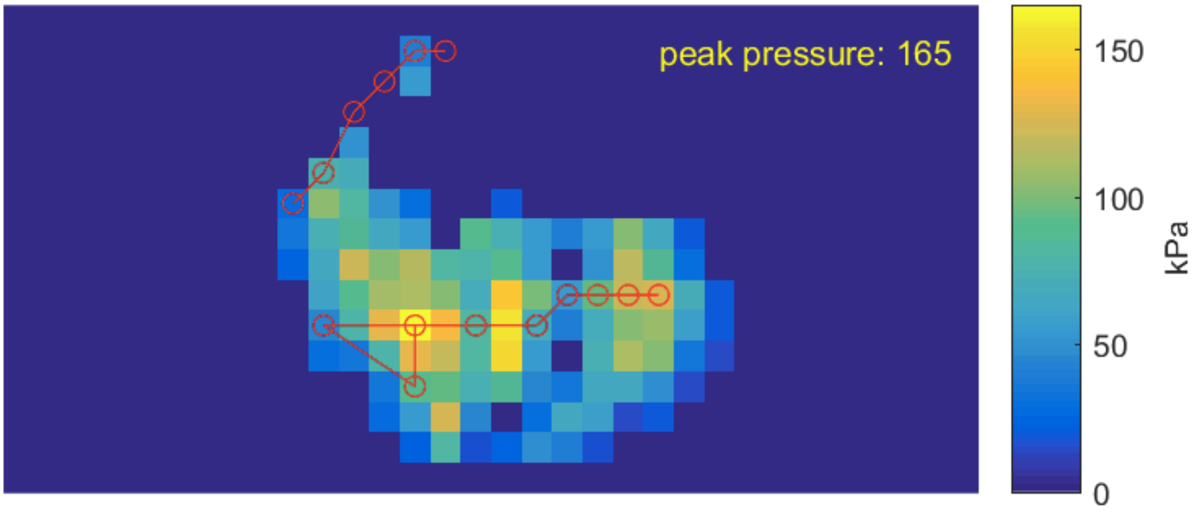


Figure 11: 3D-to-2D mapping output for 80mm diameter with thumb abducted (static). Marker arrangement as shown in Figure 5 (t4, t7, and f1-3 not shown). Peak pressure is located at 13 (MC3 head).

2.11. *Interobserver error*

A sample of 11% of the trials from across the three diameters and the three activities was used to test for interobserver error in peak pressure location identification. The peak pressure locations were assigned by a second observer (T. Kivell) and the results compared to the original peak pressure location identifications.

2.12. *Statistics and normalization*

Data was entered into and statistics run in IBM SPSS Statistics, (version 24.0; IBM Corp., Armonk, N.Y., USA), with statistical significance set at $p = 0.05$ (two-tailed).

As the entire body mass was suspended below the hand during each of the activities, and pressure is the result of force over area, peak pressure was therefore required to be normalised to control for the effects of body mass and participant hand area. The relationship between body mass (kg) and hand area (mm^2) was examined using Pearson's correlation and a non-significant positive correlation was found ($N = 6$, $r = 0.599$, $p = 0.209$). The spread of the data points and $R^2 = 0.358$ indicated that both body mass and hand area were necessary to control for via normalisation. Peak pressure was normalised by dividing it by the value of participant estimated hand area divided by body mass using the calculation: peak pressure kPa/ [(3rd digit length mm x palm width mm)/body mass kg]. Hand area was estimated for each subject by multiplying the length of the third digit by the palm width. This does assume that the participant's hand is rectangular in shape, but it allows for a rough estimate of contact area. Mean, standard deviation, and maximum and minimum values were calculated for both peak pressure and normalised peak pressure using all 189 trials for all 6 participants (see Tables 4 and 5).

A Shapiro-Wilk test was used to determine the normality of the data. The data was deemed to be not normally distributed and therefore non-parametric tests were used. Due to hand sizes in relation to mat width some trials where the thumb was abducted resulted in part of the hand being over the edge of the mat. A Mann-Whitney U test was used to determine if there was a significant difference in normalised peak pressure for all 189 trials from 6 subjects. The result was non-significant ($U = 1399.000$, $p = 0.526$) and therefore all trials were used for further analysis. The number of usable trials per activity-diameter combination varied for each participant. The mean normalised peak pressure value for each diameter-activity combination for each participant was therefore calculated in order to reduce the issue of pseudoreplication. This gave a total of 54 values, with 9 values per participant. These values were then used for the subsequent analyses involving normalized peak pressure. Unless mentioned otherwise, all further usage of normalized peak pressure refers to the mean values calculated for each participant for each diameter-activity combination.

Wilcoxon Signed Rank tests with Bonferroni correction were used to examine the differences in normalised peak pressure between the thumb adducted and thumb abducted activities for each of the diameters using the normalised peak pressure values for each of the participants. Where no difference was found, a static value was calculated by taking the mean normalized peak pressure values of the two static categories (thumb adducted and thumb abducted) for each diameter. This was calculated using the previous per participant, per activity-diameter means. A Wilcoxon Signed Rank test with Bonferroni correction was also used to investigate the differences between static and dynamic suspension.

As a result of the prior analysis, a Friedman's test was used to test for differences in normalised peak pressure between the diameters when all the activity categories were combined. In order to deal with issues of pseudoreplication due to multiple data points per participant, the mean normalised peak pressure value of all three activity categories for each participant for each diameter was calculated using the previous per participant, per activity-diameter means, and used for this specific analysis. Further Friedman's tests with Bonferroni corrections were used to examine the differences in normalised peak pressure between each of the activities categories within a diameter, and between the diameters for each of the activity categories. Dunn’s post-hoc analysis with Bonferroni corrections were used when significant differences occurred. The values used were the normalised peak pressure values for each of the participants. The effects of activity and diameter on the location of peak pressure were analysed using a multinomial logistic regression which was performed using ‘mlogit’ in Stata 15 (StataCorp, 2017). It must be noted that it was not possible to include random effects (participant ID) in this analysis and therefore there is the issue of pseudoreplication. It was also not possible to change the base outcome setting for each test. This must be taken into account when examining the results of the multinomical logistic regression and should be addressed in future research. The mode location of peak pressure for each activity-diameter combination was noted.

To examine diameter preference, data for eight additional participants were included (N = 14). Binomial tests with a Bonferroni correction were used to examine the differences in diameter preference for the first, second, and third preferences. The binomial tests were performed in VassarStats (Lowry, 2018: http://vassarstats.net). The relationship between the circumference of the diameter and the length of a participant’s hand was investigated by calculating the circumference as a percentage of the participant’s hand length. The circumference for each diameter was calculated by multiplying the diameter by π (rounded to 3.142). This method was also applied to the bonobo hand measurements (J. Neufuss, unpublished) and 120mm superstrate diameter (Samuel et al. 2018). A mean hand length value was calculated for the bonobo adults, as the hand length data (J. Neufuss, unpublished) is from a different sample to that used by Samuel et al. (2018). Based on methodology of Idani (1990) and Enomoto (1990), bonobos were classed as adults if they were fifteen or more years old.

3. Results

The sample consisted of six individuals (three males and three females) and the participant biometric data are presented in Table 2.

Table 2: Participant sex, body mass (kg), height (cm), and hand length (mm) (n=6 individuals).

Participant	**Sex**	**Body mass (kg)**	**Height (cm)**	**Hand length (mm)**
A	Male	84.0	178.0	193.8
B	Female	57.0	170.0	184.2
C	Female	69.0	172.5	178.8
D	Male	69.0	183.0	199.1
E	Male	72.0	175.0	190.5
F	Female	66.5	160.0	173.9

3.1.*Hand length and diameter*

The circumference of each diameter was calculated as a percentage of a participant's hand length. The mean, standard deviation, and maximum and minimum values are presented in Table 3 for both humans and bonobos.

Table 3: Circumference as a percentage of hand length, mean, standard deviation, maximum, and minimum values.

Human					
Diameter (mm)	**Circumference (mm)**	**Mean ‘circumference as a % of hand length’ ***	**Standard deviation**	**Maximum value**	**Minimum value**
45	141	76.3	3.6	81.3	71.0
80	251	133.5	5.7	144.5	126.3
105	330	177.4	7.6	189.7	165.7
Bonobo +					
Diameter (mm)	**Circumference (mm)**	**Circumference as a % of hand length ***			
120	377	173.9			

* Circumference as a percentage of hand length is calculated using the “normalized handle size” equation in Kong and Lowe (2005:499).

\+ Bonobo hand size data were provided by J. Neufuss (unpublished). Mean bonobo hand length was used for the circumference as a percentage of hand length calculation as the bonobo sample was different from that used in Samuel et al. (2018).

3.2. *Normalised peak pressure within diameter*

The mean, standard deviation, and maximum and minimum values for both peak pressure and normalised peak pressure for all 6 participants using all 189 trials were calculated and the results presented in Tables 4 and 5.

Table 4: Peak pressure mean, standard deviation, maximum and minimum values (N = 6 individuals, all 189 trials).

Diameter (mm)	Activity	Mean peak pressure (kPa)	Standard deviation	Maximum value (kPa)	Minimum value (kPa)
45	Thumb adducted	297.4	62.2	400.0	215.0
	Thumb abducted	355.9	74.3	537.5	280.0
	Dynamic suspension	309.8	98.2	527.5	180.0
80	Thumb adducted	236.2	45.2	330.0	152.5
	Thumb abducted	229.0	50.8	307.5	145.0
	Dynamic suspension	238.6	54.4	320.0	142.5
105	Thumb adducted	208.4	32.0	280.0	155.0
	Thumb abducted	207.9	53.1	347.5	145.0
	Dynamic suspension	239.6	75.4	370.0	142.5

Table 5: Normalised peak pressure mean, standard deviation, maximum and minimum values (N = 6 individuals, all 189 trials).

Diameter (mm)	Activity	Mean normalised peak pressure	Standard deviation	Maximum value	Minimum value
45	Thumb adducted	1.3	0.3	1.9	0.8
	Thumb abducted	1.5	0.4	2.6	1.1
	Dynamic suspension	1.4	0.5	2.5	0.8
80	Thumb adducted	1.0	0.2	1.3	0.6
	Thumb abducted	1.0	0.3	1.5	0.6
	Dynamic suspension	1.0	0.3	1.5	0.6
105	Thumb adducted	0.9	0.2	1.2	0.6
	Thumb abducted	0.9	0.2	1.3	0.5
	Dynamic suspension	1.0	0.3	1.5	0.5

In order to address issues of pseudoreplication a mean value for each participant for each activity-diameter combination was calculated and used for the subsequent analyses. The mean, standard deviation, and maximum and minimum values for both peak pressure and normalised peak pressure were calculated using these values for all 6 participants (54 trials total) were calculated and the results presented in Tables 6 and 7.

Table 6: Peak pressure mean, standard deviation, maximum and minimum values (N = 6 individuals, 54 trials). The calculations in this table use the mean value for each participant for each activity-diameter combination.

Diameter (mm)	**Activity**	**Mean peak pressure (kPa) (using per participant, per activity-diameter combination mean)**	**Standard deviation**	**Maximum value (kPa)**	**Minimum value (kPa)**
45	Thumb adducted	303.8	63.3	376.7	234.4
	Thumb abducted	357.9	73.5	486.7	282.5
	Dynamic suspension	312.0	97.5	481.9	228.0
80	Thumb adducted	228.1	40.6	298.8	193.1
	Thumb abducted	227.3	47.7	283.3	163.8
	Dynamic suspension	233.2	58.7	285.0	145.0
105	Thumb adducted	219.8	35.9	280.0	172.5
	Thumb abducted	212.2	61.0	325.8	153.1
	Dynamic suspension	224.2	59.9	326.4	153.1

Table 7: Normalised peak pressure mean, standard deviation, maximum and minimum values (N = 6 individuals, 54 trials). The calculations in this table use the mean value for each participant for each activity-diameter combination.

Diameter (mm)	Activity	Mean normalised peak pressure (using per participant, per activity-diameter combination mean)	Standard deviation	Maximum value	Minimum value
45	Thumb adducted	1.3	0.3	1.8	0.9
	Thumb abducted	1.5	0.4	2.3	1.1
	Dynamic suspension	1.3	0.5	2.3	1.0
80	Thumb adducted	1.0	0.2	1.2	0.7
	Thumb abducted	1.0	0.2	1.4	0.7
	Dynamic suspension	1.0	0.3	1.3	0.7
105	Thumb adducted	0.9	0.2	1.1	0.7
	Thumb abducted	0.9	0.2	1.2	0.6
	Dynamic suspension	1.0	0.3	1.3	0.6

3.2.1. Static thumb adducted vs. thumb abducted suspension

A Wilcoxon Signed Ranks test with Bonferroni correction (N = 6) was performed using the normalized peak pressure values for each participant for each activity-diameter combination. The Bonferroni correction set the significant value at p = 0.017. This showed that there was no difference in the normalised peak pressure for the static thumb adducted and static thumb abducted activities on the 45mm diameter (Z = -2.201, p = 0.028). The median normalised peak pressure value was 1.3 for static thumb adducted and 1.5 for static thumb abducted on the 45mm diameter. There was also no difference on the 80mm (Z = -0.314, p = 0.753) and 105mm (Z = -0.524, p = 0.600) diameters. The median normalised peak pressure values on the 80mm diameter were 0.9 for thumb adducted and 1.0 for thumb abducted. On the 105mm diameter the median normalised peak pressure values were 1.0 for thumb adducted and 0.9 for thumb abducted. All thumb adducted and thumb abducted trials could therefore be combined for comparing the static (thumb adducted and thumb abducted) normalised peak pressure values to the dynamic suspension normalised peak pressure values.

3.2.2. Static vs. dynamic suspension

During static suspension the body mass remains below the hand, but during dynamic suspension the position of the body mass in relation to the hand changes during the swing cycle. Therefore, the normalised peak pressure may differ between the two different relationships of body mass position to hand position. Mean static normalised peak pressure (thumb adducted and thumb abducted) was calculated for each participant on the 45mm, 80mm, and 105mm diameters using the mean values for each activity-diameter combination per participant and compared to the dynamic suspension normalised peak pressure values using Wilcoxon Signed Ranks tests ($N = 6$). A Bonferroni correction set the significance level at $p = 0.017$.

There was no difference observed on the 45mm diameter between the mean static normalised peak pressure and dynamic normalised peak pressure ($Z = -0.524$, $p = 0.600$). The median value for mean static normalised peak pressure was 1.4 and for dynamic normalised peak pressure it was 1.1. No difference was also found between the mean static normalised peak pressure and dynamic normalised peak pressure values for either the 80mm ($Z = -0.524$, $p = 0.600$) or 105mm ($Z = -0.105$, $p = 0.917$) diameters. On the 80mm diameter the median values for mean static normalised peak pressure and dynamic suspension normalised peak pressure were 1.0 and 1.1 respectively. On the 105mm diameter the median value for mean static normalised peak pressure was 1.0 and for dynamic suspension normalised peak pressure it was 1.0.

3.2.3 Normalised peak pressure between diameters with activities combined.

As no difference was found between the normalized peak pressure values for the thumb adducted-thumb abducted analysis, and for the static-dynamic analysis, on any of the diameters all activity categories were combined to examine the differences in normalised peak pressure between all three diameters. Issues of pseudoreplication were dealt with by taking the mean normalised peak pressure value of all three activity categories for each participant for each diameter. A Friedman's test (N = 6) was used to examine the differences in normalized peak pressure across all three diameters with the activity categories combined. The results of this analysis show that there is a significant difference (X^2 (2) = 9.333, p = 0.009) in the normalised peak pressure across all three diameters with the activity categories combined.

Dunn's post-hoc test with a Bonferroni correction showed that there was a significant difference in the combined activity mean normalised peak pressure between the 105mm and 45mm diameters (p = 0.012). The 45mm diameter had a greater combined activity mean normalised peak pressure value compared to the 105mm diameter (see Table 8). No difference was found between the 45mm and 80mm, and the 80mm and 105mm diameters.

As a result of these differences further analysis was carried out to explore the potential sources for this difference (activity category or diameter size).

Table 8: Normalised peak pressure mean, standard deviation, maximum and minimum values (N = 6). The calculations in this table use combined activity mean based on the mean value for each participant for each activity-diameter combination.

Diameter (mm)	**Mean normalised peak pressure (using combined activity mean based on per participant, per activity-diameter combination mean)**	**Standard deviation**	**Maximum value**	**Minimum value**
45	1.4	0.4	2.1	1.0
80	1.0	0.2	1.3	0.7
105	0.9	0.2	1.1	0.6

3.2.4. Differences in normalised peak pressure between activities and within diameters

Each of the different activities, thumb adducted, thumb abducted, and dynamic suspension, has a different relationship between the hand position and the positioning of body mass.

A Friedman's test (N = 6) with Bonferroni correction was used to examine the differences in normalised peak pressure between the three different activities (thumb adducted, thumb abducted, and dynamic suspension) on each of the three different diameters. The Bonferroni correction set the significance value at $p = 0.017$. The mean normalized peak pressure values for each participant for each activity-diameter combination were used.

There was no difference in normalised peak pressure between the three activities on the 45mm diameter, X^2 (2) = 6.333, $p = 0.042$. On the 80mm diameter there was no difference in normalised peak pressure between the three activities, X^2 (2) = 0.000, $p = 1.000$. There was also no difference in normalised peak pressure between the three activities on the 105mm diameter, X^2 (2) = 0.609, $p = 0.738$. Whilst there was no difference the 45mm had larger mean values, calculated using the mean normalized peak pressure values for each participant for each activity-diameter combination, compared to the other two diameter sizes. On the 45mm diameter the mean normalised peak pressure values were: 1.3 thumb adducted, 1.5 for thumb abducted, and 1.3 for dynamic suspension. On the 80mm diameter the mean normalised peak pressure values were 1.0 for all three activity categories. On the 105mm diameter the mean normalised peak pressure values were 0.9 for both the thumb adducted and thumb abducted activity categories, and 1.0 for the dynamic suspension activity category. See Table 7 for standard deviation, maximum, and minimum values.

3.3. Normalised peak pressure within activity

Friedman's tests (N = 6) with Bonferroni correction were performed in order to examine the differences in normalised peak pressure across all three of the diameters (45mm, 80mm, and 105mm) for each of the three activity categories. The Bonferroni correction set the significance value to p = 0.017. A Dunn's pairwise post-hoc test with Bonferroni correction was performed where required. The mean normalized peak pressure values for each participant for each activity-diameter combination were used.

3.3.1 Thumb adducted

The results a Friedman's test (N = 6) for thumb adducted showed that there was a significant difference in the normalised peak pressure across the three diameters, X^2 (2) = 9.333, p = 0.009. When a Bonferroni correction was applied the result remained significant. Dunn's post-hoc tests with Bonferroni correction showed that there was a significant difference in normalised peak pressure values within the thumb adducted activity between the 45mm and 105mm diameters (p = 0.012). There was no difference in the normalised peak pressure values for thumb adducted between the 45mm and 80mm, and the 80mm and 105mm diameters. The 45mm diameter had the greatest mean normalised peak pressure value, which was calculated using the mean normalized peak pressure values for each participant for each activity-diameter combination. The mean value for the 45mm diameter was 1.3. For the 80mm and 105mm diameters it was 1.0 and 0.9 respectively. Standard deviation, maximum, and minimum values are provided in Table 7.

3.3.2. Thumb abducted

Using a Friedman's test (N = 6) for thumb abducted it was demonstrated that there was a significant difference in the normalised peak pressure across the three diameters, X^2 (2) = 9.333, p = 0.009. When a Bonferroni correction was applied the result remained significant. Dunn's post-hoc tests with Bonferroni correction showed that there was only a significant difference in normalised peak pressure values within the thumb abducted activity between the 45mm and 105mm diameters (p = 0.012). There was no difference in the normalised peak pressure values for thumb abducted between the 45mm and 80mm, and the 80mm and 105mm diameters respectively. The greatest mean normalised peak pressure value, calculated using the mean normalized peak pressure values for each participant for each activity-diameter combination, was found on the 45mm diameter. The mean values for the thumb abducted activity were 1.5 for the 45mm diameter, 1.0 for the 80mm diameter, and 0.9 for the 105mm diameter. See Table 7 for the standard deviation, maximum, and minimum values.

3.3.3. Dynamic suspension

A Friedman's test (N = 6) showed that there was no difference in the normalised peak pressure between the three diameters (45mm, 80mm, and 105mm) for the dynamic suspension activity, X^2 (2) = 5.333, p = 0.069. Using the mean normalized peak pressure values for each participant for each activity-diameter combination, a mean value was calculated for each of the three diameters in the dynamic suspension activity category. The mean value for the 45mm diameter was 1.3. On the 80mm and 105mm diameters it was 1.0. Table 7 provides the standard deviation, alongside maximum and minimum values.

3.4. Location

Location of peak pressure for each trial was assessed using the mapping coordinates.

3.4.1. Interobserver error

Peak pressure location was assigned by a second observer for a sample of 11% of the total trials in order to test for interobserver error. The majority of trials (about 90%) were in agreement. However, trials where the location of peak pressure was slightly ambiguous between the base or middle of the metacarpal required further clarification.

3.4.2. Within diameter and between activities

The peak pressure location results for each of the diameters, clustered by activity category, are shown in Figures 12a-c.

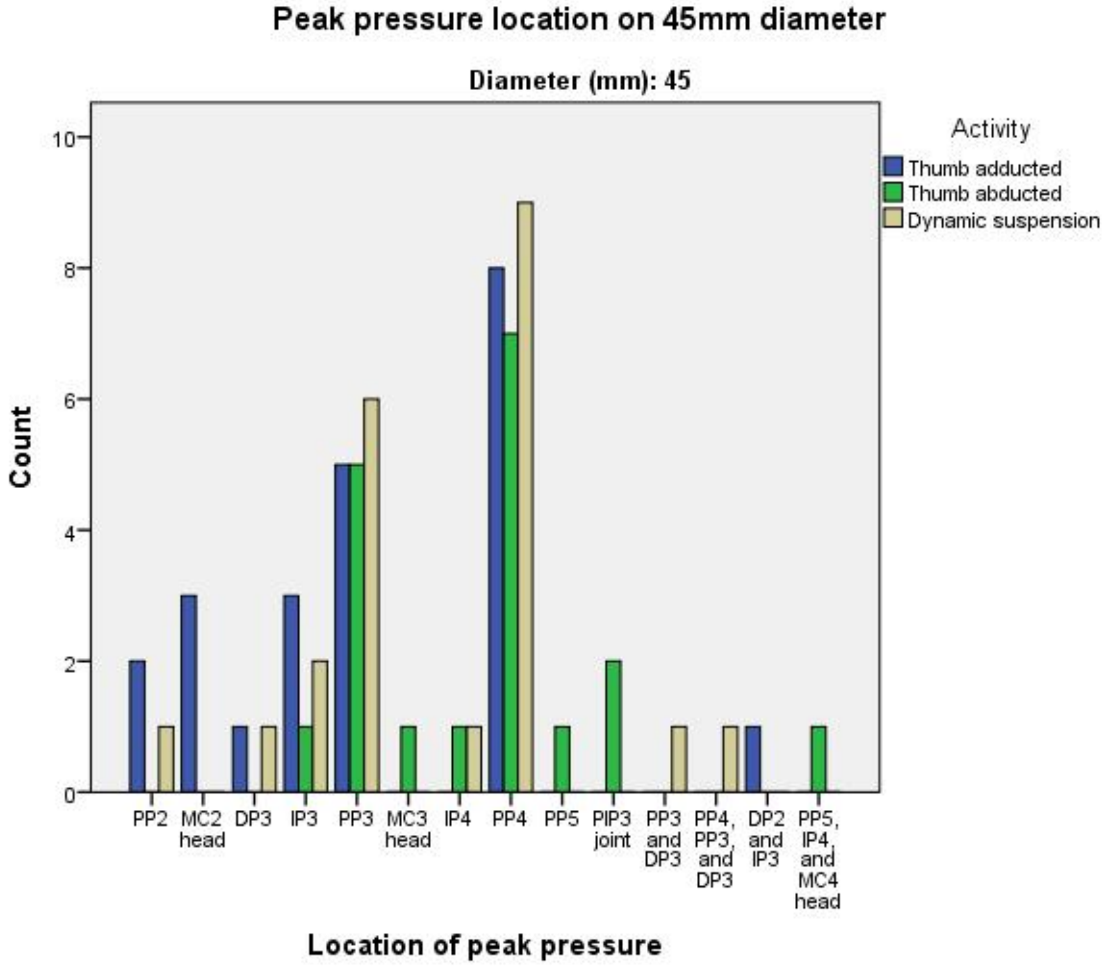


Figure 12a: Peak pressure location by activity on 45mm diameter.

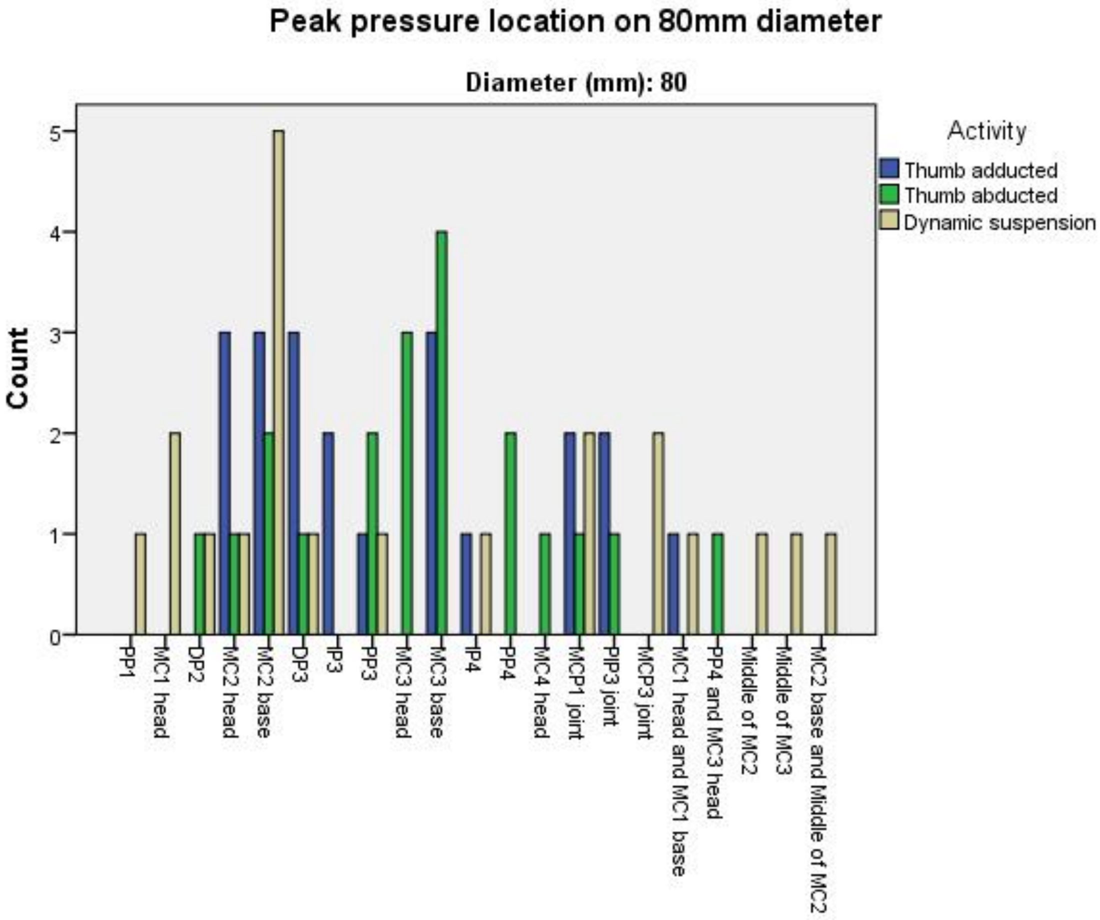


Figure 12b: Peak pressure location by activity on 80mm diameter.

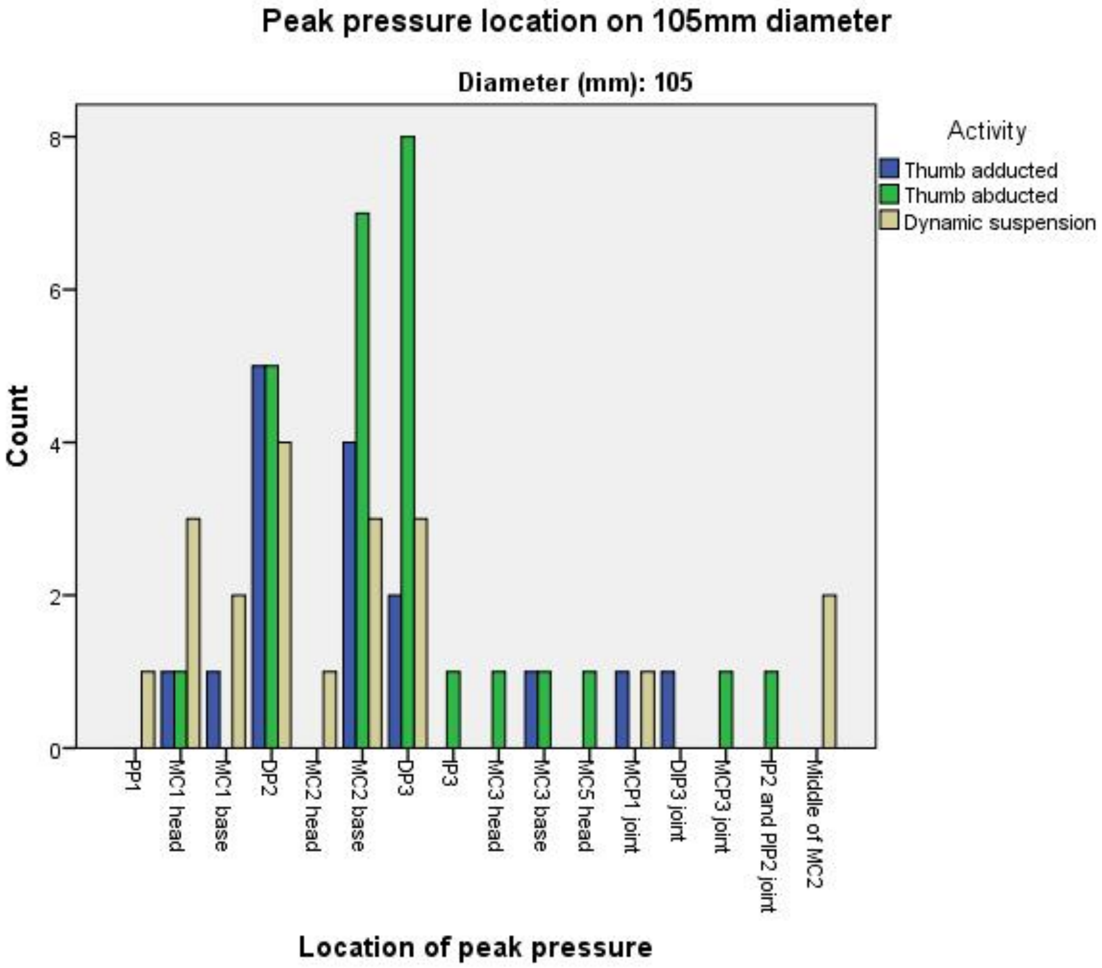


Figure 12c: Peak pressure location by activity on 105mm diameter.

A multinomial logistic regression was run to examine the effect of activity category on location of peak pressure for each of the diameters. It must be noted that it was not possible to include participant number as a random effect and therefore these results must be regarded cautiously due to the potential issue of pseudoreplication via multiple measures per participant, per activity and diameter category. The total number of participants tested was 6 and the total number of trials was 189. It was not possible to change the base outcome setting and therefore the default (mode) was used. This did mean that output data was not provided for the mode location. For the 45mm diameter the base outcome was PP4. For the 80mm diameter it was MC2 base, and for the 105mm diameter it was DP2. On each of the 45mm (N

= 64), 80mm (N = 62), and 105mm (N = 63) diameters no activity category was shown to have a significant effect on location of peak pressure relative to the base outcome.

3.4.3. Within activity and between diameters

Figures 13a-c show the locations of peak pressure for each of the activity categories, with the bars clustered by diameter.

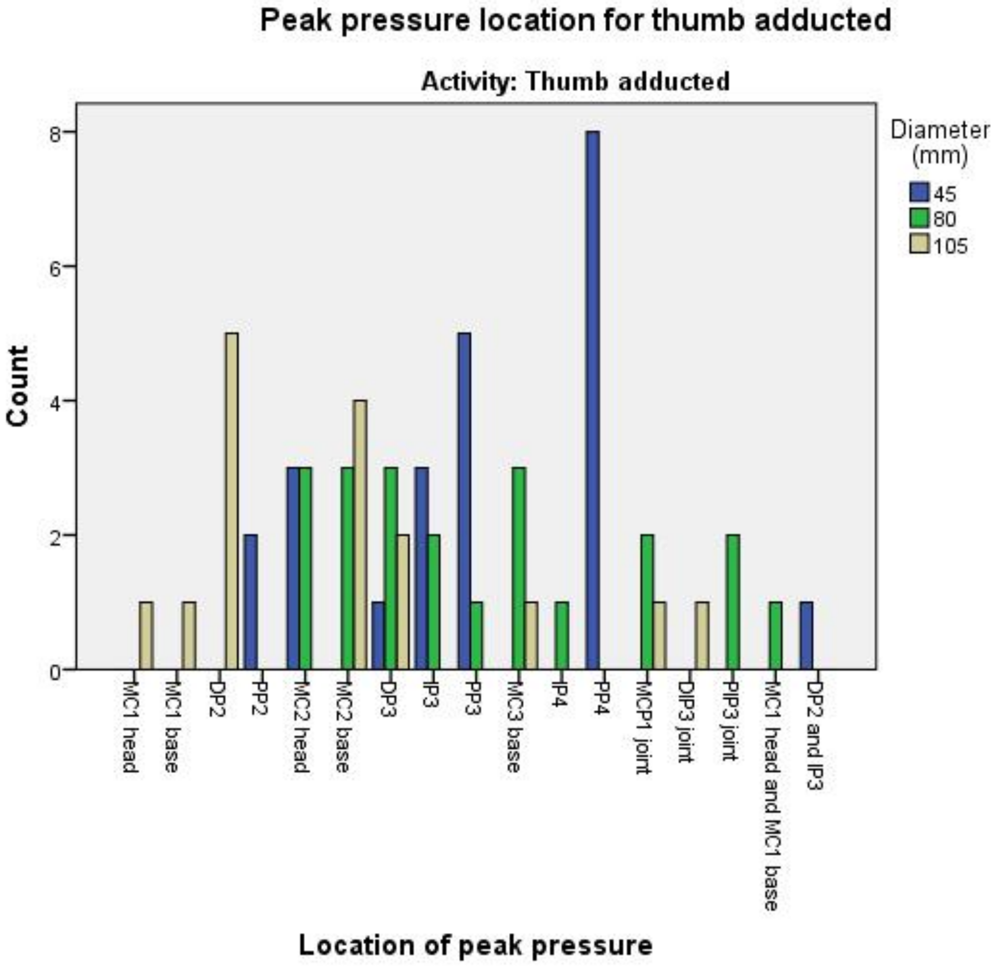


Figure 13a: Peak pressure location for thumb adducted.

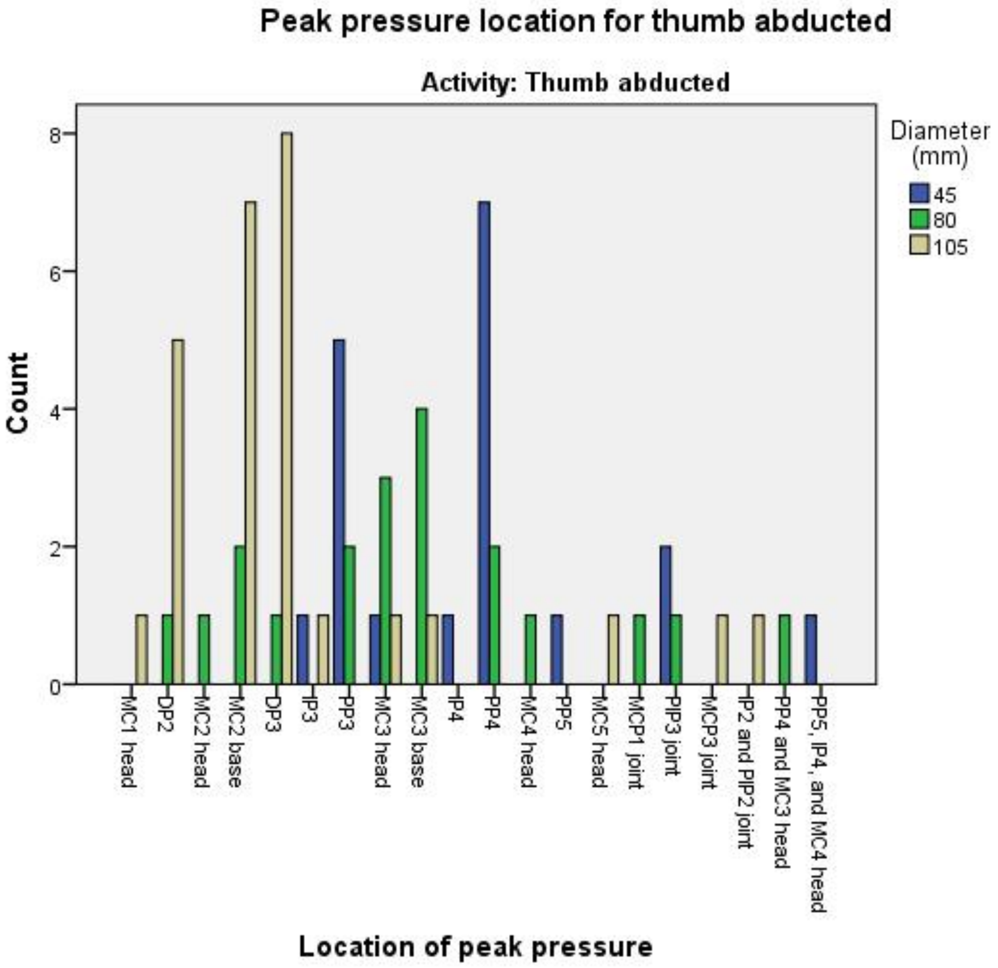


Figure 13b: Peak pressure location for thumb abducted.

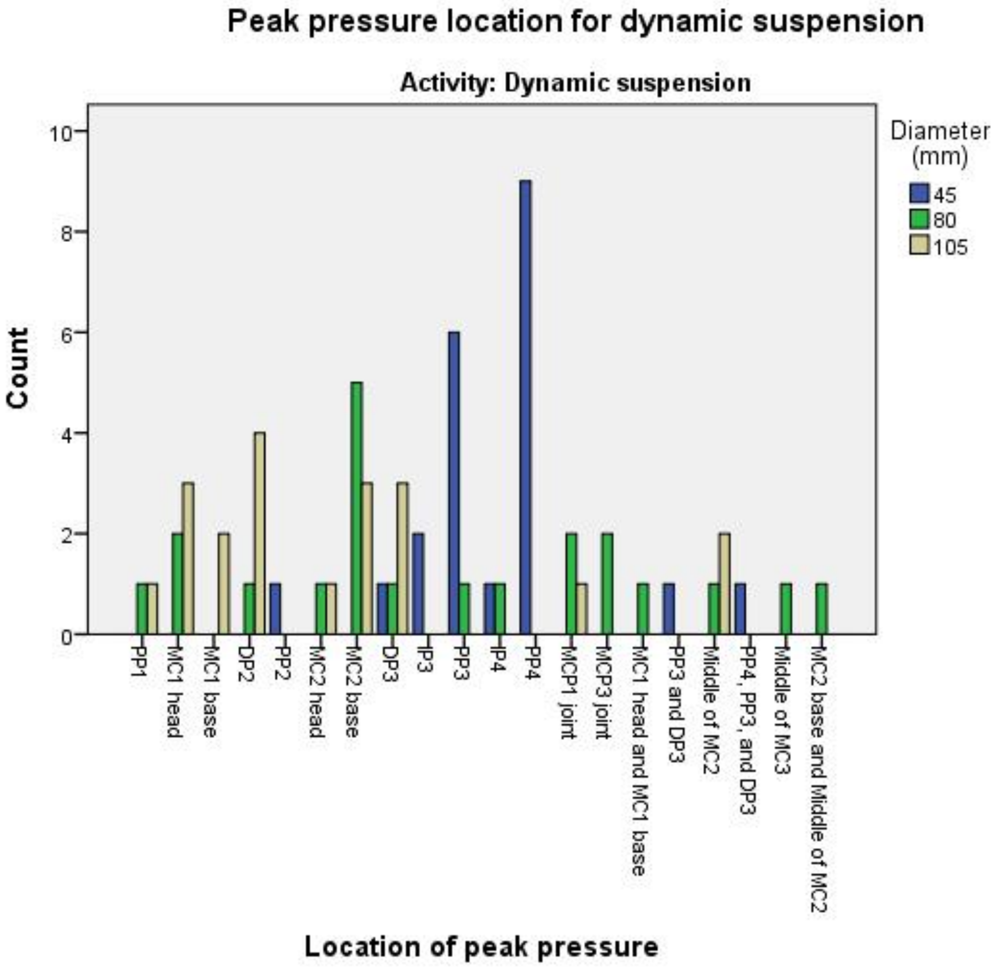


Figure 13c: Peak pressure location for dynamic suspension.

A multinomial logistic regression was run to examine the effect of diameter on location of peak pressure within each of the activity categories. It must be noted that it was not possible to include participant number as a random effect and therefore these results must be regarded cautiously due to the potential issue of pseudoreplication via multiple measures per participant, per activity and diameter category. The total number of participants tested was 6 and the total number of trials was 189. It was not possible to change the base outcome setting and therefore the default (mode) was used. This did mean that output data was not provided for the mode location. For thumb adducted the base outcome was PP4. For thumb abducted it was MC2 base, and for dynamic suspension it was PP4. Diameter was found to have no significant effect on the location of peak pressure relative to the base outcome for the activity categories of thumb adducted ($N = 60$) and dynamic suspension ($N = 63$). In the thumb abducted activity category ($N = 66$) diameter was shown to have a significant effect on location of peak pressure, relative to the base outcome (MC2 base), for the locations: IP3 (coefficient = - 0.129, SE = 0.059, $z = - 2.19$, $p = 0.029$), PP3 (coefficient = - 0.190, SE = 0.053, $z = - 3.59$, $p < 0.001$), MC3 head (coefficient = - 0.118, SE = 0.049, $z = - 2.43$, $p = 0.015$), PP4 (coefficient = - 0.120, SE = 0.053, $z = - 3.77$, $p < 0.001$), and the PIP3 joint (coefficient = - 0.184, SE = 0.058, $z = - 3.16$, $p = 0.002$). This indicates that on the third digit the metacarpal head to the intermediate phalanx, and the proximal phalanx of the fourth digit, are likely significant areas of peak pressure, relative to the base outcome of MC2 base, when the thumb is abducted during static suspension. As the diameter variable increases it is significantly less likely that peak pressure will occur at these locations compared to the base outcome (MC2 base).

3.4.4. Mode locations of peak pressure

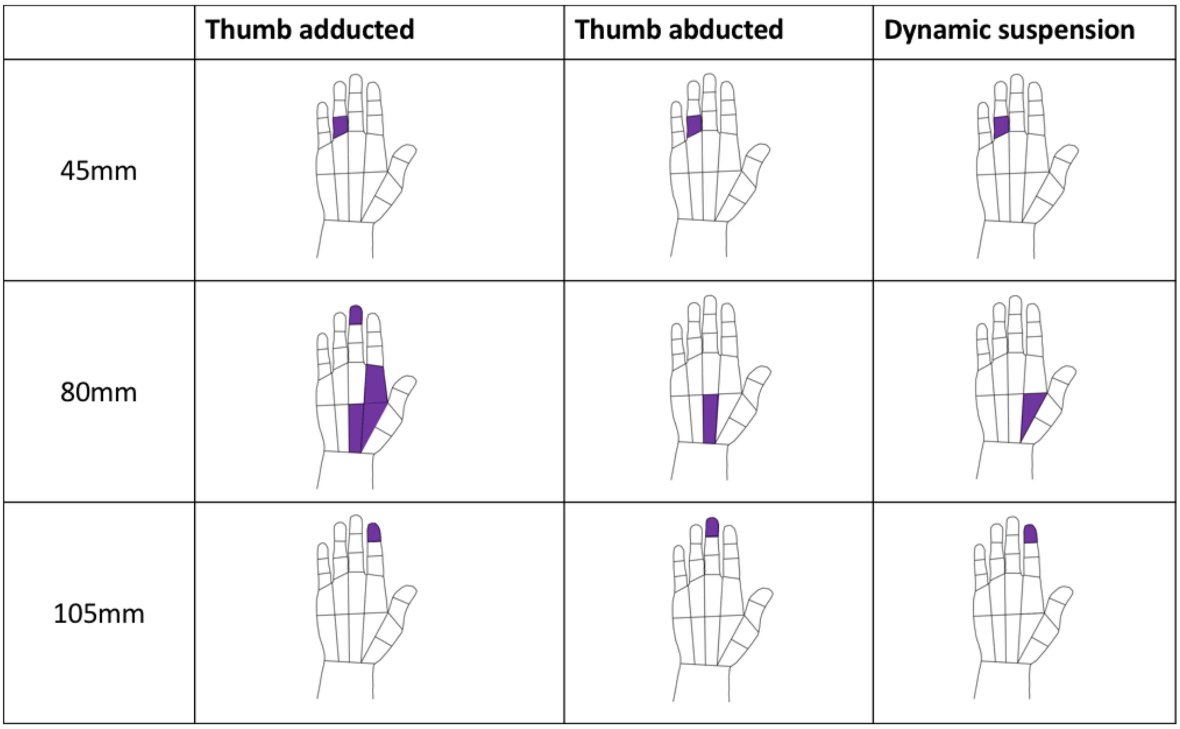


Figure 14: Mode locations of peak pressure. Split by activity category and diameter.

When examining the results of Figures 12a-c and 13a-c it was possible to observe trends in the mode of location of peak pressure for each activity-diameter combination, although this should be interpreted cautiously due to issues of pseudoreplication as all 189 trials for the 6 participants are included. The mode locations are presented in Figure 14. For the thumb adducted activity category the location of peak pressure mode was PP4 for the 445mm diameter. For thumb adducted on the 80mm diameter there were multiple locations with the mode frequency: MC2 base, MC2 head, DP3, and MC3 head. For the thumb adducted category for the 105mm diameter the location mode was DP2. In the thumb abducted activity category the location mode for the 45mm diameter was PP4, for the 80mm diameter it was the MC3 base, and for the 105mm diameter it was DP3. For the dynamic suspension activity category the location mode for the 45mm diameter was PP4, for the 80mm diameter it was the MC2 base, and for the 105mm diameter it was DP2. Whilst no specific statistical tests were used for this section of the analysis it is shown that as the diameter size increased within each of the activity categories there was a pattern in the mode of location of peak pressure, although issues of pseuoreplication should be considered. The location of peak pressure went from being more frequently located more centrally on the hand at the fourth digit on the smallest diameter to being more frequently located at the distal part of the hand on the second and third digits on the largest diameter.

3.5. Diameter preference

Binomial tests with Bonferroni correction were run with data for the current six participants. Data was also included for an additional eight participants giving a final sample size of N=14 for each of the first, second, and third preferences in diameter size categories. All p values reported here are two tailed and test for the significance of getting n or more out of the total sample size.

3.5.1. First preference

Table 9: Frequencies of first preference of diameter size.

	45mm	**80mm**	**105mm**	**Total**
Yes	11	2	1	14

A binomial test with Bonferroni correction showed that the preference for the 45mm diameter was statistically significant ($p = 0.001$) in the first preference of diameter size category. This shows that overall the 45mm diameter was the most preferred diameter size. There was no difference for the frequencies of the 80mm and 105mm diameters.

3.5.2. Second preference

Table 10: Frequencies of second preference of diameter size.

	45mm	**80mm**	**105mm**	**Total**
Yes	3	10	1	14

No difference in preference was found for each diameter for the second preference of diameter size category using a binomial test with Bonferroni correction.

3.5.3. Third preference

Table 11: Frequencies of third preference of diameter size.

	45mm	**80mm**	**105mm**	**Total**
Yes	0	2	12	14

The preference for the 105mm diameter was shown to be statistically significant ($p < 0.001$) in the third preference of diameter size category. This shows that overall the 105mm diameter was the least preferred diameter. There was no difference for the frequencies of the 45mm and 80mm diameters.

4. Discussion

This study's aims were to quantify for the first time pressures experienced by the human hand during suspension and the relationship between the peak pressure and location of peak pressure with variation in the superstrate diameter. This study also investigated variation in pressure experienced by the hand during static suspension, using two different thumb postures, and dynamic suspension.

4.1. *Normalised peak pressure*

I predicted that there would be no difference in normalised peak pressure between the static thumb abducted and thumb adducted suspension within all three diameters. This study found support for this hypothesis in relation to the normalized peak pressure values. There were no significant differences found in normalized peak pressure on the 45mm, the 80mm, and 105mm diameters. This suggests that the thumb position does not affect the amount of pressure experienced by the human hand during suspension once body mass and hand area have been controlled for.

I predicted that normalised peak pressure would be significantly higher during dynamic vs. static suspension. This hypothesis was not supported. Static abducted and adducted thumb postures were combined through calculating their mean, using the values for the mean normalized peak pressure for each participant for each activity and diameter combination, and compared to dynamic suspension. No significant difference was found for any of the three diameters (45mm, 80mm, or 105mm). This suggests that the position of the participant's body mass in relation to the hand, either statically below or moving in a pendulum-like motion below the hand, does not significantly affect the normalised peak pressure values.

Interestingly when all 189 trials were used, as well as when the number of trials per participant per activity-diameter combination was controlled for using means, the thumb abducted value on the 45mm diameter for both peak pressure and normalized peak pressure had a higher mean value than that for dynamic suspension (see Tables 4-7). This was not expected based on the general differences in pressure between static and dynamic activities in previous pressure studies (e.g. Tables 2-4 in Imamura et al. 2002). Contact area for each of the activity categories was not investigated in this study. It therefore may be possible that there was a larger contact area used during the dynamic activity which would result in lower pressure values. Kinematic analysis was only used on the hand and therefore the exact position of the rest of the body relative to the hand was not fully quantified in this study. The participant was also able to choose their preference of hand positioning (thumb adducted or thumb abducted) for the dynamic suspension activity. Therefore, the dynamic suspension category contains both thumb adducted and thumb abducted hand positions. This effect of this was not investigated in the present study. These issues should be fully addressed in future research.

As no differences in normalised peak pressure were found between the activity categories of thumb abducted and thumb adducted, and mean static and dynamic suspension, hypothesis 3 was initially tested using the mean value of the combined activity categories. I predicted that there would be a significant difference in normalised peak pressure between the three diameters. This study found partial support for this hypothesis, as there were statistically significant differences in normalised peak pressure only on the 45mm diameter compared to the 105mm diameter, with the 45mm diameter having a greater mean normalised peak pressure. No significant difference in mean normalised peak pressure was found between the 45mm and 80mm, and the 80mm and 105mm diameters. The 45mm diameter is close to the ergonomically defined optimal diameter of 30-40mm (Edgren et al. 2004; Hall, 1997; Kong and Lowe, 2005; Seo and Armstrong 2008). When the non-deformable diameters are considered, the results of this study therefore suggest that superstrates that are 5mm larger than the maximum optimal diameter in size interact with the human hand in a different way than do those that are 65mm larger than the maximum optimal diameter for the human hand. It should be noted, however, that in the present study the use of the deformable Velcro ® and the pressure mat increased the diameter by 18mm. Therefore the deformable diameter of the smallest diameter tested in this study is larger than the optimal diameter by 23mm. Diameters that are the exact optimal diameter for the human hand, or smaller than, should also be examined in future research in order to further investigate the effect of diameter size on normalised peak pressure.

In order to further investigate the significant difference in mean normalised peak pressure when the activity categories were combined, the activity categories and diameter sizes were separated out and further analysis run using Friedman's tests with Bonferroni corrections. Dunn's post-hoc tests using Bonferroni corrections were also used where appropriate. When differences in normalised peak pressure were examined within each of the diameters and between the activity categories, no difference was found. On the other hand, when differences in normalised peak pressure between the diameters for each of the separate activity categories were examined significant differences were found for the static suspension categories of thumb adducted and thumb abducted. The significant differences occurring only in the static categories compared to the dynamic category suggests that there may be differences in how diameter size affects normalised peak pressure when the body mass is positioned below a single hand between more postural arboreal suspension activities involving the hand (see the arboreal component of Hunt, 1996) and more locomotive arboreal suspension activities that use the hand (see Thorpe et al. 2007). It should be noted that in both the thumb adducted and thumb abducted activity categories that significant differences in normalised peak pressure were only observed between the 45mm and 105mm diameters.

4.2. *Location of peak pressure in humans*

I predicted that there would be a significant difference in the location of peak pressure across all three of the diameters, with the peak pressure occurring more often at the distal phalanges as the diameter increases (based on Seo and Armstrong, 2008). It should be noted that when using the multinomial logistic regression it was not possible to include random effects and therefore these results should be interpreted cautiously due to issues of pseudoreplication. It was also not possible to alter the base outcome value for each analysis. This study found partial support for this hypothesis. The location of peak pressure relative to the base outcome was not found to be significantly different between each of the activity categories within each diameter. In contrast, when the differences in location of peak pressure within each activity category were examined across all three of the diameters, significant differences were found in the thumb abducted activity category only.

A significant effect of diameter was shown for the locations of PP4, MC3 head, PP3, the PIP3 joint, and IP3 relative to the base outcome category (MC2 base) in the thumb abducted activity category. This suggests that the majority of the third digit and part of the fourth digit may be significant locations for peak pressure over different sized diameters when the thumb is abducted. It was not possible to perform post-hoc tests and therefore the exact differences in location of peak pressure between pairs of diameters for thumb abducted cannot presently be investigated. The thumb abducted position is most similar to the hand positions used by primates to grasp substrates during vertical climbing (bonobos: Samuel et al. 2018), although in the present study the thumb was not in opposition to the fingers. Therefore, analysis of how activity category and diameter size affect how pressure is experienced in the hand during vertical climbing would be beneficial for further understanding of how different types of arboreal locomotion affect how the hand experiences pressure. It should be noted that statistical analysis which takes into account random effects (participant ID) is needed before further study is done, as this will allow the effect of multiple measures per participant, per activity-diameter category to be controlled for.

The mode location, or locations, of peak pressure were examined using the cluster graphs (Figures 12a-c, and 13a-c), as well as presented visually in Figure 14. It should be noted that these graphs contain the data for all 189 trials for all 6 participants and therefore there may be some issues due to pseudoreplication, as each participant had different numbers of usable trials for each activity-diameter combination. Overall, as the diameter increases from 45mm to 105mm, for each of the three activity categories the mode locations of peak pressure move from the proximal phalanx of the fourth digit to the distal phalanges of the second and third digits. The mode location of peak pressure for the 45mm diameter for all activity categories is the fourth digit, whereas the mode locations of peak pressure on the 80mm and 105mm diameters are found most often on the second and third digits. The mode locations on the 105mm diameter for all activity categories are at the distal phalanges, which is in contrast to the fourth proximal phalanx for the 45mm diameter. Therefore, as diameter increases the mode locations of peak pressure move laterally across the hand, and to the distal areas of the hand. As previously noted, significant differences in normalised peak pressure were found in the thumb adducted and thumb abducted activity categories between the 45mm and 105mm diameters. These results, in combination with the mode location results, suggest that there is a complex relationship between the diameter of the superstrate, the activity category, and the location of peak pressure. It should be noted that as the mode location of peak pressure results are only descriptive that more robust statistical analysis is needed in order to confirm these findings.

Whilst the present study did not examine contact area, the mode location of peak pressure results are comparable to the ergonomic studies of Seo et al. (2007) and Seo and Armstrong (2008). When the thumb was opposed to the rest of the digits and no torque was applied on the 57.8mm handle the application of maximum grip force produced the highest areas of pressure at the distal phalanges, and the proximal phalanx of the third digit (Seo et al. 2007). Some high areas of peak pressure, but not as high as those at the distal and proximal phalanges were also observed around the first-to-third metacarpals (Seo et al. 2007). As the diameter increased to 83.2mm and no torque was applied the areas of highest peak pressure were observed to be at the distal phalanges, in particular the first and third distal phalanges (Seo et al. 2007). This may be due in part to the decrease in palmar contact area noted by Seo et al. 2007 and Seo and Armstrong (2008) as the diameter increases.

It should be noted, that in my study, the body mass was below the suspension pole in contrast to the experimental set up of some ergonomic studies where participants are seated (e.g. Seo et al. 2007; Seo and Armstrong, 2008). This may result in differences in the contact area of the hand on the diameter for each of the studies. The thumb is often opposed to the remaining digits in ergonomic studies (e.g. Edgren et al. 2004; Seo et al. 2007; Seo and Armstrong, 2008), whereas in my study the thumb was either adducted, thus putting the hand into a hook grip as illustrated in Alexander (1994), or abducted laterally in the coronal plane. Therefore, actual contact area when the body mass is below the superstrate being gripped should be investigated to allow further comparison to the ergonomic literature.

In the study by Choi and Robinovitch (2011), the body mass was located above the hands, as the participant ‘fell’ forward onto their hands. Overall it was found that the location of peak pressure was in-between the hamate and the scaphoid in the wrist (Choi and Robinovitch, 2011). This differs from the results of my study, where the body mass was below the hand. The tentative location results of my study (see Figure 14) suggest that the digits and the palm are modal locations of peak pressure, which contrasts the results of Choi and Robinovitch (2011) as expected due to differences in in body position in relation to the substrate. This is also likely to result in differences in contact area when the hand is in a hook grip with the body mass below, compared to a flat hand with the body mass above it. Other factors such as velocity and duration of activity may also affect how pressure is experienced by the human hand, and should therefore be considered in future research.

Whilst not directly examining the location of peak pressure, it was found that the third digit, followed by the second and fourth digits had the largest contribution to total force in the fingers across all the diameters they tested (Kong and Lowe, 2005). It should be noted that the metacarpal heads were included in their calculation of total force for each finger (Kong and Lowe, 2005), which is in contrast to the present study hand segment definitions. Whilst there are differences in how palm and digit are classified, this is somewhat in line with my study's findings that the mode location of peak pressure is found at the proximal phalanx of the fourth ray on the 45mm diameter, and then moves more distally and to the third and second rays as the diameter increases to 80mm and then 105mm, although some involvement of the distal palm is noted on the 80mm diameter.

As the hands and the feet of humans and primates are both pentadactyl limbs but are used in different ways for habitual locomotor and manipulative activities (D'Août et al. 2001; Hatala et al. 2013; Marzke and Marzke, 2000; Schmitt et al. 2016; Thorpe et al. 2007), the differences in how pressure is experienced between them may provide some insight into specialised morphologies. For example, it has been suggested that the human foot contained a pressure tripod to dissipate stress into the substrate in bipedal locomotion (Marchi, 2005). The pressure tripod of the foot consisting of the calcaneus, first metatarsophalangeal (MTP) joint, and fifth MTP joint (Marchi, 2005). This bears some similarity to the foot pressure results of Hatala et al. (2013), which found the areas of greatest pressure to be at the heel and the hallux of the human foot during bipedal locomotion. The location mode results of my study suggest that during suspensory arboreal locomotion and static posture the majority of the pressure, over a range of diameter sizes, is experienced in the second to fourth rays of the hand. Preliminary multinomial logistic regression analysis suggests third digit between the MC3 head and IP3, and PP4 play a significant roles in relation to diameter size. The negative coefficients suggest that these locations have a negative relationship with increasing diameter size, which is in line with the distal phalanx location mode results for the largest diameter (105mm) in contrast to the location mode of PP4 on the smallest diameter (45mm). The statistical significance of this, however, is tentative and should be analysed further with methods that take random effects into account. Bipedal locomotion and gripping an arboreal superstrate involve different hand and foot positions (see Alexander, 1994; Hatala et al. 2013). This suggests that locomotion on a flat surface with the body mass above the substrate produces a different pressure pattern to locomotion and static posture on a cylindrical arboreal superstrate with the body mass below the superstrate.

4.3. *Human hand anatomy*

As pressure is the result of force over area, the site of peak pressure in this study would be where the greatest force is being exerted by an anatomical section of the hand on a 1cm^2 pressure sensor. As the application of force, if it is great enough, may damage the area of anatomy it is applied to, it has been suggested by Wolff (1892) that the skeletal elements of an organism are adapted to withstand, within reason, the mechanical forces that they are habitually subjected to (see also Ruff et al. 2006). This has been widely debated within the anthropological literature, particularly in relation to entheses (musculoskeletal stress markers) (e.g. Eshed et al. 2004; Milella et al. 2015; Schlecht, 2012). It has been proposed that the curved phalanges of chimpanzees reduce the strains that the skeleton and relevant soft tissues are subjected to during grasping (Hunt, 1991). It should also be noted that olive baboons were suggested to mediate the mechanical stress on their metacarpals by using a more palmigrade-style posture when the GRF increased (Patel and Wunderlich, 2010). This suggests that the general shape and size of an anatomical region may play a role in mediating stress and the resulting strain during locomotor and postural activities.

Whilst peak pressure generally only occurred at one 1cm^2 sensor in this study, it was noted that many of the anatomical regions of the hand which were defined by the markers covered more than one pressure sensor and are therefore larger than the pressure mat sensor size. Therefore, future research should also consider the specific location of peak pressure within the broad anatomical segment locations used in this study.

The musculature of the hand has a role in determining the amount of grip force that can be exerted in a specific hand position. The flexor carpis ulnaris (FCU) along with the flexor carpis radialis (FCR) act to flex the wrist (Standring, 2016). Wrist flexion is also partially facilitated by the flexor digitorum superficialis (FDS), the tendons of which, alongside the tendons of the flexor digitorum profundus (FDP), also aid in the flexion of the PIP joints of the digits (Standring, 2016). At the DIP joints, the tendon of the FDP is the sole flexor (Standring, 2016). When the wrist is flexed along with the digits this causes an increased shortening of the tendons for the FDP and FDS, a condition which is normally avoided by wrist extension with digit flexion as this allows the extrinsic muscles to remain at a length that is close to that at which they generate maximum force (Standring, 2016). In humans it has been shown that wrist flexion at 30 degrees significantly decreased the grip strength of an individual by about 60% compared to their grip strength with the wrist in a neutral position (Bhardwaj et al. 2011).

On the 45mm diameter the theoretical contact area, calculated using the "normalized handle size" equation in Kong and Lowe (2005:499), is smaller than the length of the hand. It should be noted that the addition of the deformable Velcro ® and pressure mat increases the diameter by 18mm. Despite this, as the deformation under each area of the hand was not measured during the experiments, the theoretical contact area was calculated using the non-deformable diameter sizes. The theoretical contact area being smaller than the hand length would allow the wrist to be positioned directly below the hand, and therefore minimum wrist flexion would be likely to occur on the 45mm diameter during suspension. This is similar to the position of the hand in hylobatids using a hook grip on small diameter supports during unimanual forelimb-suspension (Sarmiento, 1988).

On the 80mm and 105mm diameters, the theoretical contact area of the hand is 100%. Due to the increasing size of the diameters, the hand would likely have to be placed further up on the diameter to prevent the force of gravity from causing the participant to slip off the diameter. This hand position on the diameter would also mean that the wrist could not be positioned directly below the hand and therefore some wrist flexion would occur. It would also not be possible to oppose the fingertips to the palm. It has been noted that wrist flexion in hylobatids increases as the diameter of the support increased (Sarmiento, 1988). It is possible that there may be a similar relationship in humans, however, muscle tendon units have been shown to be rather plastic in humans (Csapo et al. 2010). In habitual high heel wearing human females compared to non-high heel wearing females the Achilles tendon was significantly increased in cross sectional area, and therefore stiffness (Csapo et al. 2010). The length of the gastrocnemius medialis fascicles when resting in the habitual high heel wearing sample was significantly reduced compared to the non-high heel wearing sample (Csapo et al. 2010). This illustrates that the structure of muscles and tendons can be altered in individuals due to persistent long-term changes in loading (Csapo et al. 2010). Therefore, the effect of ontogeny on anatomy should be investigated in relation to locomotion in future studies.

The musculature of the hand also causes some issues with identifying the location of peak pressure. The palm of the hand can be divided into two areas: the hypothenar and thenar regions and the muscles of the thenar region attach predominantly on the first ray and the carpal bones, although some, for example the oblique head of the adductor pollicis, attach to the third and second metacarpal bases alongside the capitate (Standring, 2016). Therefore, when using the location of peak pressure identification methodology outlined in this study, care should be taken in determining the location of peak pressure when it falls around the base of the second metacarpal or the first metacarpal.

4.4. *Position of the hand on the diameter*

Previous ergonomic literature indicates that the diameter of the substrate being grasped affects the grip force that is able to be exerted onto the cylindrical handle (Seo et al. 2007). This is suggested to be related to the position of the fingertips in relation to the palm (Seo et al. 2007). How the hand is able to be positioned on the diameter may also affect diameter size preferences. Ergonomic studies show that the preference is for smaller diameters around the optimal diameter size of 30-40mm (Edgren et al. 2004; Hall, 1997; Kong and Lowe, 2005; Seo and Armstrong 2008). The most preferred diameter by all the participants in my study (N

= 14) was the 45mm diameter ($p = 0.001$), which out of the three analysed diameter sizes is the closest to the optimal diameter for the human hand. The third preference diameter was 105mm ($p < 0.001$), which is roughly 2.3 times the size of the 45mm diameter. The addition of Velcro ® and the pressure mat to the diameters during the experiment added an additional 18mm to the diameters, however, this was deformable. As previously mentioned, the extent of the deformation across the hand contact area was not measured in this study and therefore the non-deformable diameter sizes are used. Future studies should increase the range of diameters looked at and investigate the effects of deformable diameter wrappings on diameter preference.

The position of the hand varies between each of the diameters. On the small 45mm diameter it is likely that the fingertips could oppose the palm and the metacarpal heads, and the proximal phalanges and PIP joints would be positioned around the top of the diameter with the palm and wrist somewhat vertically below the proximal phalanges (Richmond, 2007; Sarmiento, 1988). This pattern was also noted for hylobatids when they passively used their hand as a hook grip during unimanual forelimb-suspension behaviours (Sarmiento, 1988), although it should be noted that the hand proportions of hylobatids and humans differ. Whereas on the larger diameter the hand would be more extended, and therefore the fingertips would be more likely positioned closer to the top of the diameter and unlikely to be able to oppose the palm (especially on the 105mm diameter) (Richmond, 2007; Sarmiento, 1988). This would put the wrist in a position of greater flexion (Richmond, 2007; Sarmiento, 1988). It should be noted that the exact joint angle measurements have not been calculated for this sample, and thus they should be considered in future research to allow further investigation of the relationship between hand positioning and the location of peak pressure.

The size of a participant's hand in relation to the circumference of the superstrate for each diameter size affects how the hand can be positioned on the diameter during suspension. For example, the circumference of each diameter as a percentage of hand length, calculated using the "normalized handle size" equation in Kong and Lowe (2005:499), for my sample indicates that the circumference of the 45mm diameter was less than the length of the third ray for all participants (see Table 3). The length of the third ray is used as a proxy for hand length. The mean value for the circumference of the 45mm diameter as a percentage of participant hand length showed that the circumference of the 45mm diameter was around 24% shorter than participant hand length. Therefore, even though their hands were positioned in a hook grip (thumb adducted) or modified hook grip (thumb abducted) their distal phalanges had the potential to be positioned opposite to the metacarpals. This would put the intermediate and proximal phalanges, as well as the metacarpal heads, closer to the top side of the diameter.

The circumferences of the 80mm and 105mm diameters were shown to be larger than the hand length of the participants in my study. The mean value for the circumference of the 80mm diameter as a percentage of participant hand length showed that the circumference of the 80mm diameter was around 34% larger than participant hand length. For the 105mm diameter, the mean value for the circumference as a percentage of participant hand length showed that the circumference of the 105mm diameter was around 77% larger than participant hand length.

As the participant was supporting their body mass fully with one hand, their hand was subject to gravitational forces as well as the reaction force from the superstrate being grasped (Hunt, 1991; Preuschoft, 2002). Therefore, the positioning of the hand on the diameter would have affected where in the hand these forces were acting. Gravity acts vertically on an object (see Figure 3 in Hunt, 1991, and Figure 1 in Preuschoft, 2002). The participant's hand would need to be positioned in a way that allowed them to secure themselves to the diameter when suspending and counteract the force of gravity via friction, orthogonal, and potentially tensile forces depending on the angle of the substrate (Preuschoft, 2004). On the 45mm diameter, as the circumference is shorter than the hand length of the participants it would be easier to position the fingertips opposite the palm. However, this would be more difficult on the larger (80mm and 105mm) diameters. It has been suggested that the opposition of the fingertips to the palm, although in a non-suspensory context, allows a greater grip force to be generated (Seo et al. 2007). A greater grip force, and subsequently pressure, would also result in the generation of a larger amount of friction which would assist in stabilising the grip on the diameter (Preuschoft, 2002).

When all the activity categories were combined via a mean, a statistically significant difference in normalised peak pressure was found between the 45mm and 105mm diameters, with the 45mm diameter having the greatest mean normalised peak pressure value (see Table 8). A similar pattern was also observed when the differences between the diameters was examined in each of the activity classes. In both the thumb adducted and thumb abducted activity categories there was a significant difference in normalized peak pressure between the 45mm and 105mm diameters. The greater the amount of pressure, the greater the amount of friction generated, which has been noted to be a component of grip stabilisation during climbing (Preuschoft, 2002; 2004). It should be noted that there is a larger theoretical contact area for the hand on the 80mm and 105mm diameters, as their circumferences are larger than the participant hand length. Therefore, as pressure is the result of force over area it would be expected that there would be lower peak pressure, and normalised peak pressure, values as the theoretical contact area increased. Hand contact area was not analysed in this study and thus it should be included in future research. Alongside this, the exact position of the hand on the diameter and the resulting joint angles should be investigated using kinematic methods, as this would provide further insight into the biomechanics of the human hand during suspensory locomotion.

4.5. *Human and bonobo comparison*

I predicted that the location of peak pressure in the human hand would be comparable to that of bonobos when engaging in suspension using the same relative diameter (i.e. 105mm compared to 120mm). As the diameter (120mm) used by bonobos for suspension in Samuel et al. (2018) is comparable to the 105mm diameter used in my study, circumference as a percentage of hand length was also calculated for bonobos. As there were no hand length data for the bonobos used in the study by Samuel et al. (2018), mean bonobo hand length was calculated from a separate sample of sixteen adult bonobos (J. Neufuss, unpublished). Mean hand length was used as the bonobos in the sample used to calculate hand length were not the same as the bonobos used in the study by Samuel et al. (2018). Bonobos were classed as adults if they were fifteen or more years old, based on the methodology of Idani (1990) and Enomoto (1990).

Using the circumference from Samuel et al. (2018) and mean hand length from J. Neufuss (unpublished), the circumference as a percentage of hand length for bonobos was calculated as 173.9%. This is just below the mean circumference as a percentage of hand length, and within the standard deviation, for the human sample on the 105mm diameter in my study (see Table 3).

The 105mm diameter used in this study is comparable to the 120mm diameter used in Samuel et al's. (2018) study of bonobo arboreal locomotion. During suspension in bonobos on a 120mm diameter superstrate Samuel et al. (2018) found that the peak pressure occurred at the distal phalanges or the proximal region of the palm. This is concurrent with my study's finding that in humans on the 105mm diameter for static unimanual forelimb-suspension with the thumb adducted and dynamic suspension the mode location of peak pressure was DP2, and for static unimanual forelimb-suspension with the thumb abducted it was DP3. This is consistent with the findings on location of peak pressure during bonobo suspension on the 120mm diameter (Samuel et al. 2018). It is also interesting to note that the thumb was not loaded during suspension in bonobos (Samuel et al. 2018), and that the thumb was also not a location mode for suspension in humans in any of the activity-diameter combinations.

The general lack of loading of the human thumb on all three diameters during suspension and the total lack of loading of the bonobo thumb during suspension on a 120mm superstrate, even though it was in contact with the pressure mat during each of the suspensory trials (Samuel et al. 2018), suggests that the thumb's role during suspensory locomotion may be minimal. This would be in line with studies that indicate that the human thumb plays a key role in other behaviours, such as during tool manufacture and use (Key and Dunmore, 2015). However, the mode location of peak pressure not occurring at the thumb does not guarantee that the thumb was not loaded at all in the human sample, further analysis of the human data should be done to investigate the loading, and contact area, for specific anatomical regions of the hand.

Given the similarities in mode locations of peak pressure in the human 105mm diameter sample in this study and peak pressure locations in the bonobo sample on the 120mm diameter (Samuel et al. 2018), this suggests that the relationship between hand size and circumference of the superstrate play a key role in determining the location of peak pressure across primate species.

Mean peak pressure in the bonobo hand during suspension was divided in palm and digit regions by Samuel et al. (2018). As no clear separation between the palm and digits was seen in the human sample during suspension on each of the diameters (45mm, 80mm, and 105mm) the peak pressure and mean peak pressure values, for all 189 trials and when there are 54 trials after controlling for the effect of pseudoreplication, are in relation to the entire hand.

The human results for mean peak pressure, once pseudoreplication has been controlled for (54 trials, see Table 6 for peak pressure results, and Table 7 for normalised peak pressure results), for all three of the activities on all three of the diameters were larger than the mean raw peak pressure results for vertical locomotion and suspension for both the digits and the palm respectively in bonobos (Samuel et al. 2018). This may be due to differences in body mass, and body mass in relation to hand size in each of the species. Hand size was taken into account when normalising peak pressure in the present study, but it was not for the bonobo pressure data (Samuel et al. 2018). Therefore, interspecies variation in hand size and body mass relationships should be investigated in future research.

4.6. *Location of peak pressure in primates*

In the study on the relationship between pressure, speed of locomotion, and hand position in olive baboons, it was found that the location of peak pressure remained at the metacarpal heads as the speed of locomotion, and consequently GRF, increased (Patel and Wunderlich, 2010). The increased contact area of the hand at higher speeds, due to a more palmigrady-like hand position, allowed the increased GRF to be spread over a larger area and therefore resulted in lower pressure values (Patel and Wunderlich, 2010). The exact contact area and joint positions have yet to be analysed in relation to the different diameter sizes and activity categories for my human sample. However, it would be beneficial for future research to examine how these variables affect peak pressure values and the location of peak pressure during arboreal locomotion in humans, as well as other primates.

In terrestrial studies of pressure in primates, the CoP is seen to migrate throughout the gait cycle. For example, that the CoP moves proximally along the lateral side of the foot and migrates medially during bipedal locomotion in bonobos (D'Aoȗt et al. 2001). In contrast, there was no medial migration of the CoP during quadrupedal locomotion in bonobos (D'Aoȗt et al. 2001). It should be noted that D'Aoȗt et al's. (2001) results are from a preliminary study, and therefore a larger sample size would be beneficial to fully assess the variation in CoP movement during terrestrial locomotion in bonobos. Whilst the present study examined the moment of peak pressure, and did not track CoP during the gait cycle, it is interesting to note that the mode locations of peak pressure were found across the second, third, and fourth digits of the hand. This demonstrates that during arboreal activities peak pressure is found on the central rays of the hand. It should be noted that as a result of pseudoreplication issues, statistical tests that include random effects are needed to verify the location findings of the present study. CoP in humans during arboreal locomotion should be examined in order to allow further comparisons to the previous primate pressure study literature.

Many of the arboreal theories for the origin of bipedalism suggest that a form of assisted bipedalism, where both the hands and feet are involved in arboreal locomotion or posture, may have been used by hominins (e.g. Hunt, 1996; Thorpe et al. 2007; Thorpe et al. 2014). This is supported by observations of extant great apes engaging in assisted bipedalism (Thorpe et al. 2007). Comparisons of how pressure is experienced by the hands compared to the feet in arboreal locomotion where both the upper and lower limbs are involved may provide an interesting insight into how morphology is related to the trade-offs between the functions of the hands and feet.

In head first descent in aye-ayes (*Daubentonia madagascariensis*), it was shown by Kivell et al. (2010) that a greater the Pressure Time Integral (PTI) was experienced by the foot compared to the hand. This differs from what would be expected when compared to the more even PTI spread in horizontal locomotion, and the greater PTI experienced by the foot relative to the hand during ascent (Kivell et al. 2010). This illustrates that, when engaging in locomotion using more than two limbs, how pressure is experienced by each of these limbs can be affected by any specialist morphology of the hands and feet (Kivell et al. 2010). Therefore, investigation of the pressures experienced by the hands and feet when engaging in assisted bipedalism, compared to those experienced during bipedal walking and suspension, may also be beneficial for examining how morphology and function of the hand are related across a wide sample of primate species.

4.7. *Implications for the fossil record*

Comparison of the location of peak pressure in humans and primates suggests that the diameter of the superstrate during arboreal suspensory locomotion may have similar effects across primate species. This remains to be tested with a wider primate sample and a range of diameter sizes. It is therefore important to take into account the diameters of the superstrates that would have been available to the hominins for arboreal locomotion, or if that is not possible, the general type and sizes of the tree species that would have been present. Consequently, an interdisciplinary approach combining both paleoecology (see Lindbladh et al. 2013, although paleoecological methods would need to be suitable for hominin environments and timeframes) and paleoanthropology is needed when investigating the arboreal locomotor capabilities of fossil hominins.

The results of the present study show that the thumb position has no significant effect on the normalised peak pressure value on any of the three diameters (45mm, 80mm, and 105mm). When location of peak pressure modes were examined none of the occurred on the thumb, and the significant locations in relation to diameter size from the preliminary multinomial logistic regression analysis were only found on the third and fourth digits in the thumb abducted category. Thus, the thumb of fossil hominins cannot be used to infer the potential locomotor capabilities of fossil hominins. It is more likely that the modern human thumb morphology has been selected for through manipulative behaviours, such as tool manufacture and use (see Key and Dunmore, 2015). Therefore, future research should investigate the differences in the forces experienced by the human and primate hand during locomotor and manipulative behaviours in order to further distinguish how the different functions are related to the morphology.

On the 45mm and 105mm diameters the mode locations of peak pressure were found on the phalanges of the second, third, and fourth digits, which suggests that their morphology should reflect the mechanical strains they habitually experienced in relation to arboreal locomotion. The distal phalanges of the second and third digits were the only mode locations of peak pressure on the 105mm diameter compared to the proximal fourth phalanx on the 45mm diameter. In contrast the majority of the mode locations of peak pressure on the 80mm diameter were on the second and third metacarpals, with the only phalanx being DP3. Therefore the size of the superstrate being grasped affects which anatomical region of the digits experiences the greatest pressure. Ventral phalangeal curvature allows the strain to be dispersed more evenly across the individual phalanges compared to straight phalanges (Hunt, 1991; Richmond, 2007; Nguyen et al. 2014). As stress causes strain (Lucas et al. 1999), peak pressure, or the normalised peak pressure value, influences the amount of strain experienced by the location of peak pressure within the hand. Therefore, as normalised peak pressure was significantly higher on the 45mm diameter compared to the 105mm diameter for each of the thumb adducted and thumb abducted activities, the phalanges on the 45mm diameter would likely be subject to a larger amount of strain.

In regard to the phalanges, on the 45mm diameter the peak pressure location mode was the proximal fourth phalanx for all three activity categories. In contrast, on the 105mm the distal phalanx of the second digit was the mode location of peak pressure for the thumb adducted and dynamic suspension activities, and the distal phalanx of the third digit was the mode location for the thumb abducted activity. This is also in line with the highly significant multinomial logistic regression result ($p < 0.001$) with a negative coefficient value for the effect of diameter on PP4 compared to the base outcome (MC2 base) in the thumb abducted analysis. It must be taken into account, however, that these results are tentative and further statistical analysis is required. This means that when considering the hands of fossil hominins who potentially engaged in arboreal locomotion it is therefore important to consider the degree of ventral phalangeal curvature as well as the differences in the degree of ventral curvature between each of the phalanges. This is especially relevant for hominins, such as

Australopithecus afarensis, where there is evidence for bipedal locomotion in the hindlimbs (Raichlen et al. 2010) alongside arboreal traits in the forelimbs (Bush et al. 1982; Kimbel and Delezene, 2009). This may provide some insight into the size of superstrate that a hominin used for arboreal suspensory locomotion, particularly when considering larger diameters (e.g. 105mm) in comparison to smaller diameters (e.g. 45mm). Also, examining the variation in phalangeal curvature in relation to pressure experienced by the hand during arboreal locomotion within humans and extant primate species would also be beneficial for the investigation of whether the potential arboreal adaptations seen in fossil hominins that are known to have engaged in bipedalism are primitive retentions or functionally adaptive. Therefore, intraspecies variation should also be considered for future research.

4.8. *Limitations*

Due to the time required for data collection and analysis, data on only six individuals were fully analysed for this study and thus these results should be treated as preliminary analysis. However, data were collected on an additional eight individuals and these data will be incorporated into future analyses and publications.

The retroreflective kinematic markers were placed on the hand at bony landmarks whose position had to be assessed through the skin and soft tissue of the upper limb. Whilst great care was taken to ensure that the markers were positioned as accurately as possible, the covering of the skeletal elements by soft tissues may have introduced a small margin of error into the positioning of the markers.

The dynamic suspension activity (forelimb swing) started from a static position, which was the same as the thumb adducted and thumb abducted activities. From this position the participant then swung themselves forward. This was due to high levels of marker drop out and marker movement when a more realistic form of dynamic suspension was used, where the participant started further back along the suspension pole with their non-dominant hand, swung their dominant hand onto the pressure mat, and then swung onto the rest of the suspension pole using their non-dominant hand before putting their feet on the floor. This may have been due to the camera positioning in relation to the hand or potentially the speed at which the activity took place in comparison to the static activities. Whilst this would have resulted in a more directly comparable form of suspensory locomotion to primate arboreal suspensory locomotion, the high marker drop out made it extremely difficult to get any usable trials using this method. Therefore, the approach using a standing start position beneath the diameter was used. Future research should alter the camera positions and settings further to include a more realistic form of dynamic suspension in the analysis.

In the analysis of location of peak pressure in relation to the effects of diameter and activity category it was not possible to include participant ID as a random effect in the multinomial logistic regression. This is particularly relevant as not every trial run for each participant was usable, so for each activity-diameter combination each participant had differing numbers of usable trials. Therefore this leads to the issue of pseudoreplication, which may result in over representation of certain location categories for specific activity-diameter combinations. This must be addressed in future research through the inclusion of random effects in the analysis.

4.9. *Future research directions*

Hand proportions may affect the area over which force can be distributed, therefore many other variables, such as grip strength, pinch strength, and hand proportions, should be investigated to further illuminate the relationship between hand anatomy and its function in relation to arboreal locomotion in humans. As pressure is the result of force over area, it is therefore probable that the relationship between body mass and hand size will affect the peak pressure experienced by the human hand during suspensory activities. Whilst hand area and body mass were both used to normalise peak pressure in the present study, the calculated hand area assumed that the participants hands were rectangular. This should be addressed using a more refined estimate of hand area in future research. Hand area analysis would be particularly useful as the olive baboons were suggested to mediate the amount of force experienced by the metacarpals as the speed of locomotion increased, and therefore GRF, by modifying the position of the hand to a more palmigrady-like position which increased the area that the force was acting on (Patel and Wunderlich, 2010).

Contact area should also be investigated, due to the mode locations of peak pressure in this study showing a somewhat similar pattern as the diameter increased to the results of Seo et al. (2007). The results of my study also suggest that the theoretical contact area for each of the diameters may influence the normalised peak pressure value and location of peak pressure for the diameters used, although a more accurate measure of actual contact area should be taken along with statistical tests that include random effects to further investigate this relationship. Comparison of human contact area to that of primates engaging in similar activities would be especially useful for examining how different hand morphologies are functionally used during arboreal locomotion.

The exact joint angles of the hand during each of the three activities were not quantified in this study. Therefore, future research should include further kinematic analysis in order to fully examine the effects of hand, and more specifically digit, positioning on the location of peak pressure in the human hand during arboreal suspension.

Other arboreal locomotor activities, such as vertical climbing and assisted bipedalism, should also be examined in order to assess whether the patterns observed in this study for normalised peak pressure and the location of peak pressure during suspensory arboreal locomotion across diameters and activity categories are altered by the differences in body positioning for different types of arboreal locomotion. This would also provide comparative data to previous kinematic (Isler, 2002a, b, 2004) and pressure (Samuel et al. 2018) studies of vertical climbing in primates. Through providing comparative data, it would also allow some inferences to be made as to the arboreal locomotor capabilities of fossil hominins. This would be particularly relevant to addressing the many arboreal related theories on the origin of bipedalism (e.g. Hunt 1996; Thorpe et al. 2007).

Tool manufacture and use should also be investigated using the combined pressure and kinematic approach. Both tool manufacture and use, and a potential transition from arboreal to terrestrial bipedal locomotion are suggested to have affected the evolution of the human hand (Hunt, 1991; Key and Dunmore, 2015; Marzke and Marzke, 2000; Thorpe et al. 2007; Williams-Hatala, 2016). As the date for the earliest known stone tools (3.3 mya, Harmand et al. 2015) is in close proximity for the earliest date of definite bipedalism in hominins (around 3.6 mya, Raichlen et al. 2010) and there are many arboreal related theories on the origin of bipedalism (e.g. Hunt, 1996; Thorpe et al. 2007), investigation of the kinematic and pressure differences between the two categories of activity is warranted.

5. **Conclusion**

In conclusion, there is a statistically significant difference in normalised peak pressure for each of the thumb adducted and thumb abducted activity categories between the 45mm and

105mm diameters. The relationship between the circumference of each diameter and the hand sizes of the participants indicates that this may be to do with the theoretical hand contact area and the exact hand position on the diameter. Whilst actual hand contact area and the kinematic positioning of the hand joints were not analysed in the present study, they should be included in future research.

The lack of differences in normalised peak pressure between the activity categories within each of the three diameters suggests that activity type does not affect the amount of pressure experienced by the human hand. In contrast, the significant differences in normalised peak pressure between the 45mm and 105mm diameters for both of the static activity categories suggests that diameter has an effect on the experienced pressure in the human hand. The 45mm diameter was also the most preferred diameter size and the 105mm diameter was the least preferred diameter size.

Whilst there were issues with the statistical analysis of the location of peak pressure it was possible to identify general trends. The combined modes for all three activity categories progress from the fourth proximal phalanx on the 45mm diameter, to the second and third metacarpals and the distal third phalanx on the 80mm diameter, to the distal phalanges of the second and third digits on the 105mm diameter. This indicates that the diameter of the superstrate being grasped may have an effect on where pressure is experienced in the human hand. The similarity of the mode locations of peak pressure on the 105mm diameter in the present study to the peak pressure locations of the bonobos on a 120mm diameter (Samuel et al. 2018) suggests that this trend may be observed across primate species. The circumference was shown to be a similar percentage of the hand length in both humans on the 105mm diameter and bonobos on the 120mm diameter. This combined with the similarity of the location of peak pressure between the two species on theses diameters suggests that the hand-diameter interaction may affect where peak pressure is experienced in the hand across primate species for a given activity. Additional comparative research across a wider range of primate species and diameters is needed before further conclusions can be drawn.

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