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Relationship of Posterior Intracranial Venous Structures in Homo sapiens and Handedness

by

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Submitted in partial fulfillment
of the requirements for the degree of
Master of Arts in Anthropology, Hunter College
The City University of New York

2020

July 24th 2020

Date

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Thesis Sponsor

July 24th 2020

Date

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Acknowledgements

I would like to thank Hunter College and the Anthropology department for the opportunity to complete my studies despite all the challenges.

I would like to extend my sincere thanks to my thesis sponsor, Dr. Christopher Gilbert, for his valuable and expert support and guidance during the development of this thesis and for his patience and encouragement during its completion.

I would also like to express my gratitude to Dr. Victoria Dominguez for her assistance and guidance as the second reader of this thesis.

Thank you to all who supported this thesis both directly and indirectly, especially Mirna Halawani for the statistical advice.

Abstract

The transverse sinus spans the endocranial surface of the occipital bone and ultimately transmits deoxygenated blood to the sigmoid sinus and jugular vein *en route* to the heart. This paired sinus tends to be more defined on either the left or right side in human crania. Left and right dominance, or the use of one side of the body more than the other, leaves traces on the human skeleton. Methods to determine handedness upon examination of various elements of the human skeleton mostly focus on the use of the extremities, while little research exists examining the skull for evidence of handedness. This thesis explores the potential correlation between asymmetries of the transverse sinus and summary statistics of handedness in human populations, connecting the results to the importance of determining handedness in physical anthropology and osteology. Data were collected on modern human crania from the American Museum of Natural History and compared to statistical data from the literature on handedness. Results of several Chi-Squared tests suggest there is little to no association between transverse sinus dominance and handedness in human populations, although there is possibly an association between transverse sinus dominance and jugular foramen dominance. Additional research using more controlled samples of known handedness is needed to more conclusively examine transverse sinus dominance and handedness in modern human populations.

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Introduction

Right and left handedness, or the predominant use of one hand in the execution and performance of tasks, is an almost universal feature among modern humans, and it has been noted to leave clear traces on the human skeletal system (see below). Handedness was perceived as a uniquely “human trait before 1987” (McGrew & Marchant, 1997), but has since been recorded in numerous non-human primates (e.g., see review in Papademetriou, Sheu, & Michel, 2005), a discovery which has had an impact on the study of stone tool making in prehistoric populations as well as the study of society and culture in prehistoric populations (Lazenby 2002). Laterality or hand preference in nonhuman primates can be thought of as the preference in the side used to complete tasks such as hanging from a tree or reaching for fruit, as these activities require dexterity and precision in the limb used (McGrew & Merchant, 1997; Papademetriou et al., 2005). Although non-human primate hand preferences during certain activities are slightly different from the study of true handedness in humans, it does provide a basis for further research on the evolution of the tasks non-human primates perform to the tasks that humans perform. Lazenby (2002) suggested early primates were left-handed, using their right hands to stabilize themselves while they reached food and ate with their left hands. The need for balancing with the right hand became unnecessary in early bipedal hominins, and side preferences are instead hypothesized to have been transferred over to the use of the right side of the body in making tools and performing tasks. This switch resulted due to the specialization of the right arm for stability and dexterity, as the unspecialized visually supported left hand that reached for food became less useful for tasks requiring precision (Lazenby, 2002).

In addition to non-human primates and the earliest hominins, studies on the evolution of human handedness and laterality extend to the archaeological record as well. For example, Bargalló, Mosquera, & Lozano (2017) studied differences in flakes (a product of stone tool

making) collected from two archaeological sites in Spain inhabited by pre-Neanderthal and Neanderthal communities, respectively. Their results demonstrated differences in the angles of the intentionally broken materials, and these differences were attributed to left and right-handed variance among the individuals making the tools (Bargalló, Mosquera, & Lozano. 2017). Thus, handedness and dominance are present in non-human primate populations, including great apes, and osteological and archaeological evidence from prehistoric populations such as *Homo erectus*, *Homo habilis*, *Homo neanderthalensis*, and *Homo sapiens* suggest that a dominant pattern of righthandedness, in particular, has been present in our own lineage for many hundreds of thousands (if not millions) of years as well (Rumbaugh et al., 2003; Lazenby 2002; Lozano et al., 2017).

As time progressed and human cognition became more advanced, handedness continued to play a role, becoming more and more entrenched in daily life. Constant & Mellet (2018), for example, demonstrated that individuals have trouble quickly discriminating between right and left depending on which side is preferred/dominant: “left-handers were significantly faster at identifying left target-hands over right target-hands, and they were significantly faster when the labeled “L” was presented over the label “R” (Constant & Mellet, 2018). These results illustrate the subconscious focus on the repetitive use of the dominant side in modern individuals, which contributes to the theoretical basis of examining increased bone density on the dominant side of the body.

The subconscious focus on the dominant side in the human body is a possible reason for osteological differences in left and right bone mass asymmetry, as one side of the body is being used more frequently and subjected to more force than the other non-dominant side of the body. This theory is supported, for example, by Kontulainen et al. (2003) in their study of bone density

and handedness in tennis and squash players; “Mechanical loading” or the act of applying force to bone has been shown to affect the asymmetry of bone shape and density, as explained by Wolff’s Law: bone tissue is dynamic, and responds according to external forces so that it is built where needed and resorbed where it is not needed (definition from White, 2000; Frost, 2001). Therefore, bones that are commonly used in physical activities and have force frequently applied to them should show asymmetric differences relating to increased bone tissue on the favored side. By using radiographic imaging to detect the density and size of the bones in the body, not only can the preferences in side be inferred, but also the frequency of use, both of which are factors that affect bone growth and development (Kontulainen et al., 2003; Blackburn, 2011). In fact, in their study of squash and tennis players, Kontulainen et al. (2003) found greater humeral cortical area (3%), total area (3%), cortical wall thickness (6%), marrow cavity area (4%), and torsional bone strength index (3%) in the experimental (nationally ranked racquet sports players) relative to the age, height, and weight-matched control (no physical activity affecting dominant side only) groups (Kontulainen et al., 2003). The “young starters”, females who began training at a mean of 8 years old, displayed even greater differences, with “20% greater cortical area and 15% greater cortical wall thickness” as well as a “26% greater torsional bone strength index” in the playing arm compared to the “old-starters” who displayed a greater density in cortical area than the average non-athlete but less than that of the “young starters” (Kontulainen et al., 2003). Kontulainen et al.’s (2003) research supports the theory that an individual’s dominant side bone structure is affected by the extended use of that side especially during growth and development periods.

Other research supports an association between handedness and skeletal differences as well, including connections between factors such as the length and density of long bones and

factors of handedness (e.g., see review by Ubelaker and Zarenko, 2012). Van Dusen (1939) demonstrated that the children aged 5 to 8 who were right-handed presented with longer right upper extremities, while children aged 1 to 4 who were right-handed presented with longer left upper extremity measurements (reviewed in Ubelaker and Zarenko, 2012). This research along with Kontulainen et al., (2003) research suggests a strong correlation between machinal loading during development and skeletal changes in bone density and length.

Genetic and environmental factors contribute to the human phenotype, including handedness, and it may be possible that handedness begins in utero, raising the questions: does handedness increase blood pressure on one side of the body due to the increase in muscle mass on the dominant side? And does this begin in utero? Blackburn (2011) surmised that physical differences in left-handedness and right-handedness may begin while the fetus is developing via a “process such as a left-right difference in blood oxygen level, which would potentially lead to unequal bone growth (Steele, 2000)”. Among the research Blackburn (2011) examined was the study by Pande and Singh (1971), which examined the upper limb anatomy of 10 fetuses and found that 9 of the samples had greater muscle and bone weight in the right limb and one had a greater weight in the left limb. Although a small sample, this ratio (90% right side dominant, 10% left side dominant) is consistent with overall population statistics for handedness (see below) and supports the theory that handedness is correlated with both environmental and genetic factors (Blackburn, 2011). Steele and Mays (1995) found that prenatal infants with longer recorded left humeri outnumbered the infants with longer right humeri 12 to 1. However, they also found that there was an increasing rightward bias that develops from infancy, and took this further to conclude “skeletal asymmetry in the long bones of the upper limb is present and correlated with the side of the dominant hand by middle and late childhood. The combination of

this research demonstrates that handedness is potentially present from birth through childhood” (Steele & Mays, 1995). Thus, in summary, there are numerous studies suggesting osteological markers of handedness in human skeletons from youth through adulthood, although very few, if any, have presented controlled data throughout ontogeny to gain a full understanding on the development of skeletal markers of handedness.

In addition to osteological markers, the brain has distinct features that suggest handedness. Geschwind and Levisky (1968) first called attention to asymmetry of the planum temporale in the 1960’s and spurred an increase in research regarding the link between brain asymmetry and cognitive function. Steele (2000) noted neurological markers of handedness that can be measured via brain scan and statistically tested to measure handedness from various studies. They include features in the planum temporale, the planum parietale, the Sylvian fissure, and the central sulcus (Steele, 2000). These features are, unfortunately, undetectable in a dry skull besides the Sylvian fissure, which is not regarded as a reliable marker. Other variations in the human brain appear to have a relationship with human handedness as well, going back to research by Dax and Broca in the 19th century. These early studies demonstrated that human brains are asymmetric with the majority of people processing language in the left hemisphere (Finger & Roe, 1994). While many of these asymmetries of the brain leave few traces on the endocranial surface of the human cranium, asymmetries in paired endocranial features do suggest possible markers linked to the venous structures of the brain. These endocranial asymmetries relate back to the hypothesized increased bone density and muscle size on dominant sides due to an increased mechanical force (e.g., Kontulainen et al., 2003; Ubelaker and Zarenko, 2012), which would potentially require an increase in blood flow and act upon the structures that contain the vessels associated with transporting the pressurized blood to the body. The heart

pumps oxygenated blood through the carotid artery to the brain, where the blood delivers nutrients to the tissues before passing through the venous sinus system and ultimately passing through the jugular foramen down the jugular vein and back to the heart. One of the largest and most important of these sinuses is the transverse sinus, present and often well-defined osteologically on either side of the midline on the endocranial portion of the occipital bone. The transverse sinus on the occipital tends to be larger on either the right or left side as it leads into the jugular foramen (Cornwall, Dias, Perumal, & Smith, 2014). Given this noted asymmetry, it is hypothesized here that the pressure on the dominant side of the body may affect the formation and size of the transverse sinus.

Several major sinuses become the jugular vein; the superior sagittal sinus, the occipital sinus and the straight sinus drain into the transverse sinus, which drains into the sigmoid sinus that then empties into the jugular vein. Cornwall, Dias, Perumal, & Smith (2014) suggest that the difference in size of the jugular foramina may be linked to handedness and dominance due to the increased blood pressure and volume on the dominant side of the body, and their research demonstrated a prevalence of larger right jugular foramina.

Across modern human populations, right-handedness appears much more common than left-handedness. In fact, a recent study suggests that “about 90% of the population are right-handed and 10% are left handed” (McManus, 2009: p.37). This conclusion for modern human populations is supported by other studies as well (Hardyck & Petrinovich, 1977; Blackburn, 2011). While historical data on handedness for individuals is sparse, McManus (2009) indicates that “it is probable that about 8% to 10% of the population has been left-handed for at least the past 200,000 years (p. 37). In addition, handedness statistics vary relative to time, geography, and sex: for example, “men are about 25% more likely to be left-handed than women” and “left-

handedness [is] more common in White, Asian and Hispanic populations” (McManus, 2009; p.37-38).

In 1986, Boyd Gibbons and Louie Psihoyos compiled the results of the “Smell Survey” from the National Geographic magazine. The survey was designed to uncover differences between male and female impressions of smells from a scratch and sniff card found in the issue. What Gibbons and Psihoyos did not realize at first is the fact they collected the largest database of left and right-handed people from the results. The smell survey was designed to trigger emotion from scent and there was a box for each participant to fill out “right-handed” or “left-handed”. The results of this survey showed there was a strong correlation to handedness and birth year: “only 3% to 4% of those born before 1920 being left handed, compared with about 11% to 12% of those born after 1950” (McManus, 2009) which may suggest an aspect of cultural or sociological significance such as religious bias against left-handedness during this time.

Handedness is a part of daily human life; it is arguable that handedness and sided dominance dictates the way in which an individual performs tasks and moves. The use of one side of the body more often than the other side of the body morphs the muscular and skeletal systems as well as the brain (see above). The purpose of this thesis is to examine a large sample of cranial data including sex, general geographic origin, and increased left or right size of the transverse sinus, and compare these data to the population statistics derived from McManus (2009) to determine if a statistically significant relationship exists between handedness and transverse sinus dominance. The reasoning for a connection between the transverse sinus dominance and handedness comes from the Cornwall, Dias, Perumal, & Smith (2014) study in which they examined the relationship between handedness and the variations in the size of the

jugular foramina. This research is extremely relevant to the proposal of this paper, as the transverse sinus eventually drains into the jugular vein through the jugular foramen.

The research presented by Cornwall, Dias, Perumal, & Smith (2014) hypothesized that the “increased use of the dominant upper limb would increase the mass of musculature of that limb and create a backpressure” that would in turn increase the size of the jugular foramen due to the pressure. They concluded that there was a higher likelihood of a larger jugular foramen size on the right side of the skull by 60% (Cornwall, Dias, Perumal, & Smith, 2014). While this data does not line up with the larger population statistics for handedness and the handedness of the sampled individuals was unknown, there is still a significant percentage of larger jugular foramina on the right side of the skull, suggesting a possible connection with right-hand dominance in the population. In fact, earlier research on jugular foramen asymmetries and handedness suggested a 78% positive correlation between jugular foramen size and handedness of the individual (Glassman and Dana, 1992; reviewed in Ubelaker and Zarenko, 2012). With this possible link made between the larger jugular foramen and handedness, there may be a connection to a larger transverse sinus and blood flow pressure on the right side of the body. However, more research is needed as both sources also suggest that a clear association is currently lacking (Cornwall, Dias, Perumal, & Smith, 2014; Ubelaker and Zarenko, 2012).

This study examines original research collected from the American Museum of Natural History in New York City of transverse sinus dominance and compares the results to the Cornwall, Dias, Perumal, Smith, (2014) research to see if jugular foramen dominance and transverse sinus dominance are correlated. By doing so, this study ultimately attempts to uncover another cranial feature diagnostic of handedness in human populations. This paper ultimately seeks to determine the significance of the deviations in size and structure of the

transverse sinus and its relationship to handedness and functional asymmetry in living modern human populations.

Methods

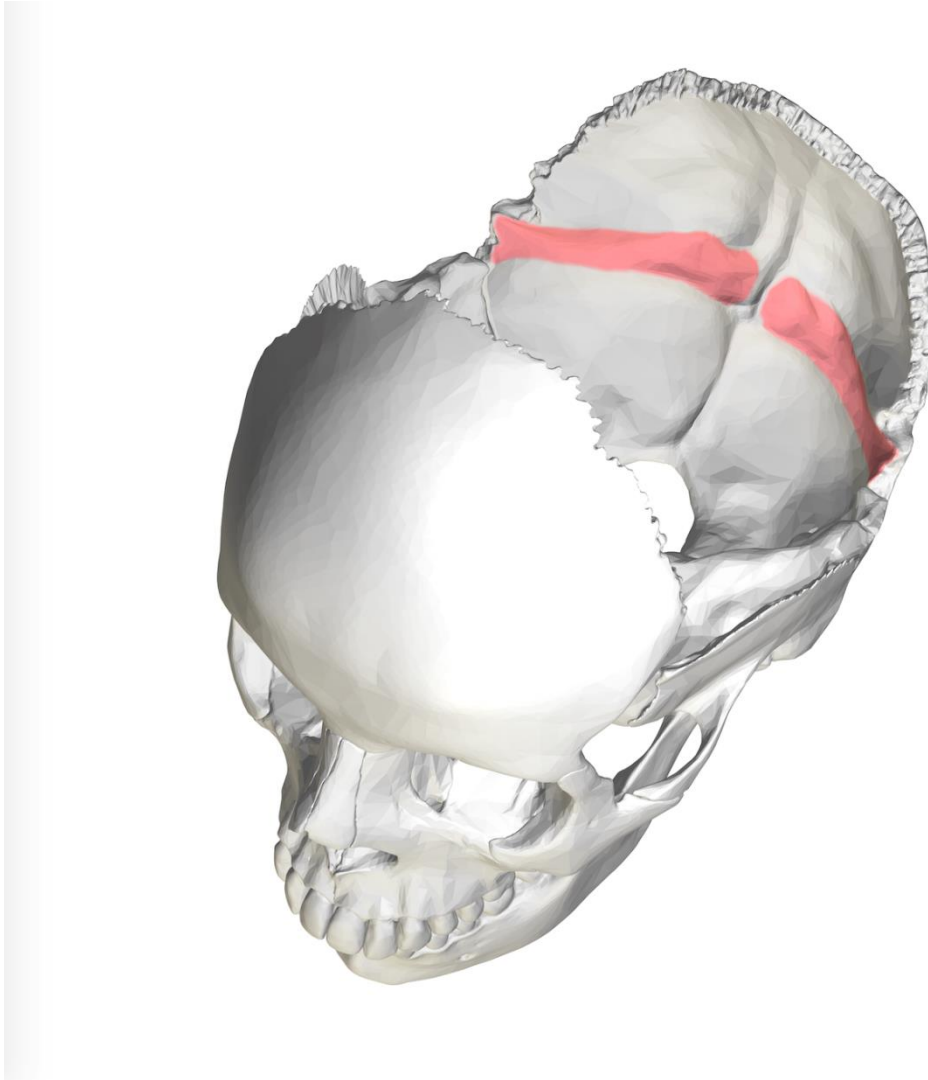
Two-hundred sectioned adult crania, defined as any age beyond “sub-adult” with all permanent teeth erupted and sectioned in a way that allowed for a clear view of the transverse sinus on the endocranial surface of the occipital bone, were examined from the collection at the American Museum of Natural History (AMNH). The geographical locations range from across North America, South America, Africa, Asia, and Europe. The AMNH specimen number and geographic location for each specimen is listed in Appendix 1. One hundred of the examined crania were from New World populations and one hundred were from Old World populations. The samples were chosen at random and examined for deviations in the shape and size of the transverse sinus by observation and palpitation of the bony landmarks associated with the sagittal venous sinus, the transverse sinus on the endo-cranial surface of the occipital and temporal bones (see Figure 1). By examining the endocranial surface of the occipital bone, it was noted if the transverse sinus was larger on one side of the bone relative the other. If there was no clear way to see the endocranial surface of the occipital bone or there was no defined deviance on the size of the paired sinuses, the specimen was excluded from the study. These specimens were not included in the final count of observed specimens due to the lack of data available on them. An example of the variation seen in the transverse sinus and the scoring system used in this thesis is illustrated in Figures 2-3.

Biological sex of each cranium was estimated by using the guidelines presented by White & Folkens (2005) and included in Appendix 1. The resulting samples were then compiled and compared to the population statistics retrieved from McManus (2009) and Hardyck & Petrinovich (1977) in Tables 1-2.

The StatCrunch (Person 2019) online statistical program was used to preform statistical analysis. Chi-Squared tests (test for independence and best fit) were performed to determine if

proportions of transverse sinus dominance seen within populations were significantly different than expected given known handedness proportions in the populations overall. The significance level was set at $p < 0.05$ to determine if a relationship was present between the observed populations from the AMNH and the expected population statistics on handedness, 90% right handed and 10% left handed based on a population of 200 for all data and 100 respectively for Old World and New World data separately (McManus 2009; Hardyck & Petrinovich 1977). In addition, data from Cornwall et al (2014) was tested against the observed data collected from the AMNH to determine if there was a statistical relationship between jugular foramen dominance and transverse sinus dominance.

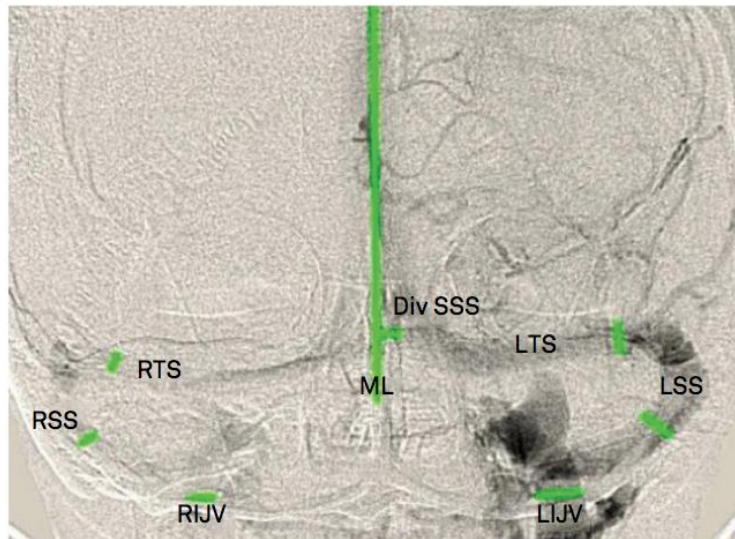
Figure 1



*Citation: CC BY-SA 2.1 jp File: Occipital bone - Groove for transverse sinus4.png Created: 9 March 2013

Figure 1. Highlighted is the transverse sinus, which spans the endocranial surface of the occipital bone of the skull and is defined by the presentation of bony landmarks which form the groove for the vein which transfers deoxygenated blood to the sigmoid sinus. Here, the right side of the sinus is “dominant” as the sagittal sinus bends to the right forming a more defined and larger right transverse sinus.

Figure 2



RTS: right transverse sinus; LTS: left transverse sinus; RSS: right sigmoid sinus; LSS: left sigmoid sinus; RIJV: right internal jugular vein; LIJV: left internal jugular vein; DivSSS: Division point of superior sagittal sinus; ML: midline.

Citation: Image from Batista et al (2017).

Figure 2: This image is from an angiogram showing the passage of blood through the transverse sinus. The vein sits in the transverse sinus, dictating the size of the depression in the bone. This image shows a left dominant transverse sinus, which means there is more pressure in the left vein creating a larger left depression

Figure 3

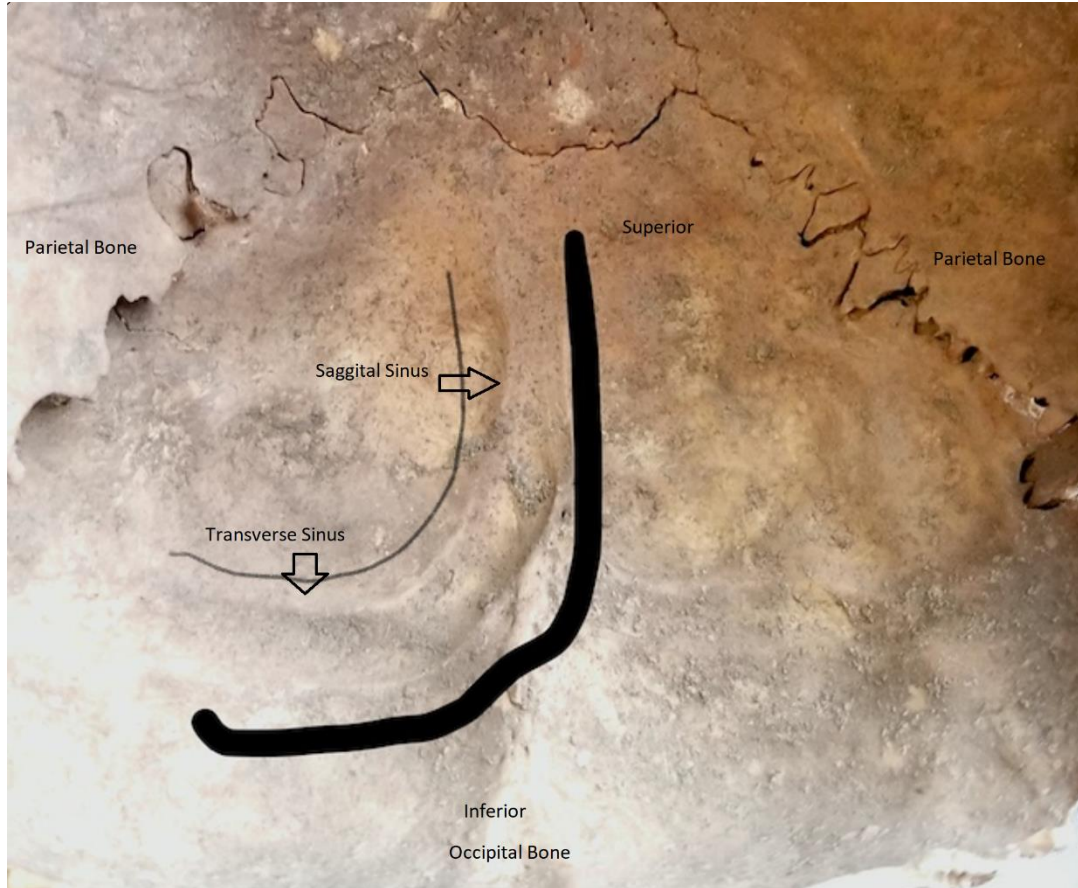


Figure 3: This is an image taken at the American Museum of Natural History in New York City demonstrating the right deviance in the transverse sinus. Image is in endocranial view, so that the right side of the specimen is on the left side of the image and vice versa. Note here the less impressive depression on the right side of the occipital bone; here the left transverse sinus is present but not significant enough to create a notable depression.

Photo credit: Brianne Finley, February 2019, American Museum of Natural History.

Results

Chi-squared tests show that data collected on transverse sinus asymmetry among 200 modern human specimens are significantly different from statistics for overall handedness in the general modern human population (Table 3). The Chi-squared tests cannot reject the null hypothesis that transverse sinus asymmetry and jugular foramen asymmetry are statistically equivalent (Table 4), suggesting that there may be a relationship between these two features.

Presentation of Data for Reference

Table 1: AMNH Transverse Sinus Asymmetry

Observed data, transverse sinus asymmetry, modern humans

	Right	Left	Total
Male	92	33	125
Female	52	23	75
Total	144	56	200

The data above in Table 1 is the count of the total right-sided asymmetrical dominant sinuses and total left sided dominant sinuses among males and females collected from Old and New World populations at the American Museum of Natural History. The data show a higher total of right dominant transverse sinus counts in both males and females. See Appendix for information on individual specimens.

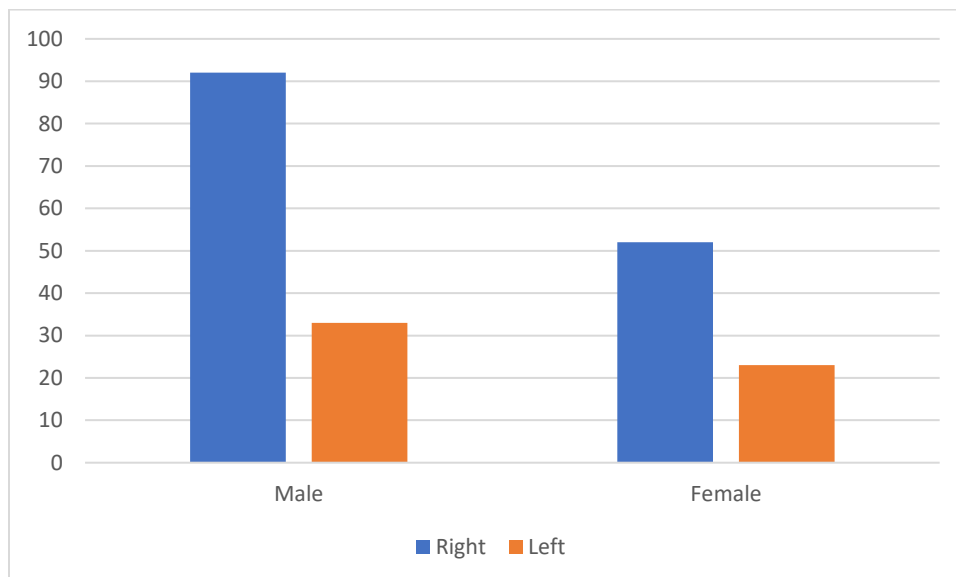


Table 2: AMNH Transverse Sinus Asymmetry v. Population Statistics

Observed data of transverse sinus asymmetry from the American Museum of Natural History and expected data reflecting population statistics from McMannus (2009)

	Right	Left
Observed	144	56
Expected	180	20

The data above in Table 2 is a comparison table of the observed transverse sinus dominant data from the American Museum of Natural History and the expected data retrieved from the McMannus (2009) study which is an idealized representation of handedness in society.

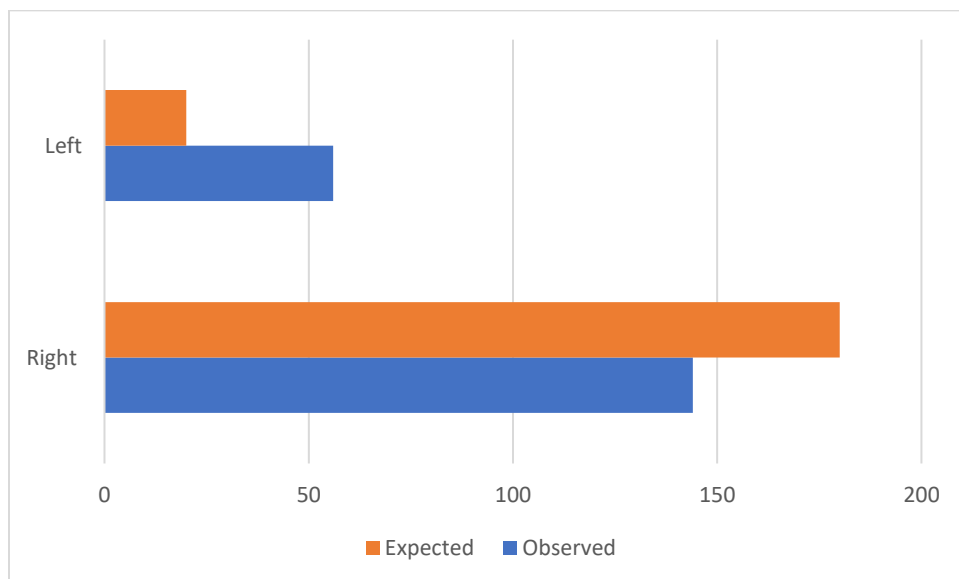


Table 3: Chi-Squared Test of AMNH Transverse Sinus Asymmetry v. Population Statistics

Chi-Square goodness-of-fit test designed to determine if the proportions of transverse sinus asymmetry seen in the data collected at the AMNH are similar to overall population statistics reported by McMannus (2009). A p-value less than <0.05 indicates that the proportions in the two samples are significantly different, and so we reject the null hypothesis that they are similar.

N	DF	Chi-Square	P-value
200	1	72	<0.0001

Observed	Expected
144	180
56	20

Table 4: Chi-Squared of AMNH Transverse Sinus Asymmetry v. Cornwall et al (2014) Data

Observed transverse sinus asymmetrical dominance data from the American Museum of Natural History vs. expected jugular foramen asymmetry data from Cornwall, Dias, Perumal, & Smith, (2014).

Chi-Square goodness-of-fit test designed to determine if the proportions of transverse sinus asymmetry seen in the data collected at the AMNH are similar to overall jugular foramen dominance data reported by Cornwall, Dias, Perumal, & Smith, (2014). A p-value of 0.4079 indicates that the proportions in the two samples are not significantly different, and so we accept the null hypothesis that they are similar.

	Right	Left	Total
Observed	144	56	200
Expected	158	51	209

Chi-Square test result:

Statistic	DF	Value	P-value
Chi-square	1	10.68493913	0.4079

Discussion

Results suggest that the observed sample of transverse sinus asymmetries is significantly different from overall population statistics on handedness, and therefore the idea that transverse sinus asymmetry closely tracks handedness in modern humans is not supported. Thus, taken at face value, the size of the transverse sinus should not be applied to the study of human osteology as a proxy for handedness given the current results. However, although the lack of an association with overall population statistics indicates that there is not a close or direct correlation between transverse sinus size and handedness, the overall prevalence of right-sided transverse sinus asymmetry dominance among the sampled crania is perhaps still noteworthy given the overall dominance of right-handedness in the overall population. In other words, although there is not a strong correlation, it is still possible that a weaker association does exist. This possibility could perhaps form the basis for future research on a more controlled cranial sample that includes information about known handedness. Because many museum skeletal collections do not have information on handedness recorded for their specimens, perhaps other medical collections could be used, or maybe known postcranial skeletal markers for handedness could be used in museum collections to estimate handedness before collecting data on the transverse sinus. This requires collections with full skeletons and not just cranial material, which are less common, but do exist.

In contrast to the lack of association between transverse sinus asymmetry and handedness, results of the chi-squared tests between transverse sinus asymmetry and jugular foramen asymmetry suggest that an association may exist (Table 4). This relationship suggests that transverse sinus asymmetry and jugular foramen size asymmetry may be connected, which is perhaps not surprising given their close anatomical relationship and creates an opportunity for a larger data pool to be referenced in handedness research (see Introduction). Again, similar to the situation with handedness and transverse sinus dominance, a more controlled sample with

specimens that are directly scored for both features (transverse sinus dominance and jugular foramen dominance) would go a long way towards resolving this issue in the future.

In summary, while this study represents a reasonable test of the connection between transverse sinus asymmetry and handedness, to more directly test this association future studies should try to find a large cranial collection with recorded handedness data; using the 90/10 ratio from McManus (2009) is not ideal. Even among the crania sampled, a different ratio may have been more appropriate, given that handedness proportions have fluctuated through time and possibly differ by sex as well as across geographic populations (e.g., McManus, 2009). In addition, the exclusion of specimens with no clear transverse sinus asymmetries may have slightly skewed the recorded transverse sinus asymmetry proportions, although the slight error involved by using this study design is unlikely to have altered the statistical results. Future research on skeletal data should include handedness, geographical location, sex, age, and details on where they were raised during critical times of coordination and specialized task development will shed much needed light on this topic and act as a more stable data set for testing research. Likewise, to confirm the results in this study for the association between transverse sinus and jugular foramen asymmetry, these features should be scored on the same sample of crania rather than on separate samples as was done here.

Recommendations

If possible, future studies should investigate the possible link directly by obtaining samples of crania from individuals where handedness is known. This type of sample may be difficult to acquire, but it is the only direct way to test the hypothesis regarding the connection between transverse sinus size and handedness. If a statistically significant relationship can be found given a more appropriate or precise sample, then applications to forensics as well as the

archaeological and fossil records may be profound (e.g., handedness in toolmaking, see Rumbaugh etc.)

Thus, several fields of anthropology could benefit from more precise data being examined regarding transverse sinus dominance and handedness. As the research in this thesis indicates, there are some suggestions of a relationship, though not statistically significant, between handedness in the population and transverse sinus asymmetry. If individuals who received an MRI scan or angiographies of their occipital, parietal, and temporal bones were administered a questionnaire which would allow the researcher to conclude the handedness of the individual and submitted both the MRI/ angiography and questionnaire, a database could be built determining biological sex, location, transverse sinus asymmetry dominance, and recorded handedness. This study would eliminate the need for the reliance on population statistics and would provide the direct response to the handedness questionnaire to the brain scan and the results would then be based on the deviations in the responses to the handedness questions and the actual way in which the transverse sinus deviates.

Conclusion

The data presented in this thesis suggests that there is no clear relationship between handedness and transverse sinus dominance in the skull. However, there is a statistical association between transverse sinus asymmetry and jugular foramen size asymmetry. More broadly, with the limited data on handedness in the sampled populations, this research is suggestive but not definitive, and future studies with more controlled samples should be completed before making recommendations to the broader field of physical/biological anthropology. With a more conclusive, controlled study, transverse sinus asymmetry data may become relevant to various fields of anthropology.

Appendences

Appendix 1

New World Sample

Specimen Number	Sex	Location	Transverse Sinus Dominant Side
991/31	M	New Jersey	R
99/8213	M	NY	L
99/6565	F	IL	R
991/829	F	FL	R
99/7895	F	TX	R
99/7958	M	New Mexico	L
99/9349	M	New Mexico	R
99/9253	M	New Mexico	L
99/8657	M	New Mexico	L
99/8744	M	New Mexico	R
99/9322	M	Colorado	L
H/16047	M	Utah	R
99/7479	F	Utah	R
99/7479	F	Utah	R
99/7712	M	Utah	R
99/9615	M	Arizona	R
99/9145	M	Arizona	L
99/9110	F	Arizona	R
VL/1203	F	LA	L
99/7302	M	CA	R
991/75-A	M	Alaska	L
99.1/183	M	Alaska	R
-/197	F	Alaska	R
-/169	M	Alaska	R
99/2682-B	M	Washington	R
99/2683	F	Washington	L
UL/274	M	Tasmania	R
UL/275	M	Tasmania	R
UL/269	F	Tasmania	R
99.1/442	F	Alaska	R
99/3768	M	Siberia	L
99/3777	M	Siberia	R
99/3767	F	Siberia	L
99/3718	F	Bearing Strait	L

99/3711	M	Bearing Strait	R
99/3709	M	Bearing Strait	L
99/1734	M	British Colombia	R
99/1737	F	British Colombia	L
99/1731	F	British Colombia	L
99/4261	M	British Colombia	R
99/4263	M	British Colombia	R
99/4269	M	British Colombia	R
99/8414	F	Greenland	R
99/7703	F	Greenland	L
99/7704	M	Greenland	L
99/A	F	Mexico	R
99/6	M	Mexico	R
99/9	F	Mexico	R
99/18	M	Mexico	L
99/2161	M	Mexico	L
99/2076	M	Mexico	L
99/9718	F	Mexico	R
99/3963	F	Mexico	R
99/4091	F	Mexico	L
99/4673	M	Mexico	R
99/163	M	Mexico	R
99.1/151	M	Mexico	R
99.1/713	M	Chile	R
99.1/726	F	Chile	L
99.1/716	M	Chile	R
1/2890	M	Brazil	R
99.1/2446	F	Brazil	L
VL/3341	M	Brazil	L
99/4530	M	Columbia	R
99.3831	F	Columbia	R
99/3832	F	Columbia	R
99/9931	M	Venezuela	R
99/9937	M	Venezuela	L
99/9922B	M	Venezuela	R
99/9773	M	Honduras	L
99/9772	M	Honduras	R
99/9776	M	Honduras	R
99/9895	F	Puerto Rico	L
99/9892	F	Puerto Rico	R
99/9894	F	Puerto Rico	R
99/9884	M	Puerto Rico	R
30/7732	M	Guatemala	R

30/9690	F	Guatemala	R
30/9692	M	Guatemala	R
30/7735	M	Guatemala	R
VL/4466	F	Peru	R
99.1/894	M	Peru	L
VL/566	M	Peru	L
99/6662	M	Peru	L
99/3675	M	Peru	R
99/3573	F	Bolivia	R
99/3358	M	Bolivia	R
B/2983	F	Bolivia	R
B/6548	M	Bolivia	R
99/3419	F	Bolivia	L
99/9493	F	Tahiti	R
99/9495	M	Tahiti	R
99/9496	F	Tahiti	R
99/9497	F	Tahiti	R
99.1/2001	M	Marquesas	R
99.1/1987	F	Marquesas	R
99.1/2017	F	Marquesas	L
VL/3359	M	Patagonia	R
VL/3353	M	Patagonia	R
VL/3354	F	Patagonia	R

Old World Sample

Specimen Number	Sex	Location	Transverse Sinus Dominant Side
3560	M	Cech, Bohemia	R
3516	F	Cech, Bohemia	L
3508	F	Cech, Bohemia	R
3528	M	Cech, Bohemia	R
3541	F	Cech, Bohemia	R
3538	M	Cech, Bohemia	R
1993	M	New Guinea	R
1451	F	New Guinea	L
2227	M	New Guinea	R
243	F	Australia	R
1627	F	Australia	L
1578	M	Australia	R
9232	M	Soloman Islands	R
9644	F	Soloman Islands	L
9234	M	Soloman Islands	R
119	F	New Hebrides	R
8076	F	New Hebrides	R
1115	M	New Hebrides	R
2897	M	New Britain	L
4645	M	New Britain	R
1121	F	Mongolian	R
8020	M	Mongolian	R
8032	F	Mongolian	L
8015	M	Mongolian	R
995	F	India	L
8422	M	India	R
2461	M	India	L
1294	M	Japan	R
4672	M	Japan	R
1634	M	Japan	R
1761	M	China	R
1737	F	China	R
1763	M	China	L
5242	M	Singapore	R
5257	F	Singapore	R
5258	F	Singapore	R

2915	M	West Africa	L
2914	M	West Africa	R
2017	M	West Africa	R
1076	F	Afganastan	R
1080	M	Afganastan	R
1077	F	Afganastan	L
1170	F	Eqypt	R
1169	M	Eqypt	R
1168	M	Eqypt	R
2920	M	Eqypt	R
2923	M	Eqypt	R
1661	M	Eqypt	R
3225	M	Eqypt	L
644	F	Eqypt	L
961	F	Myrina	R
372	M	Rosmas	R
371	M	Rosmas	R
556	M	Rosmas	R
965	M	Greece	R
942	F	Greece	R
2076	M	Greece	R
2070	F	Greece	L
2064	M	Greece	L
2062	F	Greece	R
2073	M	Greece	R
1087	M	Turkey	L
1088	M	Turkey	R
1083	M	Turkey	R
1264	M	Turkey	L
1276	F	Turkey	L
1042	F	Turkey	R
1047	F	Turkey	R
1045	M	Turkey	R
924	M	Turkey	R
1929	M	Turkey	L
967	M	Turkey	R
968	F	Turkey	R
1313	M	Syria	R
7214	F	Syria	R
7213	M	Syria	L
1214	M	Syria	R
1215	M	Syria	R
1862	F	Austria	R

1868	M	Austria	R
1525	F	Austria	R
2491	M	Austria	R
2496A	F	Austria	R
3670	F	Austria	R
3676	M	Austria	R
5037	M	Hungry	R
4930	M	Hungry	R
4936	M	Hungry	R
4938	M	Hungry	L
5221	M	Hungry	R
5219	F	Hungry	R
5172	M	Hungry	L
3583	M	Russia	R
3589	M	Russia	R
3594	F	Russia	R
3581	F	Russia	R
3392	M	Russia	R
4131	M	Germany	L
4132	M	Germany	L
4133	M	Germany	R

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