Project title: Computer Science meets Anthropology: a novel approach for reconstructing locomotion from fossil human footprints

Funding program: National Science Foundation, SBE Interdisciplinary Postdoctoral Research Fellowship

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Project abstract:

Intellectual Merit:

Our bipedal locomotion is a unique and fundamental behavior that has driven and shaped the evolution of our species. Yet the evolutionary history of human bipedalism remains poorly understood. In recent years, discoveries of several sites preserving fossil human footprints have offered an exciting new form of data from which to understand the evolution of bipedalism. However, novel techniques will be required to analyze the wealth of information contained within these invaluable sources of data. This project is transformative in its experimental approach for linking footprint morphologies to the patterns of locomotion that produced them. Experimental biomechanics will be bridged with techniques for robotic vision, to understand how details of locomotion are recorded by 3-D footprint morphology. Those data will be used to develop powerful machine learning algorithms, applying technologies from a rapidly-growing field at the intersection of computer science and statistics, to build detailed reconstructions of locomotion from fossil human footprints. By doing so, this project will shed new light on the evolutionary history of our species.

Broader Impacts:

This project is the first to apply these interdisciplinary techniques to paleoanthropological questions. Consistent efforts will be made to disseminate results to a diverse range of professional audiences in biological anthropology, evolutionary biology, and computer science. The PI will also engage the broader public in this research through ongoing collaborations with the Smithsonian Institution's Human Origins Program. Results of this research, and its implications for understanding the evolution of our species, will be presented through regular lectures and participation in educational programs at the museum's Hall of Human Origins. The PI and co-PIs plan to recruit and train research assistants from The George Washington University's Trachtenberg Scholars Program. This program supports the education and training of promising students from the District of Columbia public school system, who typically come from groups historically underrepresented in STEM disciplines.

Overview

Our bipedal locomotion is a unique and fundamental behavior that has driven and shaped the evolution of our species. Yet the evolutionary history of human bipedalism remains poorly understood, in large part because no techniques can identify absolute, unequivocal evidence of habitual locomotor behaviors from fossil human skeletal morphology alone. This study examines a different and relatively understudied type of paleoanthropological data in the form of fossil human footprints. Footprints represent direct, immediate records of the locomotion practiced by our extinct relatives. However, current methods for predicting the locomotor actions represented by particular sets of footprints are very limited in their power. This study will apply two new methods for visualizing and capturing the process of footprint formation, including biplanar x-ray to capture motions of the foot below the surface and dense scene capture for recording limb movements above the surface. These data will serve as inputs for powerful analytical techniques from machine learning, which can generate robust algorithms for predicting detailed subsurface and above-surface motion patterns from footprint trackways. These algorithms can then use data from fossil human footprints dating to 3.6 and 1.5 million years ago to generate robust predictions of locomotor biomechanics and provide a new perspective and opportunity to evaluate long-standing questions about the evolutionary history of human bipedalism.

Intellectual Merit

Fossil human footprints provide unique evidence of ‘fossilized behavior’ in that they are direct snapshots of our extinct relatives interacting with their environment in order to achieve their patterns of locomotion. In recent years, continued discoveries have greatly expanded the sample of footprints in the human fossil record and these discoveries underscore the importance of developing techniques that can use these new sources of paleoanthropological data to better understand the evolutionary history of our species. This project is transformative in its approach for experimental data collection and analysis, which bridges experimental biomechanics with the latest techniques for robotic vision. It will then use those data to develop powerful machine learning algorithms, applying the latest technologies from a budding field at the intersection of computer science and statistics, for reconstructing patterns of locomotion from fossil footprint data. This project will represent the first ever applications of these data collection and analysis techniques to research questions in paleoanthropology. Therefore, this project has the potential to spark ongoing collaborations between these fields and lead to new subfields at their intersections.

Broader Impacts

This project will be the first to apply these data collection and analysis techniques to paleoanthropological questions. As a result, consistent efforts will be made to disseminate results of the research to a diverse range of journals and professional conferences in the fields of biological anthropology, evolutionary biology, and computer science.

The PI has ongoing collaborations with the Education and Public Outreach department of the Smithsonian Institution’s Human Origins Program. Results of this research and its bearing on the evolutionary history of our species will be presented to the broader public through regular lectures and participation in interactive programs within the museum’s Hall of Human Origins.

The PI and co-PIs have established plans to recruit and train undergraduate research assistants from The George Washington University’s Trachtenberg Scholars Program. This program supports the education and training of promising students from the District of Columbia public school system, who typically come from groups historically underrepresented in STEM disciplines. Consistent efforts will be made to recruit and train students from those groups.

I. INTRODUCTION

Darwin (1871) was one of the earliest researchers to suggest that bipedalism played a fundamental role in driving and shaping our species' evolution. Habitual bipedalism is a unique behavioral characteristic that distinguishes modern humans from the other extant great apes, and which imposed novel biomechanical demands that selected for our derived anatomy and other aspects of our adaptive regime. Yet much remains unknown about the evolutionary history of human bipedalism. For example, did multiple forms of bipedalism evolve within the hominin clade? Or did all earlier hominins walk bipedally in the same manner as modern humans do today?

Paleoanthropologists have traditionally pursued answers to such questions by trying to reconstruct habitual locomotor behaviors from skeletal morphology. However, this approach is complicated by the fact that fossil taxa possess unique combinations of anatomical traits, some of which mirror the morphology of modern humans while others are more similar to nonhuman great apes. The consequences of this situation are apparent in the gridlocked debate over the locomotor anatomy of *Australopithecus afarensis*, a fossil relative of ours that lived between three and four million years ago (for a review see Ward, 2002). Through interpretations of the same skeletal anatomy, some researchers have argued for a humanlike pattern of habitual bipedal locomotion (e.g., Latimer & Lovejoy, 1989, 1990a,b) while others have argued for the retention of climbing behaviors and a facultative mode of bipedalism similar to that of nonhuman great apes (e.g., Stern & Susman, 1983; Susman et al., 1984). This debate cannot be resolved because there are currently no methods that can identify absolute, unequivocal evidence of habitual locomotor behavior from skeletal morphology alone.

Fossil hominin footprints circumvent these issues by offering direct windows to the immediate locomotor behaviors of our ancestors and relatives. They record the exact ways in which fossil hominins interacted with deformable substrates while moving across their landscapes. But until recently, the record of fossil hominin footprints predating the emergence of *Homo sapiens* (about 200 thousand years ago) was sparse; one famous set of hominin footprints dating to about 3.6 Ma was known from Laetoli, Tanzania (Leakey & Hay, 1979), and a few poorly preserved tracks dating to about 1.4 Ma were discovered at Koobi Fora, Kenya (Behrensmeyer & Laporte, 1981). Consequently, there was limited potential for footprints to shed light on whether, and how, forms of bipedalism differed and changed through time among our extinct relatives. However, the recent announcement of hominin footprint trackways dating to ca. 1.5 Ma at Ileret, Kenya (Bennett et al., 2009), and the continued discoveries and excavations of nearly a half-dozen unique footprints sites from that same locality and time period (Richmond et al., 2011, in prep), have dramatically changed this situation. These early hominin footprint sites offer a substantial data set which can shed new light on fundamental questions about the evolution of bipedal locomotion among our fossil relatives. With the right approach, comparisons of fossil hominin footprints from Laetoli and Ileret could transform our understanding of the relationships between skeletal morphology and function in the extinct hominin taxa which produced those footprints, and offer the first direct test of the hypothesis that different styles of bipedalism existed in our evolutionary history.

However, extracting detailed information about locomotion from footprints has proven exceedingly difficult. Researchers have been able to estimate velocity or cadence from the relative stride lengths of fossil hominin trackways (e.g., Charteris et al., 1981; Dingwall et al., 2013) and exclude the possibility of particular types of gait postures (e.g., Raichlen et al., 2010), but no methods exist for generating direct quantitative predictions of the kinetic and kinematic variables that are almost certainly preserved in fossil hominin footprint morphologies. Previous studies have found that only weak relationships exist between footprint morphologies and patterns of foot function as measured on plantar pressure pads (D'Août et al., 2010; Bates et al., 2013; Hatala et al., 2013). Either the foot must function differently, or patterns of foot function must be expressed in different ways, when humans walk on deformable substrates.

In light of these results, the PI's dissertation research has taken an alternative approach to analyze footprints in a new multidimensional context, using linear mixed effects models to examine how multiple biomechanical variables (kinetic and kinematic) simultaneously interact to produce footprint shape changes. Using this approach, we have found that distinct patterns of footprint shape change can be explained by certain signatures of human bipedalism (Hatala et al., in prep). For example, among a large sample of humans moving at different speeds (n=490) the first and second principal components of footprint shape variation (37% and 20% of total variance) are significantly influenced ($p<0.05$) by the fixed effects of the shape of the normal force curve and the use of the human toe-off mechanism, respectively. This finding represents the first evidence that detailed signatures of locomotor biomechanics can be inferred from the shapes of human footprints. Yet the amount of unexplained footprint shape variance that exists in these linear mixed effects models suggests that we can refine our approach to achieve more powerful predictive models for inferring foot function and overall locomotor patterns from footprints in the fossil record (e.g., Figure 1).

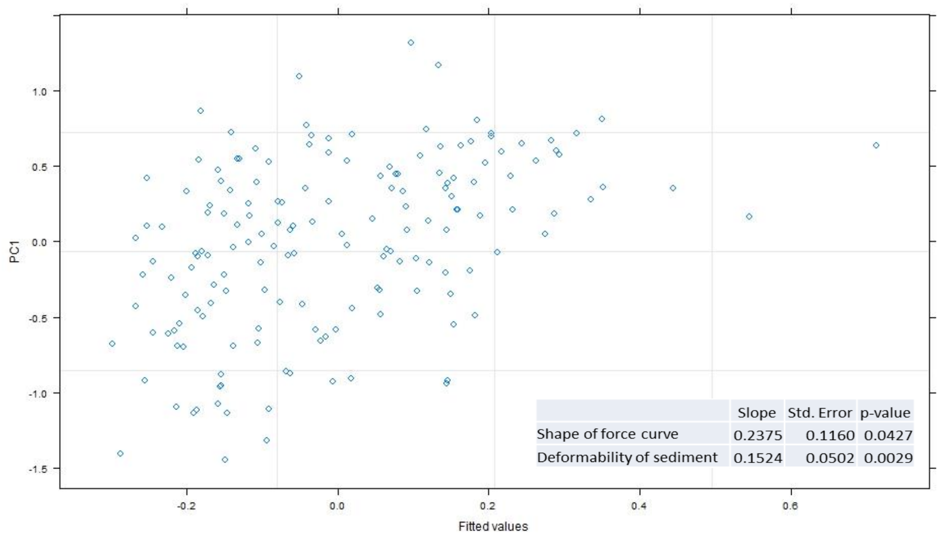

Figure 1: A linear mixed effects model explaining variation in the first principal component of footprint shape variation. This model includes two significant ($p<0.05$) fixed effects – the shape of the normal force curve and the deformability of the sediment. A linear relationship exists but considerable variance remains unexplained (high standard error).

Our results showing significant relationships between locomotor variables and patterns of footprint shape variation (Hatala et al., in prep) are important and exciting first steps towards establishing methods for inferring details of locomotion from footprints in the human fossil record. However, we can improve upon these methods, and develop new ones, by building a more thorough understanding of the mechanical processes through which locomotion is recorded in footprints. **We intend to develop such an understanding by applying two new methods for visualizing, in previously unachieved detail, the mechanical processes of footprint formation at both the subsurface and above-surface levels.** The data made available by these new visualization techniques will allow us to build the first quantitative models for predicting detailed subsurface and above-surface movements from footprints in the human fossil record. **Using experimental biomechanical data, this project will apply machine learning techniques to develop robust algorithms for predicting patterns of foot function and lower limb motion sequences from the morphology and spatial distribution of footprints.** The resulting machine learning models will be used to extract detailed locomotor biomechanics from newly-uncovered fossil hominin footprints. **This approach represents a novel combination of analytical techniques from computer science with data from anthropology, which will provide a direct test of the long-standing hypothesis that multiple strategies for bipedalism existed during our evolutionary history.**

II. RESEARCH OBJECTIVES AND METHODS

A) Visualizing the mechanical process of footprint formation

Part A of the project is a two-phase investigation of methods for visualizing the formation of footprints above and below the surface.

Subsurface visualization (Personnel: Hatala, Prof. Gatesy)

Previous studies have shown that there is a disjunction between patterns of foot function as quantified by plantar pressure pads and the morphologies of footprints produced by the same foot during the same gait sequence (e.g., D'Août et al., 2010; Bates et al., 2013; Hatala et al., 2013). As a result, no methods currently exist for actually inferring patterns of foot function from footprints. Furthermore, no pressure- or force-sensing equipment is available that can measure forces at the interface between the foot and the deformable surface, without interfering with the deformation process. Here we propose a novel approach for understanding human foot function on deformable substrates, which will in turn enable the first opportunity to quantitatively interpret patterns of foot function from footprints.

We intend to utilize X-ray Reconstruction of Moving Morphology (XROMM), a method developed by researchers in biomechanics working alongside computer scientists, in order to directly visualize the foot, and quantify its motion, as it moves through a deformable substrate (e.g., Ellis and Gatesy, 2013). These experiments will be performed at the W. M. Keck Foundation XROMM Facility at Brown University. XROMM has proven to be an accurate and reliable technique for quantifying 3-dimensional (3-D) motions visualized through biplanar x-ray (Brainerd et al., 2010; Gatesy et al., 2010). Here, we plan to apply this technology in a new way to quantify dynamic changes in 3-D plantar shape, as an individual's foot penetrates into a deformable substrate, support's the body's weight, then exits.

We will recruit 20 subjects (10 male, 10 female) to walk across a 15-meter long elevated trackway, in the middle of which will lie a 3-meter long and 10 cm deep container (inlaid to the trackway such that it is level with the surrounding solid ground) that is filled with standardized sediment. This sediment is a mixture of powder, consisting of rounded glass 'bubbles' approximately 60 microns in diameter (similar to fine-grained sand), along with ball clay and water. Although this material certainly differs from those that preserve footprints in the fossil record, its radiopacity is ideal (natural silty-clay sediments obscure x-rays), and uniform particle size throughout the material allows us to control that variable.

We will affix an array of radiopaque hemispheric metal beads across the bottom of each subject's feet, with markers spaced to divide the surface into roughly 1.5 cm triangles (approximately 100 markers per foot; Figure 2). They will be adhered to the foot using Kryolan medical adhesive which is non-toxic, appropriate for use on sensitive skin, and can be easily removed with Kryolan adhesive remover. The 3-dimensional space of the biplanar x-ray view will be calibrated before each trial, such that the markers on the foot (Figure 2) can be accurately oriented and scaled from their positions in the biplanar x-ray video.

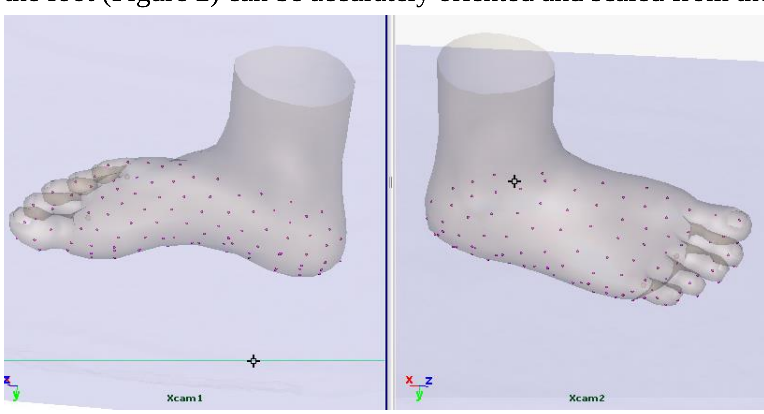

Figure 2. An animated 3-D foot model, viewed from the perspective of the biplanar XROMM cameras. An array of approximately 100 markers were evenly-spaced to produce roughly 1.5 cm triangles across the plantar surface. Only minimal overlap exists, showing that the 3-D plantar shape can be successfully digitized at this resolution.

Each subject will move across the trackway and create footprints for a total of nine trials at their self-selected comfortable walking speed. Substrate conditions will be varied to assess the influence of substrate deformability on foot function. Each subject will conduct three trials on firm ground before completing up to six more on substrates of increasing compliance. Substrates will be made more compliant by increasing the level of hydration, which will be measured using a digital hydrometer. The protocol will be thoroughly tested using cadaver feet, such that visualization parameters of the x-ray equipment can be optimized before exposing human subjects. After each footprint is created, it will be captured in several high-resolution (22.3 MP) photographs from different angles and orientations, such that detailed and accurately scaled 3-D dense surface models can be rendered using Agisoft PhotoScan photogrammetry software (AgiSoft LLC, St. Petersburg, Russia). Given that the majority of fossil human trackways analyzed in this project were likely produced at walking paces (Raichlen et al., 2008; Dingwall et al., 2013) the production and analysis of experimental footprints at walking speeds are of highest priority. Furthermore, the number of trials per subject must be limited to operate within safe limits for x-ray exposure. Consequently, the effects of speed will not be explored in detail in these experiments.

Once 3-D motion data are collected, movements of marker beads will be digitized using Autodesk Maya software (Autodesk Inc.; San Rafael, CA) to provide 3-D x-y-z coordinates for each point at each frame during ground contact. We will be able to quantify the dynamic shape of the foot throughout the step, and also during the ontogeny of the footprint. With these data we can compute relative accelerations of each marker, and subsample points to quantify average accelerations of areas that correspond to particular anatomical regions of the foot (e.g., the heel, or the medial longitudinal arch). This will provide the first quantitative data on the external function of the human foot when traversing deformable substrates. Furthermore, these data will tell us the exact 3-D position of the foot as it progressively forms a footprint. We can address for the first time the question of whether footprint shape actually matches the maximum vertical descent of the dynamic shape of the foot or whether infill, sediment pushup, and other aspects of the substrate actually cause track morphology to deviate from a direct representation of the foot's dynamic shape. With these data we can test three hypotheses:

H_1: The patterns of dynamic shape change to the plantar surface of the foot are influenced by the compliance of the substrate on which locomotion occurs.

H_2: Areas of the plantar foot which experience maximum accelerations during the time of ground contact will correlate with the deepest points of the footprint.

H_3: The 3-D shape of a footprint represents a mirror image of the foot's dynamic 3-D shape changes that occur throughout the gait cycle (i.e., foot motion is not distorted or lost).

Above surface visualization (Personnel: Hatala, Prof. Sibley)

With the spatial distribution of footprints, we can be certain of the locations of sequential foot placements that occurred during a locomotor event. Previous research has shown that the length of a stride measured from a human trackway can be informative of the speed or cadence at which an individual was moving (e.g., Charteris et al., 1981; Dingwall et al., 2013). Our most recent analyses from the PI's dissertation research are providing the first evidence that 2-dimensional (2-D) joint kinematics significantly influence the internal shape of footprints (Hatala et al., in prep). For example, among a large sample of humans moving at different speeds (n=490) the third principal component of footprint shape variation (which explained 13% of total variance) was significantly affected by angular excursions at both the hip and knee joints (Figure 3). These 2-D results suggest that gross kinematic variables, such as velocity, as well as more subtle patterns of limb motions leave signatures that can be detected from a combination of the spatial distribution and the internal morphology of consecutive footprints. However, controlled 3-D data are necessary in order to fully investigate and understand these relationships.

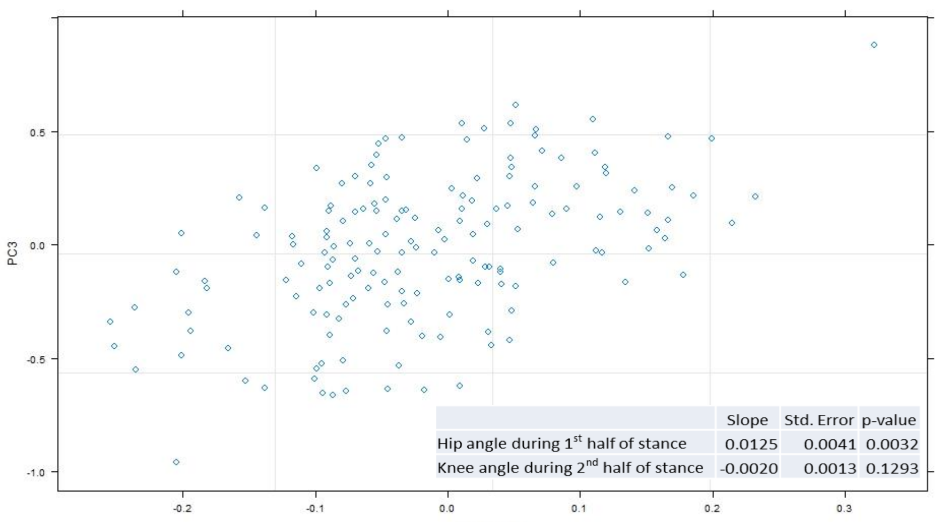

Figure 3: A linear mixed effects model for the third principal component of footprint shape variation. Only hip excursions have a significant independent effect, but knee excursions are also present in the model with lowest AIC value. As in Figure 1, a linear relationship exists but considerable variance remains unexplained (high standard error).

We intend to use a newly developed instrument for large-scale, real-time 3-D dense surface modeling at sub-millimeter resolution (Figure 4), which will allow us to render detailed 3-D scene captures of humans interacting with a deformable substrate during the creation of footprints. The quantification of the relationships between 3-D motion patterns and both the spatial distribution and the internal morphology of footprints will enable us to unlock much of the biomechanical information that is stored within the footprints of our fossil ancestors.

This portion of experimental data collection will take place at The George Washington University (GWU), in the Motion Capture and Analysis (MOCA) laboratory. Recent support from NSF-MRI 1337722 has made possible the instrumentation of the GWU MOCA lab with a novel system capable of large-scale, real-time, dense 3-D motion capture (Figure 4). This system fuses simultaneous data inputs from infrared optical motion capture (VICON), depth cameras (RGB-D sensors), grey-scale cameras, color cameras, and long-range laser scanners (LiDAR), to allow for real-time dense surface modeling of a focused 2 m^3 volume, with sub-millimeter resolution, at a rate of 30 Hz. The rest of the room is captured at sub-centimeter resolution. This instrument can therefore capture in detail the progressive deformation of a footprint as it is being created within that focused volume. Simultaneously, VICON optical motion cameras can capture (at up to 120 Hz) the 3-D joint kinematics of the subject producing that footprint.

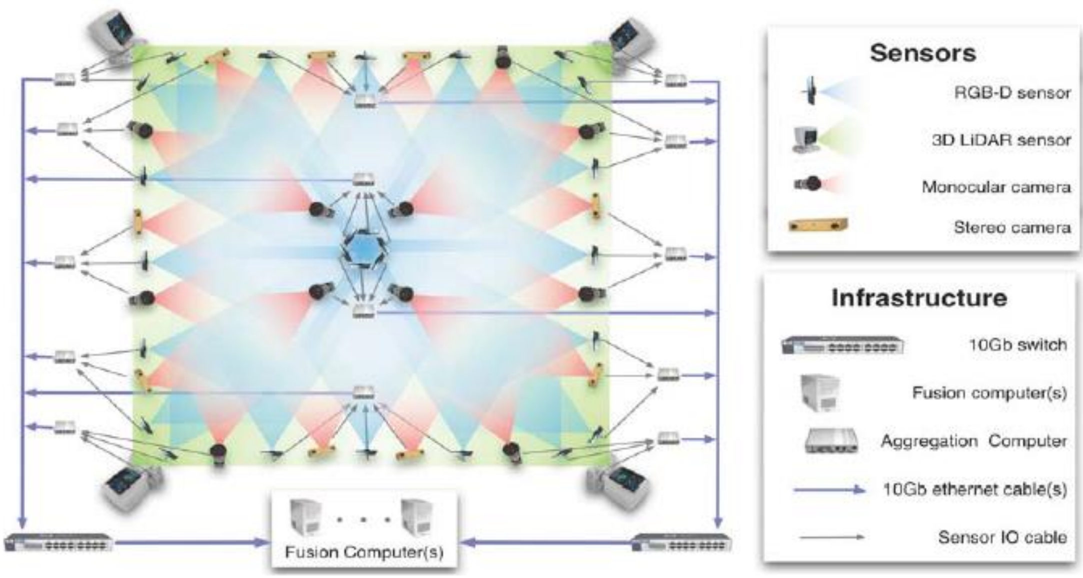

Figure 4. Sensor-suite, networking and computing architecture covering the GWU MOCA laboratory. 20 RGB-D Sensors ring the room, and 6 more sit in the center on the ceiling (total of 26). LiDAR, stereo cameras and monocular cameras provide high-resolution imagery for model texturing and for focused 3D depth estimation. 10 GB networking infrastructure and high-end multi-GPU workstations fuse data from the array of sensors in real-time.

We plan to construct a 15 m long wooden trackway, elevated 10 cm from the ground. A 3m long section in the middle will consist of a container holding sediment taken directly from a layer which preserves 1.5 million year old fossil hominin footprints at Ileret, Kenya (this sediment has already been exported to the US by the PI). This sediment will fill the 10 cm depth and will be leveled such that it is continuous with the rest of the wooden trackway. The focused ceiling camera rig, including the depth cameras, will be focused on the center of this sediment patch.

We will recruit another 20 subjects (10 male, 10 female) to walk and run across this trackway for a total of 36 trials each (three sets of 12 trials per subject). Three sets of trials will differ based on sediment hydration levels, as water will be added to the sediment to reach 0%, 15%, and 30% hydration, measured by a digital hydrometer. For each sedimentary condition, each subject will conduct twelve trials by employing four different self-selected speeds: three trials at a comfortable walk, three at a fast walk, three at an endurance running pace, and three at a sprint. In each trial, the dense scene will be captured at 30 Hz and sequentially modeled by the fusion computers (Figure 4). Meanwhile, subject kinematics will be captured in high-resolution at 120 Hz by channeling the lab's 10 Vicon T160 cameras to a separate computer with Vicon Nexus software (Vicon Motion Systems Ltd., Oxford, UK).

The real-time dense surface capture of the sediment as a subject produces a footprint will allow us to track and quantify vectors of shape deformation to the substrate as the subject interacts with the surface. The simultaneous capture of the subject's kinematics will allow us to quantitatively relate deformation of the substrate to above-surface subject 3-D motion patterns. Furthermore, at least for walking trials (stride lengths during fast running may exceed 3m) we can gather data on the 3-D topography *and* spatial relationships between consecutive footprints. Even if both footprints do not occur within the $2m^3$ densely captured volume, we can use handheld photogrammetry to capture any desired part of the sediment trackway at sub-millimeter resolution. Simultaneous capture of subject kinematics will again allow us to establish quantitative relationships between detailed 3-D scenes and the motion patterns that produced them. These data will allow us to test two hypotheses that are imperative for decoding the biomechanical variables recorded within footprints:

H_1: Subject kinematics will change according to sedimentary conditions. When hydration levels are increased, and the substrate becomes more readily deformable, kinematic strategies will be altered to compensate for the conditions in which locomotion is being produced (e.g., angular excursions at the hip and knee may increase when traversing more deformable substrates).

H_2: Rates and amounts of substrate deformation will correspond to patterns of 3-D coordinated limb motions. For example, the greatest amount of substrate deformation will occur while the limb is achieving its greatest cumulative accelerations (e.g., during initial contact or propulsion).

B) Developing predictive models for inferring locomotion from fossil human footprints

Part B of the project involves the development and application of predictive models for interpreting locomotor variables from footprint assemblages.

Building predictive models (Personnel: Hatala, Prof. Sibley)

The application of these new visualization techniques will produce two 'big' multidimensional data sets that both permit and require analytical techniques that can make appropriate use of such large amounts of data. Taking advantage of Prof. Sibley's expertise in computer vision and estimation theory and in analyzing such high-dimensional data, we intend to develop machine learning algorithms to model the events captured by each data collection process. The rapidly-growing field of machine learning takes advantage of advancing computational technologies to implement statistical models which learn to predict patterns based on multidimensional training data (e.g., Murphy, 2012). Such an approach is highly relevant to the proposed study and the application of these methods is novel to paleoanthropology.

First, we wish to develop a model for predicting from the internal 3-D topography of a footprint the sequence of foot shape changes that produced it. The high-resolution photogrammetric models of the footprints created during XROMM experiments will provide our training data of footprints that were produced by known patterns of foot shape changes. We can extract the detailed 3-D morphology of those footprints using surface semilandmark methods from geometric morphometrics (Gunz et al., 2005). We will define landmarks (features) at the tip of the big toe, posterior-most heel, and the borders of the fifth and first metatarsal heads, then apply an evenly-spaced mesh of 200 sliding semilandmarks across the internal surface of the print. With feature engineering and high-dimensional training data, we will learn probabilistic models to predict the 3-D shape of the foot (i.e., the marker grid on the foot during XROMM experiments) from foot strike through toe-off. We will train and test the performance of predictive models within our experimental data set such that they can learn to provide the most accurate predictions of foot postures during footprint creation.

Second, we will build a model for predicting overall subject movement patterns from the internal morphology and the spatial distribution of footprints within a trackway. Here, we will use the end point of our dense captures of 3-D footprint scenes (after the subject has departed) as the training data input for the output of the specific locomotor sequence that produced those footprints. Because each dense scene consists of calibrated spatial coordinates, we can extract from them measures of stride length and the orientation of footprints relative to the direction of travel. We will also remove ‘chunks’ of the dense scene containing individual footprints and digitize them using landmarks and surface semilandmarks, as described above. We can then build and improve models for predicting 3-D patterns of limb motions from the spatially calibrated 3-D dense scene of the footprints that those motions produced.

Applying predictive models to fossil human footprints (Personnel: Hatala, Prof. Richmond)

Once predictive models have been developed and improved using these substantial sets of ‘ground-truthed’ experimental data, they can be applied to the analysis of footprints from the human fossil record. **This will result in the first-ever detailed reconstructions of the subsurface and above-surface motion patterns that are represented by the 3.6 Ma fossil hominin footprints at Laetoli, Tanzania and the 1.5 Ma trackways at Ileret, Kenya**.

Before applying these predictive models to analyze those two assemblages of fossil hominin footprints, fossil data must be captured in a manner through which it will match the format of the experimental data set. In the past few years, the 3.6 Ma fossil trackways at Laetoli were partially re-excavated and they were captured using high-resolution photogrammetry (Matthews et al., 2011). Dense 3-D surface models of the Laetoli trackways, at sub-millimeter resolution, are therefore available for analysis through collaboration with the site directors.

Fossil hominin footprints at Ileret, Kenya continue to be unearthed from more than a half-dozen unique sites (Richmond et al., in prep). The PI has been working on the excavation of these footprint sites alongside Prof. Richmond throughout his dissertation research. As a result, the PI has already used photogrammetry to capture high-resolution 3-D dense surface models of all individual footprints that have been uncovered to date. However, at all of these sites, additional footprints continue to be uncovered, and certain trackways lead directly into walls of excavation areas. Consequently, the fossil sample is certain to increase substantially within the next 2 years. The PI plans to continue his work with Prof. Richmond to excavate these footprint sites at Ileret, and likely discover new ones, in order to build upon the fossil dataset which this project will be able to analyze in innovative ways.

Once these data have been collected, they will be used to test two fundamental hypotheses:

H_1: The fossil hominin footprints at Ileret and Laetoli record evidence of different forms of bipedalism that existed within our extinct relatives.

H_2: The Ileret footprints, dating to 1.5 Ma, record a form of bipedalism that more closely resembles our own than do the Laetoli footprints from 3.6 Ma.

III. SIGNIFICANCE OF PROPOSED RESEARCH

Intellectual Merit

Bipedalism is a fundamental modern human behavior yet paleoanthropologists have struggled to understand its evolutionary history. Debates over the interpretation of locomotor modes from skeletal anatomy have reached an impasse because no currently available analytical methods can offer unequivocal evidence of habitual locomotor behaviors. The proposed study will produce the first robust quantitative methods for reconstructing locomotor patterns represented by footprints in the human fossil record. These will provide direct data regarding the strategies used for locomotion by our extinct ancestors at a remarkable level of detail that has never been achieved. These results will offer new and exciting ways to address long-standing questions about the evolutionary history of human bipedalism.

This project is transformative in the manner by which it brings together new technologies and innovative techniques from multiple disciplines to address a question that is fundamental to the understanding of our evolutionary history. It will integrate recently-developed visualization methods (XROMM, real-time 3-D dense scene modeling) to capture the process of footprint formation on subsurface and above-surface levels, in ways which were never before possible. These data will then form the input and ground truths to develop machine learning algorithms for predicting detailed locomotor biomechanics from the internal morphology and distribution of footprints within a trackway. These analytical methods come from a rapidly-growing field at the intersection of computer science and statistics, and this project will represent their first application within the field of biological anthropology. **By providing the first applications of these data capture and analysis techniques to paleoanthropological questions this project has the potential to foster extensive collaborations between anthropology and computer science, and could lead to the emergence of new subfields at their intersection for developing and applying innovative approaches to long-standing anthropological questions.**

Broader Impacts

This project will be the first to apply these data collection and analysis techniques to research questions in biological anthropology. Consistent efforts will be made to disseminate the results of this research to a diverse range of journals and professional conferences, within the fields of anthropology, biomechanics, and computer science.

Results of this research, and their implications for the evolutionary history of our species, will consistently be presented to a broad public audience. The PI will continue his ongoing work with the Education and Public Outreach department of the Smithsonian Institution's Human Origins Programs. He regularly gives 'HOT (Human Origins Today) Topics' lectures in the Hall of Human Origins, and participates in the 'Scientist is In' program, in which he sets up a temporary interactive exhibit cart with 'hands-on' materials to demonstrate his latest research to museum visitors. Following publication of original data, the PI and co-PIs will work with the Human Origins Program's web developers to build interactive webpages where online visitors can visualize and understand our research and how it helps advance our understanding of our evolutionary past. Building on recent coverage of the PI and co-PI's (Prof. Richmond's) research on fossil human footprints (e.g., NPR in 2010, *Science* in 2011 and 2013, History Channel in 2012) the PI and co-PIs will continue to work with popular media outlets to communicate their research in accessible ways to engage a large public audience.

Over the course of this project, the PI will continue to train undergraduate students at various stages in the careers, who are seeking first-hand research opportunities. Undergraduates will be recruited from both anthropology and computer science, in order to provide critical training in interdisciplinary STEM research. The PI and co-PIs have established a plan for specifically recruiting students from GWU's Trachtenberg Scholars Program. This program supports the education and research training of high-achieving students from the District of Columbia public school system. These students typically come from groups underrepresented in the STEM disciplines, and consistent efforts will be made to recruit and train students from those groups. The PI has already co-mentored, along with a co-PI (Prof. Richmond), one GWU undergraduate as she conducted her senior honor's thesis project related to the interpretation of fossil human footprints. They encouraged and worked with this student to present at professional conferences (Dingwall et al., 2011, 2012), and submit her thesis for publication (Dingwall et al., 2013). This trainee is now pursuing a doctoral degree at Harvard University. The proposed study will provide many opportunities for undergraduate training and the PI and co-PIs will continue to mentor students in ways that foster their potential to design, perform, and communicate their own innovative research.

IV. TRAINING OBJECTIVES AND CAREER GOALS

The study proposed here will help me achieve both my immediate objective, and career goal, of being a biological anthropologist at the forefront of developing new inter- and transdisciplinary methods and approaches for addressing fundamental questions about our evolutionary history. As an NSF-IGERT trainee for the past five years, I have gained a deep appreciation of the benefits that come from crossing the traditional boundaries of our discipline, and I have learned in many cases how techniques from other fields can help solve problems in our own. In this postdoctoral fellowship, I will further advance that interdisciplinary training and develop my own research skills by learning newly developed data collection and analysis techniques from a vertebrate paleontologist/comparative biomechanist (Prof. Gatesy) and a computer scientist (Prof. Sibley), and applying those techniques to address a long-standing research question from biological anthropology. I will emerge from this fellowship with well-established interdisciplinary collaborations, and confidence in my abilities to develop new collaborations that synthesize diverse fields of study to approach decades-old questions in new and exciting ways. As I pursue the next steps of my research career, I will be able to integrate seamlessly with a variety of departments, or interdisciplinary programs, as my own interests and skills will complement those from a wide range of traditional fields. Furthermore, this fellowship will provide me with first-hand experience to guide my own development as a mentor who encourages and enables my students to conduct their own interdisciplinary research. I hope to be the kind of mentor who drives students to think outside the box and develop proficiencies across diverse fields, which will allow them to pioneer their own innovative and transformative research.

V. JUSTIFICATION OF SPONSORING SCIENTIST AND HOST INSTITUTION

The fellowship will be overseen by a team of co-mentors. Each of these mentors has expertise in a particular area but they are all scientists who have histories of conducting interdisciplinary research. The Lead Mentor (Prof. Sibley) has expertise in robotic vision, specifically the automated visualization and comprehension of 3-D deformable environments. Understanding the process of footprint formation involves a different problem but it requires an identical approach to interpreting a 3-D deformable scene. Fossil human trackways are 3-D scenes that represent a past process of deformation, and we want to work backwards to understand the event (locomotion) that created them. This project represents a novel application of analytical techniques for which Prof. Sibley is particularly well-versed. We plan to use new equipment and techniques for real-time 3-D capture of the interaction between locomotion and a deformable surface, which results in footprints. In doing so, we will develop the ability to work backwards and predict the locomotor event that led to a particular pattern of deformations (i.e., footprints). Prof. Sibley is responsible for the development and the active improvement of the algorithms which capture and fuse data that enable real-time 3-D capture of deforming scenes at sub-millimeter resolution. These techniques are essential to this project. Furthermore, Prof. Sibley maintains active collaborations at GWU with experts developing new machine learning algorithms (Profs. James Hahn and Claire Monteleoni). Should we require assistance at any point in building, training, and testing new algorithms for predicting locomotion from footprint trackways, these collaborators have offered their consultation. Given the fact that Prof. Sibley, and the MOCA lab which is instrumented for large-scale, real-time, dense 3-D motion capture, are at GWU, this is the most feasible host institution.

The other co-mentors also offer unique perspectives that will enable certain aspects of this interdisciplinary project to occur. The first, Prof. Gatesy, is a widely-respected expert on the evolution of locomotion in vertebrates, and has been at the forefront of developing techniques for interpreting the locomotion of dinosaurs from their fossilized trackways. His expertise will be particularly helpful in foreseeing both obstacles and opportunities in the collection and analysis of experimental footprint data. Most importantly to this proposal, he has spent more than 20 years developing techniques for visualizing and analyzing motion through biplanar x-ray. He is part of the team responsible for founding and developing XROMM, as a technique for visualizing and analyzing 3-D skeletal motion. Prof. Gatesy is an active member of the research group that utilizes the XROMM facility at Brown University, and he will advise and oversee that portion of data collection. Combining his expertise in the application of XROMM with his interest, and vast experience, in analyzing fossil trackways make this collaboration a natural fit. The second co-mentor, Prof. Richmond, acted as Ph.D. advisor to the PI. Prof. Richmond directs field research at Ileret, Kenya, where his research team (which includes the PI) is continuing to discover and excavate numerous assemblages of fossil human footprints, which form the rapidly-growing paleontological data set that will be analyzed in this project. His expertise and direction in the appropriate excavation, documentation, and interpretation of these newly emerging forms of fossil data are critical to the project. Furthermore, Prof. Richmond has a unique history of bringing interdisciplinary analytical methods to common use in paleoanthropology. His research was the first to take finite element analysis, an engineering technique, and apply it to paleoanthropological research through interdisciplinary collaborations. He will provide important guidance to the PI on making techniques from typically detached disciplines applicable and accessible to the field of biological anthropology.

VI. INTERDISCIPLINARY NATURE OF THE PROJECT

This project bridges novel methods from diverse fields to develop the exciting potential to answer a long-standing fundamental question in paleoanthropology. The study will require the PI to learn new data collection techniques for motion visualization, including biplanar x-ray and real-time dense 3-D capture of dynamic scenes. These methods have been developed and applied in the fields of comparative biomechanics and computer science, respectively, yet neither has ever been utilized in biological anthropology. Additionally, the development and application of analytical techniques from machine learning, which have surged in popularity among computer scientists and statisticians, will be entirely new to paleoanthropology. The PI has coordinated a unique team of researchers with focused expertise in different areas, but who are similarly motivated to push the boundaries of their disciplines by pursuing the answers to long-standing research questions through innovative interdisciplinary approaches. By training with this team of mentors, the PI will develop new skills that come from multiple disciplines, and that will enable him to engage in future collaborations across traditional academic boundaries. Furthermore, the PI will gain valuable experiences to guide his development as a mentor who will lead his future students to pursue transformative interdisciplinary research.

VII. SPONSORING SCIENTIST STATEMENT (Prof. Sibley)

As the Sponsoring Scientist for this fellowship, I will provide hands-on training to the PI on the application of a newly-developed system for large-scale, real-time, 3-D motion capture. This system employs data fusion techniques that are new to the field of robotic vision, and I am actively developing new algorithms for improving the accuracy and efficiency of dense scene captures. The PI will be trained on the basics of how these systems work, and how they can be altered to optimally capture desired motions (in this case the process of footprint formation). These techniques are at the forefront of research in the field, and no other methods exist which can capture an event such as the formation of a footprint in real-time and at such high resolution. The PI will be trained in such a way that he will be able to apply these emerging techniques to other research questions in human biomechanics. I will also train the PI on the specialized techniques required for managing and analyzing the massive high-dimensional data sets involved in such a project. These kinds of 'big' data sets are rare in anthropology but common in computer science, and the PI will gain unique skills to implement these approaches to address other questions in biological anthropology. I have extensive experience with the application of machine learning techniques to analyze massive multidimensional datasets. Furthermore, I maintain close collaborations with other researchers at GW (Profs. James Hahn and Claire Monteleoni) who are actively developing more accurate and efficient algorithms for building machine learning models. My own experiences and those of my colleagues make me an appropriate mentor to train and guide the PI on the ways in which machine learning can be applied to questions regarding motion and vision. My position at GWU and within the MOCA laboratory research collective ensure the availability of the resources and collaborations necessary to analyze these data in new and inventive ways.

The application of these techniques to an anthropological research question will also represent a novel and exciting application of the methods which I routinely employ. These methods have never been applied in such a manner and are likely to generate new collaborations between fields of robotics and natural sciences. A collaborative project such as this will lead to advances within the fields of computer science, as well as anthropology, and could inspire new lines of investigation at their intersection.

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