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A biplanar X-ray approach for studying the 3D dynamics of human track formation

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ABSTRACT

Recent discoveries have made hominin tracks an increasingly prevalent component of the human fossil record, and these data have the capacity to inform long-standing debates regarding the biomechanics of hominin locomotion. However, there is currently no consensus on how to decipher biomechanical variables from hominin tracks. These debates can be linked to our generally limited understanding of the complex interactions between anatomy, motion, and substrate that give rise to track morphology. These interactions are difficult to study because direct visualization of the track formation process is impeded by foot and substrate opacity. To address these obstacles, we developed biplanar X-ray and computer animation methods, derived from X-ray Reconstruction of Moving Morphology (XROMM), to analyze the 3D dynamics of three human subjects' feet as they walked across four substrates (three deformable muds and rigid composite panel). By imaging and reconstructing 3D positions of external markers, we quantified the 3D dynamics at the foot-substrate interface. Foot shape, specifically heel and medial longitudinal arch deformation, was significantly affected by substrate rigidity. In deformable muds, we found that depths measured across tracks did not directly reflect the motions of the corresponding regions of the foot, and that track outlines were not perfectly representative of foot size. These results highlight the complex, dynamic nature of track formation, and the experimental methods presented here offer a promising avenue for developing and refining methods for accurately inferring foot anatomy and gait biomechanics from fossil hominin tracks.

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1. Introduction

Studies of tracks (i.e., ‘footprints’) have been influential in paleoanthropology, but for a long time just a scant record of tracks was known from the hominin fossil record. A famous set of Pliocene hominin tracks was discovered at Laetoli, Tanzania in 1978 (Leakey and Hay, 1979), and an assemblage of early Pleistocene hominin tracks was uncovered at Koobi Fora, Kenya that same year (Behrensmeyer and Laporte, 1981). For the roughly 25 years following these discoveries, many researchers studied these specimens (particularly those from Laetoli). However, a lack of new hominin track discoveries meant that there were no comparative samples from other times and places that would enable one to use tracks alone to study temporal or evolutionary patterns in hominin anatomy and locomotion. Within the past 10–15 years, this paradigm has started to change, with discoveries of more and more Plio-Pleistocene sites across Europe and Africa that preserve the tracks of fossil hominins (Mietto et al., 2003; Bennett et al., 2009; Ashton et al., 2014; Hatala et al., 2016b; Liutkus-Pierce et al., 2016; Masao et al., 2016; Roach et al., 2016; Panarello et al., 2017; Hatala et al., 2017; Altamura et al., 2018).

Longer histories of ichnological research in other subfields of paleontology have demonstrated the variety of ways in which tracks can offer valuable insights into the anatomy, locomotion, ecology, and behavior of fossil taxa (e.g., Hitchcock, 1836; Lockley and Meyer, 2000; Falkingham, 2014). In many ways, these immediate snapshots of behavior, which are typically formed in quick succession by animals that presumably lived in close proximity and potentially interacted with each other, provide windows to the past that are unparalleled in the skeletal fossil record. Some recent investigations

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of hominin track sites have begun to explore questions regarding ecology and social behavior (Roach et al., 2016; Hatala et al., 2016b), but most analyses have focused exclusively on the potential for fossil hominin tracks to provide data on foot anatomy and locomotion. This trend can be linked to a long history of research into the evolution of hominin bipedalism and an equally long history of persistent debates regarding the exact manners of bipedalism that were used by particular hominin taxa (Ward, 2002).

Throughout the 1980s and into the 1990s, several studies were focused on inferring locomotor data from the Laetoli footprints. Some predicted patterns of foot anatomy and motion from internal track topography (e.g., Day and Wickens, 1980; White, 1980), others predicted gait parameters such as walking speed from the spacing and orientation of the footprints (e.g., Charteris et al., 1981, 1982; Alexander, 1984; Tuttle et al., 1990), and still others merged study of the footprints with that of foot skeletal fossils in order to draw both anatomical and functional conclusions (e.g., Stern and Susman, 1983; White and Suwa, 1987; Tuttle et al., 1991). While predictions of stride length and speed rarely generated much conflict, functional interpretations derived from internal track topography were inconsistent and extended, rather than resolved, debates stemming from functional interpretations of fossil skeletal anatomy (e.g., Stern and Susman, 1983; contra White and Suwa, 1987). Even in more recent analyses of the Laetoli tracks, which have continually applied the newest experimental and analytical methods, there is still no consensus on whether or not the internal morphologies of these tracks are consistent with a completely human-like pattern of bipedalism (e.g., Berge et al., 2006; Bennett et al., 2009; Raichlen et al., 2010; Crompton et al., 2012; Hatala et al., 2016a; Raichlen and Gordon, 2017). These contradictions are almost certainly linked to our generally limited understanding of the complex mechanical interactions between anatomy, motion, and substrate through which tracks are formed (Padian and Olsen, 1984; Falkingham and Gatesy, 2014).

Recent studies are gradually beginning to address this problem through controlled experiments that test hypotheses about whether and to what extent certain biomechanical variables are reflected in track topographies. For example, multiple independent research teams have demonstrated the lack of a direct correlation between depths measured within footprints and the measured distribution of force/pressure beneath the foot (D'Août et al., 2010; Bates et al., 2013; Hatala et al., 2013). This correlation had been one of the most common assumptions made in studies of hominin footprints, regarding the link between locomotor biomechanics and track morphology. Other studies have shown that broader patterns of limb kinematics are reflected in track morphologies (Raichlen et al., 2010; Hatala et al., 2016c; Raichlen and Gordon, 2017), but, given the lack of correspondence between pressure distributions and footprint topographies, the precise mechanisms by which these whole limb kinematic patterns are recorded in tracks are still unknown. These results underscore the need for new approaches to understand how we might more accurately interpret locomotor variables from hominin tracks.

Track formation is difficult to study because of two characteristics inherent to this process. First, there is a fundamental conflict between data collected using stiff-surfaced instruments, such as force plates and pressure pads, and their utility for understanding the foot's interactions with deformable substrates during track formation. Second, direct observation of the foot's external motions during track formation is hindered by foot and substrate opacity. To overcome these obstacles, a recent experimental study of guineafowl track formation applied biplanar X-ray and X-Ray Reconstruction of Moving Morphology (XROMM) methods to directly visualize and measure 3D foot movement both above and below a deformable ground surface (Falkingham and Gatesy, 2014). This new approach highlighted a potentially promising avenue for accessing the hidden process of human track formation, and understanding more directly how patterns of human and fossil hominin foot motion are recorded in tracks.

Similar methods are not easy to apply directly to studying human tracks. Plantigrade human feet are surrounded by voluminous soft tissue compared with those of small, digitigrade birds, so human tracks are less likely to closely resemble the pedal skeleton. Further, the mechanical interactions between deformable soft tissues moving through a deformable substrate are likely to be highly complex. Existing biplanar X-ray methods are either employed to reconstruct bone motion (e.g., You et al., 2001; Tashman and Anderst, 2003; Brainerd et al., 2010; Gatesy et al., 2010) or to measure internal soft tissue strain (Azizi and Roberts, 2009; Camp et al., 2016). In this study, rather than treating the skin as a rigid surface or attempting to mathematically model its properties, we used superficial markers to directly image and reconstruct the dynamic conformation of the foot's plantar surface. By using biplanar X-rays and customized methods derived from XROMM for visualization and analysis, we captured the 3D motion of the external surfaces of human feet as they traversed deformable substrates and created tracks. We then explored a few applications of this method by analyzing how patterns of human foot deformation (and motion) vary across substrates with different levels of compliance, and also by evaluating whether and to what extent certain features of track morphology preserve faithful representations of foot anatomy and/or motion.

2. Methods

2.1. Subjects

Our substrates, markers, trackway configuration, and X-ray technique (i.e., selection of appropriate X-ray settings) were developed, and subsequently tested and refined, using a human cadaver foot. Only after a successful and repeatable procedure was established, and all radiation risks were accurately calculated, did we recruit human subjects for this study. Here, we present data and results from three healthy young adults (two female, one male). All subjects provided informed consent to participate, in accordance with a protocol approved by the Institutional Review Boards of Brown University and The George Washington University.

2.2. X-ray equipment and technique

X-ray video recording was performed in the W.M. Keck Foundation XROMM Facility at Brown University. This facility includes: two EMD Technologies model EPS 45-80 X-ray generators (EMD Technologies, Saint-Eustache, Quebec, Canada) connected to Varian model G-1086 X-ray tubes (Varian, Palo Alto, CA, USA) suspended from the ceiling on telescoping cranes, two Dunlee model TH9447QXH590 image intensifiers measuring 40.64 cm in diameter (Dunlee, Aurora, IL, USA) mounted on mobile-arm bases, and two Phantom v10 high-speed digital video cameras (Vision Research, Wayne, NJ, USA) that record in both planes at 1760 by 1760 pixel resolution. To minimize exposure, X-ray emissions were pulsed (50 Hz with 2 ms pulse width) rather than continuous, at energies of 50–90 kV and currents of 300–400 mA. To counteract the dramatic difference in radiolucency between our substrates and air, the Phantom cameras' Extreme Dynamic Range feature was set to 300–400 μs. Overexposure was further reduced by fixing a plasticine filter (12 × 5.5 × 2.5 cm) in front of the top half of each collimator housing during mud trials. Two additional Phantom v9.1 cameras captured standard light videos of external foot and lower limb movements, both at resolutions of 1600 by 1200 pixels. All

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