Perspective article

Virtual anthropology meets biomechanics

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ABSTRACT

A meeting in Vienna in October 2010 brought together researchers using Virtual Anthropology (VA) and Finite Element Analysis (FEA) in order to explore the benefits and problems facing a collaboration between the two fields. FEA is used to test mechanical hypotheses in functional anatomy and VA complements and augments this process by virtue of its tools for acquiring data, for segmenting and preparing virtual specimens, and for generating reconstructions and artificial forms. This represents a critical methodological advance because geometry is one of the crucial inputs of FEA and is often the variable of interest in functional anatomy. However, we currently lack tools that quantitatively relate differences in geometry to differences in stress and strain, or that evaluate the impact on FEA of variation within and between biological samples. Thus, when comparing models of different geometry, we do not currently obtain sufficiently informative answers to questions such as "How different are these models, and in what manner are they different? Are they different in some anatomical regions but not others?" New methodologies must be developed in order to maximize the potential of FEA to address questions in comparative and evolutionary biology. In this paper we review these and other important issues that were raised during our Vienna meeting.

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Finite Element Analysis (FEA) is a computer-based engineering technique that has been widely used in clinical biomechanics and is now being used as a tool in evolutionary biomechanics (see reviews in Richmond et al., (2005); Rayfield, (2007); Panagiotopoulou, (2009), Cobb, (2010); see also Curtis, (2010) for Multibody Modeling). Key steps for both areas of application include model creation (capturing geometry, assigning material properties, specifying simulated forces, and imposing constraints), model validation (entailing a comparison of FEA results with *in-vivo* or *in-vitro* experimental data), and virtual experimentation (altering the geometry or model parameters in order to inspect the biomechanical consequences of these changes). Regarding all three of these components, methods and tools that have been summarized as "Virtual Anthropology" (VA) (for more details see Weber and Bookstein (2011) or www.evan.at) can be of considerable help. While in the recent past many newly developed methods and tools in VA have been applied to humans and other primates, all of them can in principle be applied to any biological (or even non-biological) structure and indeed this has been the case. When we use the term "VA" (which is already in use in our discipline), it is meant as a synonym for these techniques (that include Geometric Morphometrics — GM), and we hope to address researchers from as many fields as possible with similar questions.

In October 2010, a two-day meeting in Vienna was organized by the European Virtual Anthropology Network Society (www.evan-society.org) to bring together researchers using VA and FEA and to teach software for form and shape analysis (the EVAN Toolbox). Participants of the "*Virtual Anthropology meets Biomechanics Workshop*" represented institutions from four continents and included anatomists, anthropologists, archeologists, behavioral scientists, bone biologists, engineers, paleontologists, statisticians, and dental morphologists. The goal of the meeting was to explore the problems facing a collaboration between VA and FEA, and the ways either of these approaches might benefit the other.

FEA can be used to examine how objects of complex geometry respond to external loads, and thus has the potential to test mechanical hypotheses in functional anatomy. However, clinical or evolutionary questions often cannot be answered from mechanics alone. For example, an evolutionary biologist might ask, "Does this aspect of skeletal morphology represent an adaptation to the performance of a particular behavior?" Mechanics may contribute to answering this question, but obviously only in a context that considers how the morphology of interest differs from other such forms or shapes. The geometry of the specimens being analyzed is crucial because it is one of the

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fundamental inputs of FEA. Hitherto, VA has complemented FEA by virtue of its tools for acquiring data by volume-based or surface-based scanning procedures, for segmenting substructures and electronically preparing virtual specimens, and for generating reproducible reconstructions of fragmented and deformed shapes. However, rigorous hypothesis testing requires tools that (1) quantitatively relate differences in geometry to differences in stress and strain and (2) evaluate variation within and between populations. FEA does not currently provide these tools, and this is an area where the combined use of FEA and VA may advance the field. The Vienna meeting lingered on the obvious divergences between VA and FEA, particularly (1) the discrepancy between FEA's basis in deterministic computations and VA's emphasis on variability and uncertainty, (2) the absence from FEA of any formalism of "similarity" analogous to the Procrustes form distances that drive VA, and (3) the absence from VA of any formalism for the strain tensors or their variations that are the actual output of a FEA simulation.

Recent attempts to analyze the feeding biomechanics of early hominins by three independent research groups (Strait et al., 2009, 2010; Wroe et al., 2010; O'Higgins et al., 2010) illustrate the possibilities and also the problems facing a union of VA and FEA. Biomechanical simulations, for instance, require models to have complete and undistorted geometry. In the case of a fossil skull this requires reconstructing even small surface patches that might be left missing in a mere comparison of gross morphology. While in a typical VA application one might separately analyze the mandible, the teeth, the endocranial cavity and would only rarely consider the border between cortical and trabecular bone, FEA needs all this information simultaneously to complete a model — a difficult task to accomplish using heavily mineralized fossils that may be millions of years old.

In one study (Strait et al., 2010) finite element models (FEMs) of the crania of *Macaca fascicularis* and *Australopithecus africanus* were subjected to isometrically scaled loads, meaning that any differences in strain observed between them were strictly a consequence of differences in shape (Dumont et al., 2009). The first question to be asked about these models by an evolutionary biologist would be "Are the stresses and strains in the models different from each other?" The simple answer is "yes," because FEA is a deterministic process and thus the differences in geometry necessarily imply differences in stress and strain. This is not a sufficiently informative answer, and hence a series of secondary questions would then ensue. "How different are these models? Are they different in strain magnitude, orientation, and distribution, or only in one or some of these? Are they different in some anatomical regions but not others? Can these differences be summarized quantitatively?" FEA produces an enormous amount of quantitative data (many types of stress, strain and displacement at hundreds of thousands or millions of nodes), so one might have expected that FEA can easily and comprehensively address these questions. Surprisingly, however, it cannot; the computational power of FEA is directed toward a focal specimen, not to a comparison between specimens. There are not currently any tools *that preserve information about form and its variation* that allow comparisons of strain or other patterns in geometrically different models. Indeed, it is typical for assessments of model differences to rely only on a very small subsample of quantitative data contextualized by subjective interpretations of visual representations of either model deformations (images depicting magnified displacements before and after loading) or stress or strain distributions (e.g. color maps as shown in Fig. 1). In short, there is no objective standard about what "similar" or "different" ought to mean. The quantitative data is there in the outputs of each model, but we need statistical tools allowing rapid and comprehensive extraction and comparison of FEA data from homologous locations on different models.

There was disagreement at the meeting concerning how or even whether statistical rigor could be brought to bear on FEA-derived results that focus on shape (randomization methods exist in FEA but cannot be easily applied to complex geometries). Statistical analysis is the core strength of VA. Using geometric morphometrics, mean forms and variation within and between subsamples can be readily computed in order to assess the differences. These results are then often visualized by deformation grids, color maps and other graphs, yet, in contrast to FEA, they represent summaries of statistical comparisons, not individual cases, i.e. the link between specimens has been already made. [In other words, conventional multivariate pattern analyses, such as principal components, can sometimes be straightforwardly applied to these data, but never the corresponding significance tests, as the "null model" to be accepted or rejected involves every detail of the rules of correspondence between specimens as well as the usual issues like sample provenance and structured (colored) measurement noise.] The differences between any two FEM computational outputs generally cannot be interpreted in this manner. It is not just that the tools for describing model differences are not fully developed, but also that the nature of modeling does not easily lend itself to the types of interpretations typical in comparative morphology. Indeed, there
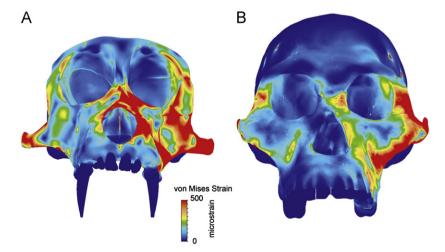

Fig. 1. Von Mises strain in cranial finite element models of (A) *Macaca fascicularis* and (B) *Australopithecus africanus* during simulated bites on the premolar teeth. Are the strain patterns similar or different? How should we be assessing "similarity" of strain patterns, anyway?

was disagreement concerning even whether or not "homologous locations" exist at which to compare stresses or strains in different specimens insofar as there is no notion of "mechanical homology" analogous to biological homology.

Along with specifying the differences between models goes the question "Are these differences meaningful?" The answer can be addressed by considering variation within and between populations or species, but this is something that FEA is not designed to do. FEA is excellent at simulating the mechanical performance of *particular* geometries, but cannot easily provide information about the mechanical consequences of morphological variation (unless the morphology in question is simple and can be easily parameterized). The long time needed to create and analyze FEMs (e.g., weeks, in the case of crania of extant species; longer in the case of fossils) means that we cannot routinely produce large numbers of models. VA can be of assistance in this regard because it provides tools that allow FEA studies to draw conclusions about the biomechanical impact of morphological variation without having to create an inordinately large number of models. For instance, VA can produce artificial variants of whole forms (e.g., a species mean form, a hypermale form, or a hypothetical form in an interpolated or extrapolated ontogenetic series). Alternatively, VA allows a researcher to find the one real specimen that is closest to a computed average geometry, or a researcher may create a mean configuration and extreme forms along a principal component of form variables by warping (Pierce et al., 2008; O'Higgins et al., 2010). VA can also help select those real specimens nearest to the extremes in a computed morphospace. Although Procrustes distance has nothing at all to do with mechanics, at least in terms of the input geometry one can bracket the observed range of morphological variation. Unfortunately, regarding fossil taxa, one is forced to use the specimens that are best preserved, even though they might not be the most representative specimens of their species.

VA can also complement FEA during the creation and modification of FEMs. Analyses of extinct taxa may be faced with the complication that there may be no fully complete, undistorted specimens of any of the species of interest known in the fossil record. In the case of the *A. africanus* cranium, a composite of two specimens was created using reproducible, quantitative techniques with the goal of "approximating" the form of the originals (e.g., Strait et al., 2009). VA has successfully developed both anatomically based and reference-based reconstruction methods to correct distortion and to produce sufficiently complete geometries (Gunz et al., 2009; Benazzi et al., in press). Biomechanical analysis may profit from those advances as long as the corresponding uncertainties of reconstruction are reported alongside the results of deterministic simulations.

VA might also be used to alter FEM geometries so as to perform modeling experiments. This can be applied to whole forms or only locally altered ones in order to examine the biomechanical effects of relatively discrete anatomical changes (e.g., increased robusticity of the brow ridge). But it is not yet clear how to do this in a quantitative fashion that is also biologically realistic. When varying either whole or local forms, internal features have to be warped together with the outer surface, and the covariance of these parameters is not properly understood in any real data sets pertinent to extant taxa, let alone fossils (O'Higgins et al., 2010). Thus, for example, while a change in cortical thickness is not important for GM computations such as discrimination between taxa, it could matter considerably in FEA.

A cautionary note was sounded concerning problems at the biomathematical foundation of all this work. It was noted that at present GM has nothing to do with FEA at the level of formal equations and formal information processing. Starting from first

principles, the fundamental deformation models of GM are incompatible with those of FEA; for instance, GM cannot correctly simulate the deformation of a bar under cantilevered load. GM is incapable of handling the variations of material properties that characterize the FEA world or even the embedding of finite biomechanical forms in an ocean of air (i.e., constraining models in space). And present-day FEA makes no use at all of the existing GM expertise in the representation of the uncertainty of strain fields, their principal components of variation, and their correlations with causes or effects of load. Other concerns were expressed by some participants regarding the lack of model validation in some FEA studies and, more generally, the lack of objective criteria for validation. In validation studies, strains derived from *in-vitro* or *in-vivo* bone strain experiments are compared to those extracted from FEMs at nodes or elements corresponding to strain gage sites. In practice, there is no figure of merit summarizing any such comparison, and no statistical model specifying when the fit is "close enough" to justify the inferences drawn from FEA. In absence of such criteria, it is unclear when researchers might ever consider their models to be invalid.

In summary, FEA and VA both address the same aspect of organismal biology — geometry in three-dimensional coordinate space. But at present the information they may hold in common goes completely unformalized. Our Vienna meeting demonstrated some of the problems related to a collaboration, but also made clear that a convergence between the domains of VA and biomechanics has the potential to increase the strength of arguments regarding the functional anatomy of heterogeneous, variable forms. At present, the envisioned collaboration between these two fields is nascent. More work, especially on informatic and statistical foundations, will be necessary if it is ever to reach its full potential.

Conflict of interest statement

None of the authors have any financial and personal relationships with other people or organizations that could inappropriately influence (bias) this work.

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