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Lead Book Review

Complexity, Modularity, and Integration in the Human Head. The Evolution of the Human Head. By Daniel E. Lieberman (2011). Cambridge, Mass: The Belknap Press of Harvard University Press, 768 pp., $41.50 (hardback), ISBN 978-0-674-04636-8.

The intricacies of head morphology are powerful lures for those of us interested in the relationships and behavior of fossil primates. The many functional systems in the head make it a rich source of data on how fossil primates ate, saw, heard, walked, and climbed. We can learn about the evolution of the size and shape of the brain, how primates held their heads, what they ate, and even about their social group structures. Daniel Lieberman's new book, *The Evolution of the Human Head*, is a bold new attempt to put all these pieces together in an integrated whole, to make sense of the complexity through the lenses of development and function. It builds on a rich tradition in the study of primate, mammal, and vertebrate heads, from William K. Gregory's *Our Face From Fish to Man* (Gregory, 1929), through Moore's *Mammalian Skull* (Moore, 1981), to Hanken and Hall's three volume *Skull* series (Hanken and Hall, 1993). However, Lieberman's book differs from these in being focused exclusively on primate, and especially hominid, heads. Moreover, he reviews the important functional and developmental principles of all the head systems, then takes these data and uses them to interpret the developmental 'how' and functional 'why' of fossil hominid skull evolution. This ambitious agenda stretches the book to 750 pages in length, but it is well organized, mostly well indexed, and Lieberman's clean, relaxed style makes it easy to read. The book is also nicely illustrated, with crisp, clean diagrams, plenty of graphs, and some data in tables, the rest of the data being available in Lieberman's papers, or – if my past experience is anything to go by – probably from Lieberman himself.

The book starts with a preview chapter, summarizing Lieberman's view of the head and laying out his plan for the book. Lieberman posits that despite their complexity, heads are evolvable because "they consist of many functionally important modules integrated in a special way to accommodate one another" (p. 15). Lieberman postulates that heads evolve through "tinkering" (Jacob, 1977): "When new organisms make new use of preexisting or modified modules, these tinkered novelties often tend to work because they are made of modules that already function appropriately and come with existing mechanisms for adjusting to one another" (p. 15). These are interesting and important ideas that we will return to below.

Lieberman then presents two chapters on skeletal tissues (Chapter 2) and embryonic development of the head (Chapter 3). The skeletal tissue chapter includes developmental origins of bone, including patterning and morphogenesis, and a too brief treatment of dental tissues, cartilage, tendons and ligaments. There are a few pages on Moss's functional matrix hypothesis, with an appropriate nod to van der Klauuw, as well as more recent researchers, such as Cheverud, Zelditch and Hallgrimsson. I do not agree with Lieberman's use of the term "remodeling" to refer to the wholesale bone deposition resulting in drift and displacement of sheets of cortical bone. This should be referred to as *modeling*: *remodeling* should be reserved for *Haversian* remodeling, formation of osteons mainly, which improves bone material properties while maintaining gross bone shape. This chapter also includes some elementary bone biomechanics. This chapter is sufficient introduction for what is to come in the rest of the book, but when I recommend a readable account of bone tissue level biomechanics and development, I will still refer students to John Currey's book, *Bone*: *Structure and Mechanics* (Currey, 2002).

Chapter 4, *Modular Growth of the Fetal and Postnatal Head*, provides a succinct review of how the skull grows after the embryonic period. Lieberman makes liberal reference to Enlow's work on growth fields, and nicely reviews the literature on growth and development of the cranial base, vault, and face, including much of his own contributions to these areas. On the whole, the chapter presents a thorough review of a large and intimidating literature and is well worth your time. (Note that the arrows illustrating nuchal plane rotation in chimps and humans on page 104 are swapped.) Having described the modular growth of the head in Chapter 4, Chapter 5 attempts to put the pieces together again by discussing the *Integration of the Head during Fetal and Postnatal Growth*. As with Chapter 4, there are plenty of great data here, and some nice reviews of the concepts of integration. However, Chapters 4 and 5 are the two that I find the most problematic from a theoretical perspective, and I return to these issues below.

Chapter 6, on *The Brain and Skull* has a lot of interesting and important material in it regarding the evolution of brain size, differential increases in brain parts in hominid evolution, blood supply, venous drainage of the brain, how brain temperature is regulated, and the role of the skull in protecting the brain. The literature on adult brain size and brain ontogeny is also reviewed. All in all, this is a good review of the relationships between brain and skull, although for a complete picture, one should also read the previous two chapters. The only (minor) corrections needed are that the outer layer of dura is *endocranial*, not *endosteal* (Figure 6.11), the Circle of Willis is not below the tentorium (p. 220), and the myelencephalon is not the spinal cord (Figure 6.2).

Chapter 7 on *Chewing and the Head*, including a description of mastication, needs revision and correction before I would recommend it to my students to read. There is some truth to the statement that "[d]uring mastication, the mandible is pulled both forward and backward (retracted)" (p. 225) but lateral-medial movements of the teeth are much more important in primates. In attempting to explain mandibular condylar translation during chewing (Figure 7.8), Lieberman also perpetuates a dubious hypothesis about jaw mechanics that I think is erroneous (Greaves, 1974, 1980; Crompton et al., 2006;

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Rak and Hylander, 2008). The argument is that "In a simple jaw with a hingelike joint, the occlusal plane is in line with the TMJ, and the teeth occlude with a primarily vertical (orthal) direction (sic)" (p. 243). As the ramus increases in depth, the trajectory of the lower teeth becomes increasingly more anteriorly directed relative to the upper teeth (Crompton et al., 2006), a trajectory that is "corrected by translating the joint posteriorly during adduction" (p. 243). The problem envisaged by Crompton et al. (2006) and traceable to Greaves (1974) is shown in Fig. 1A. This is a geometrically impossible arrangement in any animal, because only the posterior teeth would be in occlusion when the jaws are shut. Fig. 1B presents more realistic jaw geometry: offsetting the axis of rotation from the plane of the upper tooth-row lies. Once this more realistic arrangement of upper and lower jaws is appreciated, it is clear that the tooth-rows can be displaced inferiorly as much as needed (to augment adductor cross-sectional area, for example) changing the angle of approach of the teeth and without necessitating condylar translation. Thus, it is *not* correct to argue that condylar translation is *necessary* to ensure that teeth occlude vertically when the ramus is tall (Crompton et al., 2006). It *may be one possible* solution, but the challenging control and stability problems associated with it suggest to me that condylar translation is not the design path of least resistance. This is especially the case if, as shown in Fig. 1B, this problem does not exist in the first place. Natural selection has plenty of difficult design challenges to face: a simple vertical displacement of the upper tooth-row relative to the jaw's axis of rotation is not one of them. Of course, once condylar translation is an entrenched component of jaw system design, the magnitude of condylar translation will increase as jaw joint height increases (Wall, 1999; Terhune, 2010, 2011; Ross et al., Submitted for publication), but that does not mean that condylar translation is *necessary* to maintain vertically oriented tooth movement during occlusion. Lieberman's book would have been better served by a fuller explication of the sarcomere stretch hypothesis, currently the best explanation for condylar translation in primates (Hylander, 1992b).

Chapter 7 also includes a biomechanical error concerning analysis of the mechanical advantage of the masseter muscle in frontal view. The mechanical advantage (MA) of a jaw muscle is the ratio of a muscle's lever arm to the load arm of the bite point. In Figure 7.10 (reproduced here as Fig. 2), the line of action of the masseter in coronal planes is represented by a vector running from the angle of the mandible through the lateral surface of the zygomatic arch, and its lever arm in this projection is presented as the perpendicular distance from this vector to the frontal projection of the working side temporomandibular joint (TMJ). The bite force is represented as a vector directed inferiorly at the M^1, and its moment arm is the perpendicular distance from this vector to the working side TMJ. MA is then calculated as the ratio of the lever and load arms. This is incorrect. Calculation of mechanical advantage requires correct placement of the location of the fulcrum of the lever system. Figure 7.10 places the fulcrum between the masseter vector and the bite force vector, but with the fulcrum in this location, both forces act to rotate the mandible in a clockwise direction, generating no reaction forces. Reversing the direction of the bite

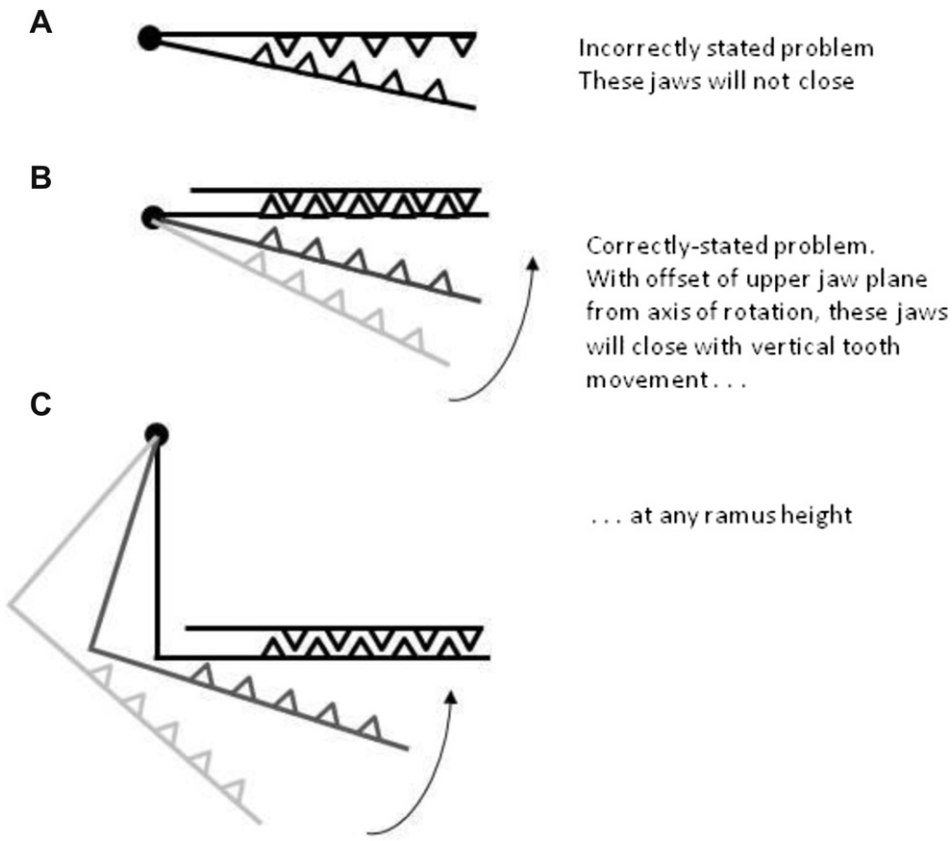

Figure 1. Diagrams illustrating problems with Lieberman's explanation for condylar translation in primates. A. Following Greaves (1974) and Crompton et al. (2006) Lieberman suggests that if the upper toothrow is in line with the axis of rotation of the jaw joint, the teeth occlude in an orthal direction. However, as is clear from this diagram, when these jaws close only the posterior teeth are in contact, and nor are the teeth moving in an orthal direction. This is a biologically unlikely geometry. B. Once a more realistic geometry is defined, it is clear that, in fact, it is possible for the teeth to occlude with an orthal movement at any jaw joint height (C). Condylar translation is not *necessary* for maintaining vertical tooth movements during occlusion. Moreover, I would argue that it is unlikely to be a preferred solution, given that the problem (anteriorly moving lower teeth during occlusion) may actually not exist, and even if it does, simple geometric solutions are available that do not entail a translating condyle.

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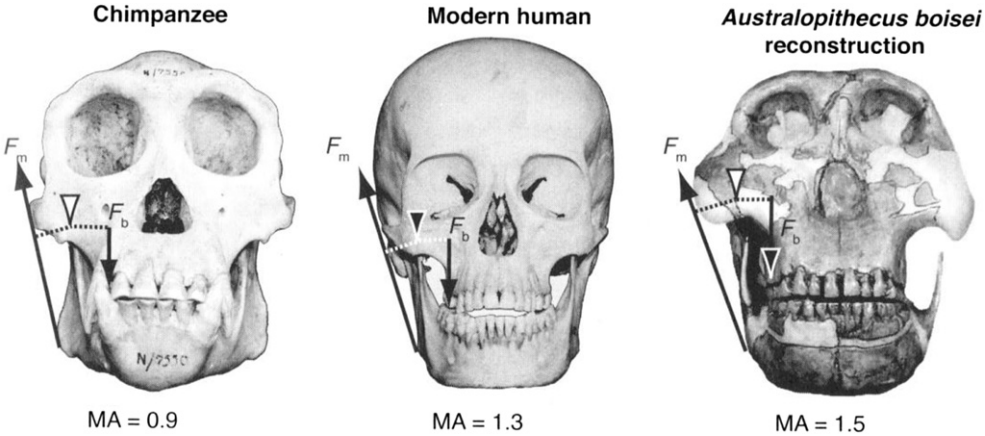

Figure 2. Reproduction of Figure 7.10 from Lieberman (2011), *The Evolution of the Human Head*. This figure illustrates the erroneous calculation of the mechanical advantage of the transverse component of the masseter muscle.

force vector would be a mathematically correct but biologically implausible solution. It is generally accepted that it is more appropriate to place the fulcrum at the balancing side joint (Hylander, 1992a; Spencer, 1998, 1999), and with the fulcrum in that location the illustrated lateral shifts in the masseter line of action in *A. boisei* would have trivial effects on the MA of the masseter. (Note that, although one can take moments about any point in a free body in order to calculate an unknown reaction force, this is not the same as calculating mechanical advantage. Consider, for example, that if one took moments about the bite force location, the MA of the masseter would go to infinity.)

Consideration of the text on page 246 suggests that Lieberman is trying to quantify the "efficiency of transverse force generation". The easiest and probably best way to do this would be to compare the magnitudes of the lateral components of the masseter muscle forces in these three taxa. These would be larger in *A. boisei* because its masseter muscle force vector is directed more laterally, but strictly speaking, this would not be a measure of efficiency. In any event, this error means that Lieberman's discussions of masseter MA in the coronal plane in Chapters 11 and 12 are incorrect.

Figure 7.1 also contains some errors that will confuse the uninitiated. In the top row of diagrams, the protoconid is *not* labeled with an asterisk as the legend states, the paraconid is. Also, this mesial view gives the impression that the food is primarily broken down by contact between the paraconid *shearing past* the buccal cusps on the upper teeth, with no crushing between the protoconid and the lingual cusps of the uppers. The "buccal" and "lingual" labels must have been swapped and the arrows seem to have been placed by someone who doesn't know anything about mastication. Parenthetically, equating Mills' "buccal" phase and "lingual" phase with Phase I and Phase II is incorrect, as Mills thought they occurred simultaneously on opposite sides of the jaws; the hyoid in Figure 7.5 is nearly in the superior mediastinum; and the effects of gravity on jaw depression are trivial compared with passive tension in the jaw elevator connective tissues (p. 239). Before leaving the feeding system, I do note that one should be careful not to accept Figures 7.12 and 11.15 at face value. These figures plot estimates of bite force at M^2 against the estimated area of M^2, using methods of (Demes and Creel, 1988), and the claim is made that "Bite force increases linearly with tooth surface area, keeping occlusal pressures similar across species". However, linearity does not mean isometry, and Lieberman's claim is only correct if the slope of the line in the plots is close to 1.0 (assuming the units on the *y*-axis are areas, which is not clear). This information is not provided, so it is not possible to evaluate these claims.

Chapter 8, *Pharynx*, *Larynx*, *Tongue and Lung*, presents a readable treatment of the development, function and recent evolution of the nose, pharynx, larynx and tongue. Lieberman nicely reviews the functions of these areas in respiration, swallowing and speech. The anatomy is clearly and simply described and illustrated, the biomechanics of airflow through tubes is summarized, and the changing relationships of these structures to the evolving cranial base are presented. This chapter is Lieberman at his best, using clear writing and simple analogies to cover a complicated topic. I think those of us preparing lectures on topics such as the evolution of speech will find this chapter very useful.

Similarly, Chapter 9, *Holding Up and Moving the Head*, is a clear presentation of some of the basic biomechanical issues involved. The discussion here is simple and concise, and a useful review. Lieberman covers foramen magnum position and orientation, nuchal plane orientation, the function of the semicircular canals in vestibule-ocular reflexes, and the results of Spoor and colleagues. Dave Strait and I showed that basicranial flexion does not reflect head and neck posture, but that foramen magnum and nuchal plane orientation adjust so as to reflect the orientation of the cervical vertebral column (Strait and Ross, 1999). Therefore, I was surprised to read in Chapter 9: "because the Strait and Ross analysis included only one bipedal species with a very flexed cranial base (*Homo sapiens*), one cannot conclude that a more flexed cranial base is unrelated to being bipedal" (p. 347). In fact, Strait and Ross (their Table 4) showed that basicranial flexion across a range of values of flexion is driven by relative brain size and is not related to head posture. It is foramen magnum orientation relative to the orbits that reflects posture. This is shown in Fig. 3, a plot of foramen magnum (FM) orientation relative to the orbital plane (OP) against the orientation of the orbital plane relative to the dorsal surface of the neck (the head neck angle, HNA). This plot illustrates that as the dorsal surface of the neck becomes more vertically oriented and closer to parallel with the OP, FM becomes more horizontally oriented (and orthogonal to the OP in an upright human). Thus, FM orientation relative to OP is a good indicator of head and neck posture in fossil taxa and it is clear why basicranial flexion is not related to head and neck posture among primates: foramen magnum orientation accommodates head and neck posture as needed.

Chapter 10, on *Sense and Sensitivity*, covers vision, hearing, olfaction and taste. This is a lot to cover in 39 pages, but Lieberman does a reasonable job. The eye section is perfunctory, but most of the variation in primate eye design is at higher taxonomic levels anyway. There is a decent section on the hearing apparatus and

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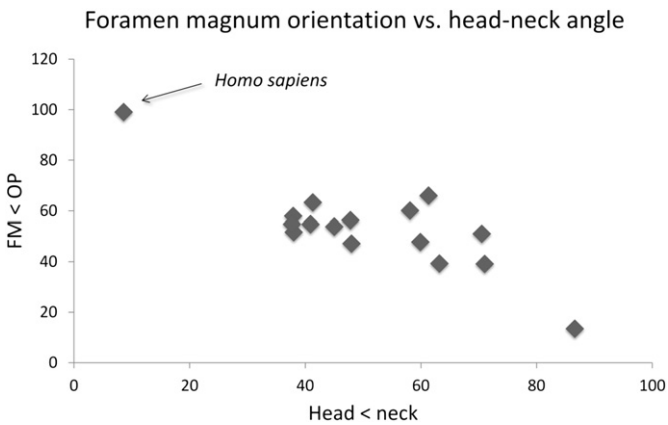

Figure 3. Bivariate plot of foramen magnum (FM) orientation relative to the orbital plane (OP) (the angle is FM < OP) against the orientation of the orbital plane (OP) relative to the dorsal surface of the neck during locomotion (head-neck angle, or head < neck). Primates locomote with the OPs facing forwards (Strait and Ross, 1999). This plot illustrates that as the dorsal surface of the neck becomes more vertically oriented and closer to parallel with the OP, FM becomes more horizontally oriented (and orthogonal to the OP in an upright human). Note that this figure is equivalent to Figure 14 in Lieberman et al. (2000), but with two important differences. First, FM orientation is calculated relative to OP instead of the OA (90° difference), making these numbers directly comparable with those in (Zollikofer et al., 2005). Second, as a result of an error of mine, the values for AOA and AFK for *Homo sapiens* in Table 7 of Lieberman (2000) were incorrectly given as 163 and 154, respectively, instead of 115 and 122 (Ross and Henneberg, 1995). (Note also that IRE5 for *H. sapiens* should be 1.184.) Because FM < OA is calculated as AOA – FM < CO (clivus ossis occipitalis orientation), and FM < OP is calculated as 90-FM < OA, these corrections alter our understanding of the relationships between FM orientation and head and neck posture in human evolution.

how it might inform us about hearing in fossil hominins, and there are sections on noses and smelling, and on tongues and taste.

Armed with these data from living hominids, Chapters 11–13 take the biomechanical, comparative and developmental studies and apply them to explain the evolution of hominin skulls. The written reviews of the fossil morphology are adequate: the illustrations, based on casts and line drawings are again crisp and well presented. The interesting aspects of Lieberman's contributions are his specific hypotheses about the developmental mechanisms that might account for the changes in morphology through human evolution–grist for dissertation mills in the future. For example, Lieberman presents two alternate pathways whereby the skull of *Pan* might be transformed into that of *Sahelanthropus* through growth field reversals, shortening of basioccipital and protraction of the upper face. The extent to which these different hypotheses are testable certainly varies, but it's good to ask the questions. There are some weird things in these chapters. For example, on p. 472 in Chapter 11 (early hominin skulls), Lieberman associates flat, shallow preglenoid planes (i.e., small articular eminences) with large anterior teeth and "anterior chews", and large articular eminences with small anterior teeth and "posterior chews". However, "anterior" and "posterior chews" are undefined (I certainly don't know what they are), and Lieberman ignores a robust literature on the size of anterior dentitions, dietary category, gape, and mandible morphology (Hylander, 1975; Kay, 1984; Ungar and Spencer, 1999; Vinyard et al., 2003, 2009).

Overall, I like the book. I like the idea of laying out general developmental and functional principles, then applying them to the fossil record. It covers a lot of ground, so inevitably it is somewhat uneven in places (such as the feeding system), but I can see myself referring graduate and senior undergraduate students to it for readable introductions to topics ranging from the evolution of speech, hearing, and head posture, to the development of the cranial base that are well enough referenced to provide an entrée into the literature. I also applaud Lieberman's framing the book in terms of the complicated and important concepts of *complexity*, *modularity*, *and integration*. However, my most serious reservations about the book lie with Lieberman's use of these terms.

Complexity

Lieberman notes (p. 8–9) that the head is complex and, without defining complexity, attributes it to three sources: functional diversity – the head performs many functions; the number and diversity of the head's modules – "distinct, partially independent units"; and the degree of integration – "the counterpart of modularity, describes the way in which different components (modules) of a system are combined into a whole". There is no doubt that the head performs many functions, but it depends on how you count them, and it probably does not perform more than the rest of the body combined. Thus, functional diversity as a *measure* of complexity in the head is a red herring. McShea has made a good case that if we are to measure and compare complexity between organisms then we should define a system's complexity as a function of the *number of its parts or interactions* without incorporation of derivative notions, such as functional diversity (McShea, 1996; McShea and Brandon, 2010). Extending this logic to comparisons within organisms, we can ask whether heads are more complex than other body regions; e.g., do heads consist of more parts and/or interactions than abdomens, or thoraces. Lieberman does not do this comparison (no-one has) but he argues that primate heads are complex in that they consist of many different parts with many and diverse functions.

This is interesting to Lieberman – and the rest of us – because it raises two important questions, the answers to which are the central themes in this book. First, how can something as complex as the head evolve (p. 12)? West-Eberhard (p. 182) suggests that modularity, flexibility and the hierarchical organization of development confer evolvability on all lineages (West-Eberhard, 2003). In this context, it is indeed provocative of Lieberman to argue that heads might actually be *more evolvable* than the rest of the body (p. 12)! Second, how do the multiple parts of the head (defining its complexity) grow, develop, and function in such close association with each other (p. 8)? Lieberman's answer to this second question – *integration* – is also one answer to the first, and we will turn to this next. His other answer to the first question is that "heads may have evolved such exuberant variation not in spite of but because of the considerable intensity of selection on heads" (p. 13). There are more functions in the head, so selection has more things to target, so there is more evolution in the head than elsewhere.

My interpretation of all of this is that Lieberman is arguing as follows: heads are complex in the sense that they have *many modules*; because these modules perform many *different* functions (i.e., they are diverse) selection targets them in different ways, and so the head evolves a lot; this is made possible by "integration" of these modules through developmental mechanisms. But isn't it important to point out that it is the packing of these modules into a *small volume* that results in more interactions than if they were separate, and doesn't this result in higher rates of evolution within and between the modules than if they were separate? In fact, it seems to me that there is good evidence that the complexity of the head (lots of parts) combined with the spatial proximity of the parts leads to compromises and potentially undesirable interactions between different modules, requiring morphological solutions that would not be needed if the modules were well separated in space. For example, selection for convergent orbits seems to have resulted in divergence of the planes of the orbits

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and temporal fossae, necessitating evolution of postorbital ossifications to protect the eye from unwanted movements during chewing (Cartmill, 1970, 1972; Heesy, 2005). Increased frontation of the orbits due to basicranial flexion, increased frontal lobe size, and/or the need to fixate on food objects immediately in front of the mouth, combined with possession of a retinal fovea, necessitates evolution of a postorbital septum to protect the eyes from unwanted movements in the temporal fossa (Cartmill, 1980; Ross, 1995a, 1995b). Increasing facial kyphosis, or increasing face size in animals with convergent, frontated orbits and small brains appear to cause the orbits to protrude out of the head, necessitating possession of a supraorbital torus to protect the orbital contents (Shea, 1986a, b; Ravosa, 1988, 1990; Hylander et al., 1991; Ravosa, 1991a, b). All of these features seem to be necessitated by the close spatial packing of modules in the head. Consider, in contrast, the simple displacement of abdominal organs with changes in relative size, or the common vertebrate solution to accommodate relative movements of trunk organs, in which connectivity rather than precise spatial precision is not needed – slippery celomic sacs such as pleura, serous pericardium, and peritoneum. On this basis, it seems reasonable to hypothesize *that the close proximity of multiple functional modules in the head creates more interactions between them than if they were separate, necessitating mechanisms for maintaining their functionality during growth, development, and use* (McShea, 1996; McShea and Venit, 2001). As Kathleen Smith notes (p. 74), "a wide variety of epigenetic mechanisms – both mechanical and molecular – require spatial and temporal proximity to function" (Smith, 1996). Perhaps spatial proximity necessitates increases in complexity.

Modules

The next question is: What is a part? "There is general agreement that a part is a system that is both integrated internally and isolated from its surround" (McShea and Venit, 2001: 292) with degrees of internal integration and external isolation (Wagner, 1996; McShea and Venit, 2001; Klingenberg, 2008). Wagner (1996) also requires a functional component to the module: a module "is a complex of characters that 1) collectively serve a primary functional role, 2) are tightly integrated by strong pleiotropic effects of genetic variation and 3) are relatively independent from other such units" (Wagner, 1996). This sounds an awful lot like a module as defined by Lieberman – "distinct, partially independent units" – or, if defined from a process perspective, "types of subprocesses that are integrated and partially autonomous" (Schlosser, 2004, 521). Thus, Lieberman argues that heads are complex in that they consist of many modules that are internally integrated and at least partially isolated from each other. However, they have to interact with each other during development, jostling for space, position, and orientation, while remaining functional. This spatial proximity makes them even more complex because there are more interactions. These things make the head a perfect laboratory for studying how complex phenotypic systems evolve.

But Lieberman does not clearly and precisely identify or define modules. I could not find "module" in the index, and despite hunting through the book I could not find a specific delineation of the modules of the head. One would think that the chapter entitled *Modular Growth of the Fetal and Postnatal Head* would be a good place to start. On p. 97 we read that the brain, eyes and jaws are modules. On p. 145 we read that brain, eyes, mouth and pharynx are modules. But how are these soft tissue parts integrated with the skull? This would be a good place to introduce Moss's functional matrices, but they do not appear to be modules (p. 122–123). The next chapter, Chapter 5, starts with some properties of modules that promote "evolvability", then asserts that the embryological origins, growth and development of the modules in the head "were described and discussed in Chapters 3 and 4", which is true, but the modules themselves were not defined. I thought I was going to run into some modules on page 146, where we read of "widespread integration and covariation among diverse anatomical units", including the fairly regular orientation of the posterior maxillary plane relative to the orbits. But the emphasis here, again, is not on integration *within* modules, but *between* head "components" (modules?); integration can spread the effects of changes in components throughout the head, with "profound evolutionary consequences".

Thus, modules are not identified in this book in a way that can be evaluated, tested, or utilized. Rather, the primary focus appears to be on interactions *between* modules, rather than the integrative forces *within* them. I thought that maybe this perspective was typical of the modularity/integration literature, with which I was not especially familiar. To address this possibility, I went on a module hunt in the literature on mammal head evolution using Schlosser's definition of modules – "types of subprocesses that are integrated and partially autonomous" (Schlosser, 2004). Schlosser uses this definition in two ways, depending on the nature of its more inclusive process and of the class of possible perturbations. *Developmental modules* are those that "(1) make an integrated and context-insensitive contribution to the development of an organism in the face of (2) perturbations that do not need to be heritable", whereas *evolutionary modules* "(1) make an integrated and context-insensitive contribution to [their] own reproduction in subsequent generations in the face of (2) variations that are heritable" (Schlosser, 2004: 524). Functionally integrated traits are excluded from Schlosser's pantheon, but they could reasonably be included, following Wagner (1996). *Functional modules* are those that (1) make an integrated and context-insensitive contribution to the functioning of the organism in the face of (2) variations that are heritable or non-heritable. Following Wimsatt, in which a function is system-, environment-, and purpose-specific (Wimsatt, 1972), *integration* in a functional module is a process whereby functional performance is maintained while the system is buffeted by heritable or nonheritable forces. Examples are symmorphosis, internal accommodation, and compensatory changes.

Armed with three separate kinds of modules, the question then is: how they are related? Cheverud uses the term *module* specifically to refer to the effect of genetic integration: "Genetic integration occurs when sets of morphological elements are *inherited together*, as a module, more or less independently of the other element sets of modules" (Cheverud, 1996: 45, emphasis added). Genetic integration is a population level phenomenon because co-inheritance involves passing the morphological elements, or modules, between generations. He contrasts it with developmental integration, an individual-level phenomenon that occurs when elements interact during development, and functional integration, which occurs when "functional interaction of morphological elements affects their joint performance". Although functional and developmental integration can in theory occur without genetic integration, empirical studies and quantitative genetic models suggest that stabilizing selection and correlated mutation produce genetic integration that mirrors developmental and function integration (Lande, 1980; Cheverud, 1982, 1984, 1988). Indeed, functionally and developmentally related traits exhibit higher levels of phenotypic, genetic and environmental correlation than unrelated traits, causing them to be co-inherited, impacting how heritable variation evolves: this is what makes modules of importance for the study of evolution (Ackermann and Cheverud, 2004; Cheverud, 1982, 1995). As heritable products of genetic integration, Cheverud's *modules* correspond to Schlosser's *evolutionary*

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modules, his developmentally integrated traits correspond to Schlosser's *developmental modules*, and his functionally integrated traits can be labeled as *functional modules*, as I define them above.

The real strength of Cheverud's and Schlosser's definitions is that by separating different kinds of modules, and quantifying them, we can ask how they are related. They need not be related, but Cheverud makes a strong case that genetic integration mirrors functional and developmental integration, suggesting some mapping of evolutionary, developmental and functional modules. Consider, in contrast, Wagner's (p. 38) suggestion that "a modular unit of the phenotype has to fulfill three criteria": "it is a complex of characters that 1) collectively serve a primary functional role, 2) are tightly integrated by strong pleiotropic effects of genetic variation and 3) are relatively independent from other such units" (Wagner, 1996). Strict application of this definition would prevent identification of developmental or evolutionary modules that might be constraining functional performance.

But none of these considerations enter into Lieberman's definition of modules, let alone his application of the term. After we have examined how Lieberman uses the term "integration", it will become clear why this is a problem.

Integration

Lieberman argues that integration is the key to understanding the *evolvability* of the head: "heads (like many other complex biological structures) "work" not *in spite* of their complexity, but *because* the many modules that comprise the head are complexly integrated in a special way" (p. 11). The *interactions between the parts*, or modules, Lieberman labels as "integration": "the way in which different components (modules) of a system are combined into a whole". We read (p. 123) that this is partly achieved through "the critical role of epigenetic interactions in helping to integrate the face as it grows and develops", that "interactions among neighboring units" (modules?) "accommodate their simultaneous growth", and that "[i]ntegration occurs throughout ontogeny through a variety of processes, including the effects of mechanical forces generated by organ growth and activities such as chewing and respiration".

Lieberman's interpretation of the aim of these integrating processes – "a highly integrated head" – recalls the holistic definition of integration advanced by Olson and Miller: "the summation of the totality of characters which, in their interdependency of form, produce an organism" (1958, v). This holistic sense of "integration" has many manifestations, including the unity of the genotype (Mayr, 1963; Lewontin, 1974; Mayr, 1976) and "systems views" of organisms (Riedl, 1978; Gould and Lewontin, 1979). But these holistic perspectives are only scientific when they are converted into testable predictions of functional, adaptive, fitness advantages for organisms. Cheverud rescued this metaphysical holism when he defined it in terms of function: "Each part of an organism is formed so that the role it plays in the *function* of the whole is performed harmoniously with respect to all other parts. An organism's phenotype is an organized, integrated, *functional* whole" (Cheverud, 1982: 499, *emphasis* added). This latter phrase reappears in Cheverud's later work, giving the holistic perspective the respectability necessary for its continued usage and widespread influence in studies of mammalian skull evolution. But the use of integration to refer to the functional integrity of the *whole organism* is an assumption of the approach, a motivation, if you like, for the importance of studying integration. Like Olson and Miller, what Cheverud and his colleagues actually document are patterns of phenotypic covariation and correlation among certain groups of traits or measures *within* organisms (Ackermann and Cheverud, 2000, 2002, 2004; Marroig and Cheverud, 2001; Ackermann and Krovitz, 2002; Ackermann et al., 2006; Hallgrimsson et al., 2009). As noted above, some phenotypic measures covary more strongly than others, and they seek to explain this by asking whether these phenotypic modules (if I may be so bold) correspond to predictions based on functional or developmental models. If these phenotypic modules are inherited (or their different components are co-inherited), this reflects genetic integration, and these modules are therefore evolutionary modules. This seems to me to be the most useful application of the concept of *integration*: as a measure or description of covariation *within* developmental, evolutionary and functional modules (Hallgrimsson et al., 2009).

But this is not how Lieberman uses the term "integration" in this book. He presents integration as both the *process* whereby modules interact and accommodate each other during growth and development, and the end result, the *integrated whole*. Elsewhere, Lieberman and colleagues define integration as both "the genetic and epigenetic *processes* that cause coordinated changes among different units of the skull that result in a distinctive pattern of covariation and correlation" (Lieberman et al., 2002) (p. 721), and the "*patterns* of covariation that result from interactions between components of a system" (emphasis added) (Lieberman et al., 2002). I do not have a problem with using the term "integration" to refer to empirical pattern and presumed process (cf. "adaptation") (Hallgrimsson et al., 2009), but I do *not* think it is useful to refer to "integration" as interactions *between* modules until and unless it is contrasted with the integrative processes that act *within* them. Consider the stark contrast between Lieberman's definition and the definitions of integration that refer to processes and interactions that act *within* modules, such as Schlosser's, or Wagner's: "A module, therefore, is a part of an organism that is integrated with respect to a certain kind of process (natural variation, function, development and so on) and relatively autonomous with respect to other parts of the organisms" (p. 921) (Wagner et al., 2007).

This may seem like pedantry to some readers. After all, aren't there two different phenomena at play: processes intrinsic to modules, that create and define them, and processes that connect modules to each other, allowing them to interact with each other, and creating the integrated, Olson and Miller's holistic organism? Does it really matter which we call which? I think it does, for two reasons. First, surely the interactions and processes that act within a module, holding it together, defining it, and creating it, have stronger claims on being "integrative" (Wagner et al., 2007) than an ill-defined almost metaphysical notion of organismal "wholeness". Second, different phenomena should be referred to using different names, unless and until they can be shown to be the same. This enables us to study them. Are the integrative processes acting within modules the same as the interactive processes acting between them? Surely the first place to start is to define the modules themselves, *then* ask how they interact and whether their intrinsic integrative processes are the same as those that accommodate the influences of other modules?

Let's consider some examples of how Lieberman's use of "integration" fails to clarify. On p. 115 we read that bones of the cranial vault "participate in the growth of the face and cranial base", and that these "connections integrate the neurocranium with the face and basicranium". This suggests that Lieberman sees the face, neurocranium and basicranium as modules, and the vault bones that connect and bridge them serve to "integrate" these modules in some unspecified way with some unspecified advantage. Perhaps they bridge the gaps between the modules? If this is the case, Lieberman does not present the frontal bone this way on pages 126–129. And why is this good for the organism at all? One functional advantage of a smoothly curving frontal bone might be

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strengthening the calvaria against blows from the outside world, according to biomechanical principles outlined by Lieberman in Chapter 6. However, in contrast with these principles, the frontal bones of many primates actually manifest protruding ridges of bone above the eyes which are ideal places for blows to fall. I suppose one could look at the frontal bone as *integrating* "the neurocranium with the face and basicranium". But this wouldn't be necessary if the face didn't stick out so far in the first place, so shouldn't we be focusing on what makes that happen? It seems to me that the preponderance of evidence suggests that supraorbital morphology is *compensating* for or *accommodating* changes in the facial module relative to the neurocranial module, a possible example of complexity resulting from close packing of the modules. I do not think we know at present whether this is due to integrating processes acting *within* those modules. To answer this question you need to focus within the modules first. *Vide supra*.

Another example is Lieberman's treatment of the role of integration in facial growth. "Facial growth has to accommodate not only many different components of the face but also the cranial base and neurocranium". The upper and middle face grow down and forward from the cranial base, and the mandible grows down separately, "requiring many aspects of skull growth to be coordinated and integrated to prevent malocclusion between the lower and upper jaws" (p. 123). Rephrased in terms defined above: there seem to be two separate developmental modules here, the upper and lower jaws that need to function together in an integrated fashion (i.e., to form a functional module). How do they achieve it? This is not some airy fairy whole organism integration (holism), but a question of how functional integration is achieved in spite of some aspects of developmental integration and with the aid of others. Lieberman asks this question but, because he focuses on integration *between* modules rather than within them, he focuses on the problem rather than the solution: there is no discussion of the fundamental mechanisms that integrate these separate modules so that they remain functional (Cheverud and Midkiff, 1992; Bastir et al., 2004; Bastir and Rosas, 2006a, 2006b; Bastir et al., 2010a). The obvious candidates here are tooth movement due to alveolar bone remodeling, and phenotypic plasticity of the palate and temporomandibular joint (Ravosa et al., 2006, 2007a, 2007b, 2009), processes acting *within* the two developmental modules (upper and lower jaws) to accommodate the pushing, pulling and jostling coming from the basicranial and neurocranial modules. If ever there were *integrative* mechanisms, these are them, yet they receive short shrift in this book. Again, I think this is because Lieberman focuses on inter-module interactions, not integrative processes within modules. Instead, we are subjected to the idea that "permanent tooth crown size is influenced... by mechanical loading" (p. 234, see also p. 279). (How such a process might produce functional integration of occluding tooth crowns is beyond me!)

So, I think Lieberman (and others) pay too much attention to interactions between modules (which I think is a confusing and trivial use of the term *integration*), without attention to what's going on within modules (which are defined in part by *integration*, including functional integration). He pays too much attention to how changes in some modules result in changes in other modules without considering how these interactions between modules are accommodated. I think that this is not an effective research strategy because the integrative processes that define a functional module act *within* it, maintaining functional performance and developmental trajectories in the face of external corrupting influences, including those from other modules. It would help if we had other terms for these inter-module interactions other than "integration", so that we could ask how or whether these interactions differ from the integrative processes within modules.

A case in point: Browridges

The problem with not clearly defining modules is well illustrated by Lieberman's treatment of the role of "integration" in explanations for interspecific variance in browridge anteroposterior dimensions. Franz Weidenreich suggested in 1941 that browridge lengths were driven by "neurocranial-orbital disjunction", and this hypothesis had received support from several careful studies in the late 1980s and early 1990s, most notably those of Ravosa (Weidenreich, 1941; Shea, 1986a,b; Ravosa, 1988, 1991b). Weidenreich's hypothesis posits that the more the orbits stick out in front of the neurocranium, the longer the browridge. Elegantly simple (could it be any other way?) and well validated, this hypothesis then begs the question, what makes the face project beyond the neurocranium? By 1998 two important possibilities had been suggested and supported by interspecific and ontogenetic data: increases in facial size and changes in facial orientation. The *facial size* model suggests that as the face gets bigger the browridges also get bigger, either as a pleiotropic effect – browridges are part of a facial module – and/or because a bigger face projects more and hence needs protecting from above. The facial *orientation* model suggests that because the orbits are part of the face – again, a facial module – changes in orientation of the face (klinorhyncy or facial kyphosis and airorhynchy) will rotate the orbits back underneath or out in front of the neurocranium, reducing or augmenting the browridge. Lieberman's (1998) *facial projection* model can be added to these, as it suggests that browridges evolve when the face projects beyond the neurocranium due to anterior displacement. Note that all three of these hypotheses imply that the orbits are part of a facial module, and that their position relative to the neurocranium (neurocranial module) can be driven by changes in size, orientation or position of the facial module. However, rather than testing this idea rigorously, Lieberman (1998) argued that browridge reduction in the lineage leading from archaic *Homo* (AH) to anatomically modern *H. sapiens* (AMHS) was due to "a single ontogenetically early shift in cranial base growth" that was related to the evolution of several features characteristic of AMHS (Lieberman, 1998). He claimed that shortening of the sphenoid body in AMHS resulted in reduced facial projection, which he argued is the "main influence on browridge size and frontal angulation in nonhuman primates", and apparently all the things that make being a human being worthwhile: cranial globularity, shortening of the orophraynx (facilitating speech), and improving leverage of the chewing muscles. (Lieberman's measures are defined and illustrated in Fig. 4.)

A subsequent paper revealed that several AH (Gibraltar 1, Kabwe, Monte Circeo) actually have very short ASLs, and that, as a result, ASL is not highly correlated with midfacial projection (MFP) among human species (Spoor et al., 1999). Forced to abandon his argument for the importance of ASL, Lieberman adopted a more multifactorial model for the determinants of browridge anteroposterior length in humans: including facial size, facial orientation, and (in spite of lack of evidence) facial projection (Lieberman, 2000). (I do note, however, that facial projection slips into *Evolution of the Human Head* Figure 5.9 via Figure 8.C of Lieberman (2000), albeit with an erroneously short ASL in Figure 5.9d.) Lieberman (2000) focuses on explaining variance in browridge length with reference to basicranial flexion and facial orientation. He suggests that because the orbital roofs are also the floor of the anterior cranial fossa, the face "rotates with the anterior cranial base as a block" (p. 171), so that facial orientation is strongly influenced by basicranial flexion. The reason for this, as long noted (Dabelow, 1929; Cartmill, 1970; Ravosa, 1991a; Ross and Ravosa, 1993; Ross and Henneberg, 1995), is orbital approximation below the olfactory tract that integrates the face and anterior cranial base. As a result,

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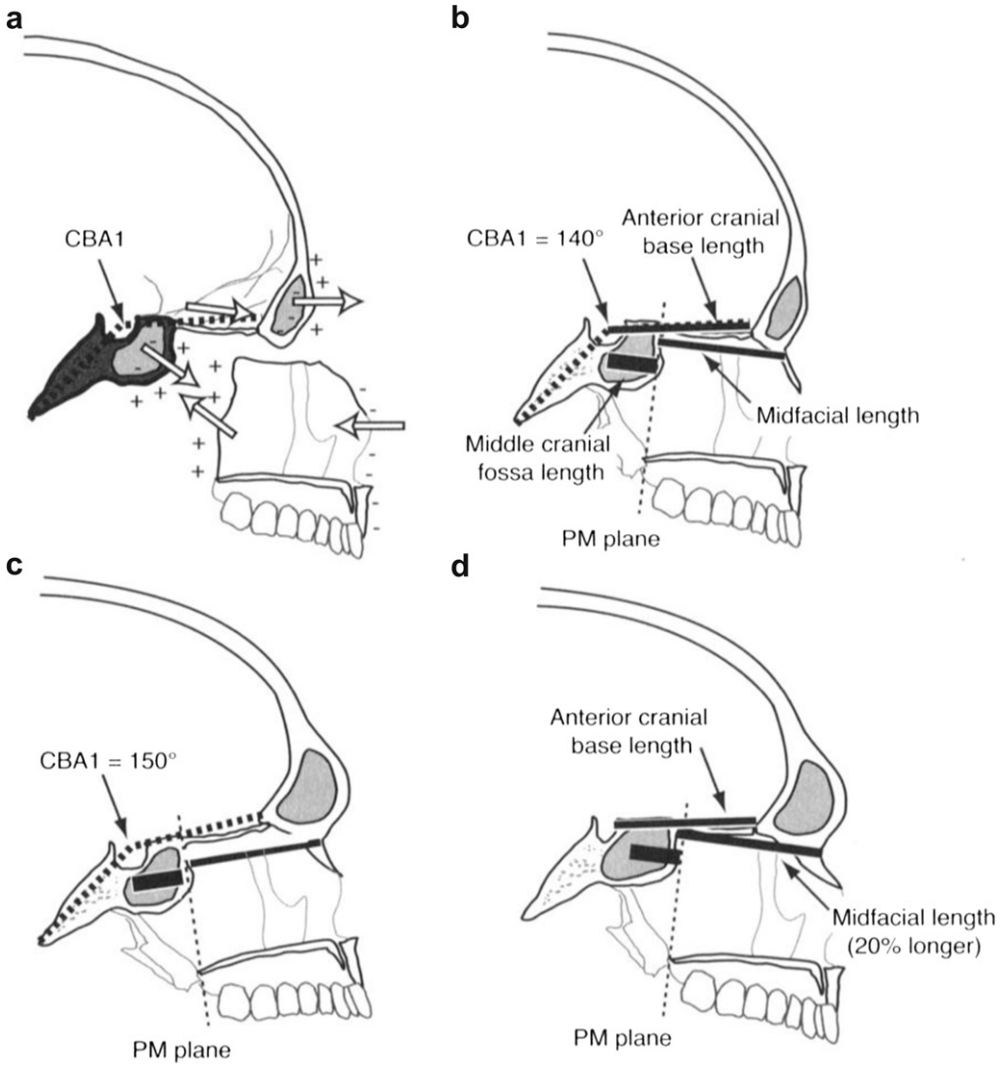

Figure 4. Reproduction of Figure 5.9 from Lieberman (2011), *The Evolution of the Human Head*.

when the posterior cranial base flexes relative to the anterior, it also flexes relative to the facial module. With this relationship in hand, Lieberman uses Figure 5.9 (this paper's Fig. 4) to argue that basicranial flexion is an especially important influence on facial projection "because a more extended cranial base rotates more of the face in front of the [anterior cranial fossa] increasing upper facial projection" (p. 174).

But this makes no sense: if the facial module is integrated with the basicranial and/or neurocranial modules, then by definition flexion within the cranial base will not affect the spatial relationships between face and anterior cranial base. Think about it this way: *Ceteris paribus*, relationships between the facial module and the anterior cranial base are not going to be affected by flexion of the posterior cranial base relative to the anterior, they are going to be affected by *changes in relationships between the face and the anterior neurocranium* (Ross and Henneberg, 1995). But, let's assume that Lieberman's hypothesis is true, and it is upward or downward flexion of the facial module by around 10° (the difference in basicranial flexion between AH and AMHS in Figure 5.9) that accounts for changes in projection of the face relative to the anterior cranial base. Assuming that the center of rotation is at sella and the front of the face is 47.8 + 14.6 = 62.4 mm away from sella (ACL + MFP from Lieberman, 1998, Table 2), the largest possible increase in MFP is given by |62.4 mm – cos10° * 62.4 mm| = 0.948 mm. A sub-millimeter change in browridge dimensions is not what we need to explain here, so simple geometry argues against changes in facial and browridge projection being driven by changes in facial orientation in turn driven by changes in basicranial flexion.

Lieberman also suggests that increases in frontal lobe size might reduce facial projection and (presumably) browridge length in AMHS. I think this argument might have some legs, but not for the reasons advanced by Lieberman. He argues that increases in frontal lobe size will result in increases in anterior cranial base length, and that this increasingly protruding ACL places the face more and more underneath the anterior cranial base, reducing MFP and browridge length (p. 174 and 176). But this argument cannot explain small browridges in humans either because, *Ceteris paribus*, increase in ACL relative to facial length would actually push the cribriform plate and browridge forward, *increasing* browridge length in AMHS, the reverse of Lieberman's predictions! Moreover, my data confirm that, indeed, humans have long sella-foramen cecum distances relative to palate length (Fig. 5) but it is clear from Lieberman's own data (2008, Table 2) that AMHS do *not*

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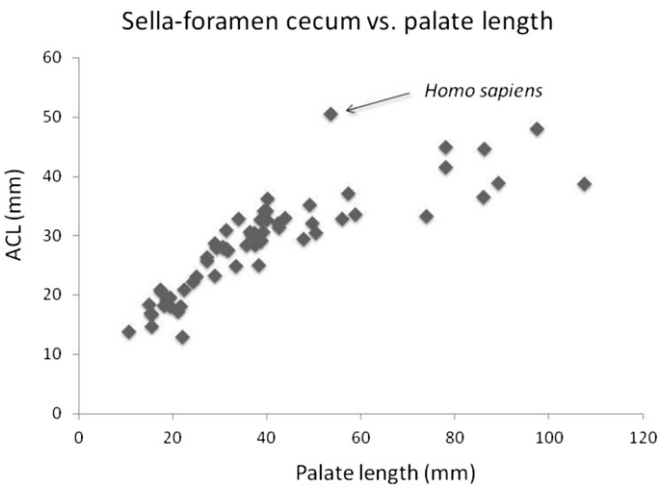

Figure 5. Bivariate plot of anterior cranial base length (ACL) against palate length. Humans have long ACLs relative to palate length. However, this is not because they have long ACLs, but because they have short palates.

have absolutely longer ACL than other primates. Thus, it must be reduction in overall facial size that causes browridge reduction in humans. I think Lieberman's belief in ACL lengthening in humans derives from a geometric morphometric analysis presented elsewhere (Lieberman et al., 2002), and reproduced here in Fig. 6. Lieberman et al. use this analysis to argue that humans have a more retracted face in part because of their long anterior cranial bases. However, these data have been scaled to a common geometric mean, so that decreases in facial size (the blue lines) *must be* associated with increases in other parts of the skull to maintain a constant centroid size. That is why anterior cranial base length *appears to be* longer in AMHS when, in fact, as Lieberman's (1998) data clearly show, it is not (Fig. 6).

This lengthy exegesis shows that there is *good evidence that variance in browridge projection in the lineage leading from AH to AMHS is NOT driven by variance in basicranial flexion, anterior cranial base length, or facial orientation*. In contrast, there is plenty of evidence that browridge projection is highly correlated with facial size. Ravosa clearly shows that palate length is one of the most consistent correlates of browridge length both in interspecific and ontogenetic comparisons (Ravosa, 1991a, b). Lieberman's rejection of facial size as the primary determinant of browridge length on the grounds that Neanderthals have more mid-facial projection than predicted by their midfacial length (2000, Figure 11) is based on a much smaller sample and on a different measure (midfacial length instead of palate length). It seems to me that the question of the influence of facial size on browridge dimensions could be quickly tested using a geometric mean of facial measures rather than single linear measures, but I'll wager that Ravosa will turn out to be right about this.

In sum, the available data suggest that selection for integration of the browridges with the rest of the face was necessary to ensure that there was always enough bone there to protect the orbital contents from blows to the head (Hylander et al., 1991) in the context of neuro-orbital disjunction caused by kilonrhynchy or increases in facial size (Weidenreich, 1941; Shea, 1986a, b; Ravosa, 1988, 1991a). In this sense, the browridges are part of the facial module as a whole. Subsequent selection for increases or decreases in size of the face would then also act on browridge size, making browridges a nice example of how functional integration producing functional modules can be achieved through developmental integration to produce developmental modules, and this in turn creates a genetically integrated evolutionary module (Cheverud, 1982). Moreover, this explanation probably also applies to the well documented positive allometry of orbit size relative to eyeball size (Schultz, 1940; Kirk, 2006). If Lieberman had focused more on defining these modules and less on the interactions between disparate parts in the head, I think he would have got better traction on these important questions.

The future of integration and modularity studies in primate crania

Studies of the causes and effects of cranial base angulation, which Lieberman neatly summarizes, show that the degree of basicranial flexion is positively correlated with the size of the brain relative to basicranial length and negatively correlated with facial length (Biegert, 1963). This has been confirmed many times since Ross and Ravosa (1993), but I confess that I still do not really understand why increases in facial length (which Ravosa and I measured as palate length) should be associated with decreases in basicranial flexion. If the face grows down and forward from the cranial base, as it does, there is plenty of room for a large face even with a flexed cranial base. But, the effect of facial size is certainly there, as nicely shown in Lieberman et al.'s recent study (Lieberman et al., 2008), and we simply do not understand why, from either mechanical, developmental, or functional perspectives. There is either some profound interaction between facial and neurocranial modules at the cranial base, or the way we are measuring the variables is not giving us the answers. If we define the brain + basicranium and the face as both *developmental and evolutionary modules* sensu Schlosser (processes that make an integrated and *relatively* context-insensitive contribution to the development and reproduction of the organism in the

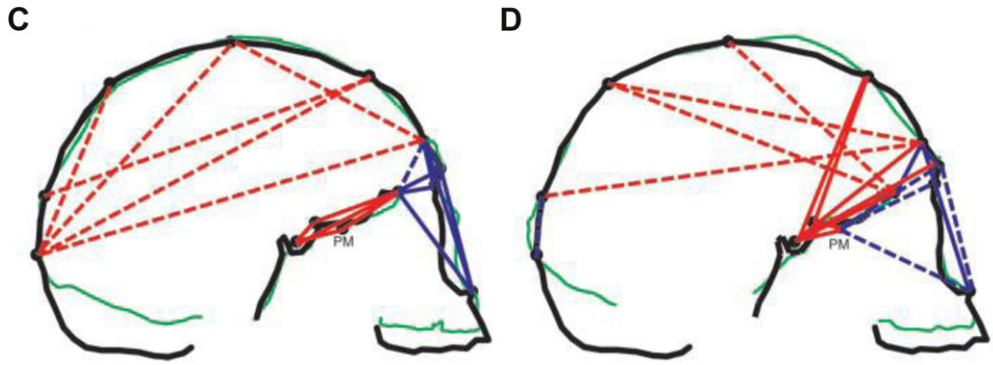

Figure 6. Reproduction of part of Figure 2 from Lieberman et al., (2002). This figure is used by them to argue that the AMHS anterior cranial base is longer than that of AH. However, this conclusion runs counter to Lieberman's (1998) data. In fact, AMHS is distinctive in having a smaller face, including a shorter palate (Figure 5).

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face of perturbations), where is the boundary between them? Perhaps the brain and endocranial surface of the basicranium constitute a neurocranial module, whereas the face and external surface of the basicranium constitute another module, predicting that endocranial basicranial measures will covary most with brain size and shape (Strait, 1999, 2001), whereas the external measures will covary with the facial module. Under this model, recalling ideas of Enlow and van der Klauww (Enlow, 1990; van der Klaauw, 1945, 1948), the "basicranium" straddles the border of two modules, with its developmental and evolutionary processes allowing changes in the two adjacent modules to accommodate each other.

In my opinion, it is at this boundary between neurocranium and face that important research on morphological integration and modularity in the primate cranium needs to be done. We need a better understanding of how the different parts of the cranial base interact with or are part of (integrated within) different cranial modules during development and evolution. I have to say, that I do not see how this can be achieved by defining cranial base flexion using the angle between a line running from basion to sella and another running from sella to foramen cecum. Sella is not even a bony point, and these lines cross so many synchondroses where important growth processes occur, thereby traversing multiple modules, that they cannot hope to provide clear signals on what the modules are and how they interact. Others have said this before very clearly (Cartmill, 1970; Sirianni and Swindler, 1979), it informed our choice of flexion measures in 1993 and since (Ross and Ravosa, 1993; Ross and Henneberg, 1995; Ross et al., 2004), and I still think it is true. The best work currently being done on integration and modularity at this important interface is the meticulous work of Markus Bastir, Antonio Rosas and their colleagues, which not only quantifies morphology at the level of detail that I think is required, but recognizes the importance of morphological changes off the mid-sagittal plane as well (Bastir et al., 2004; Bastir and Rosas, 2004a, b; 2005; Bastir et al., 2006; Bastir and Rosas, 2006b; Bastir et al., 2007, 2008a, 2008b, 2009; Bastir et al., 2010a, 2010b, in press, 2011). As high resolution 3D images of a broad sample of primate crania become more easily accessible, Bastir's results are tested across a wider range of primates, and Cheverud's approaches (Cheverud, 1982, 1995; Ackermann and Cheverud, 2000, 2002, 2004; Marroig and Cheverud, 2001; Ackermann and Krovitz, 2002) are extended to include more landmarks inside the cranium, I think we can expect to see our understanding of integration and modularity in the evolution of the primate head rapidly improve. Combined with developmental experimental approaches being pursued by Hallgrimsson and Lieberman (Hallgrimsson et al., 2004a, 2004b, 2007; Boughner and Hallgrimsson, 2008; Lieberman et al., 2008; Marcucio et al., 2011), and finite-element modeling measures of functional performance and developmental interactions (Kupczik et al., 2009; Curtis et al., 2011; O'Higgins et al., 2011), the road ahead looks exciting.

Conclusions

In sum, Lieberman's book is an innovative attempt at a synthetic treatment of hominid skull evolution. It seeks to summarize developmental and functional principles governing head evolution then apply them to understanding of the fossil record. This is an ambitious book and it has variable success. The early chapters where the important theoretical and conceptual foundations of the book are laid out are interesting from a theoretical perspective, but I think that in failing to precisely and accurately define and use "complexity", "module" and "integration", terms which are central to the ideas promulgated here, Lieberman misses an opportunity to advance the field in a meaningful way, and gets tangled up in explanations for (e.g.) browridge evolution that just do not hold water. That said, this may not be Lieberman's problem, but, rather, reflective of broader problems with these concepts. The idea of the book is a good one and if a second edition were prepared that addressed the theoretical problems laid out above, and corrected the biomechanical errors and errant figures, then this book would be enormously useful. Until that time, I can recommend this book to critical, independent undergraduates looking for an introduction to the literature on primate head evolution. A graduate student looking for research projects will certainly find some low-hanging fruit here, but they will need to be prepared to read thoughtfully and critically. Finally, there is plenty here for researchers like me who have grappled head-on with many of the exciting questions addressed in this book.

Acknowledgments

I am grateful to Dan Lieberman for many stimulating discussions on head evolution over the years. He has generously shared data and resources with me and many others in order to further our understanding of this most fascinating part of the primate body. I apologize to Lieberman and Ravosa for my error in our 2000 Yearbook paper, and I appreciate the *Journal of Human Evolution* providing the opportunity to set the record straight. I appreciate helpful comments from Richard Smith and an anonymous reviewer that improved this review.

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