



## SYMPOSIUM INTRODUCTION

### Multifunctional Structures and Multistructural Functions: Integration in the Evolution of Biomechanical Systems

S. C. Farina,<sup>1,\*</sup> E. A. Kane<sup>†</sup> and L. P. Hernandez<sup>‡</sup>

\*Department of Biology, Howard University, 415 College Street NW, Washington, DC 20059, USA; <sup>†</sup>Department of Biology, Georgia Southern University, 1332 Southern Drive, Statesboro, GA 30458, USA; <sup>‡</sup>Department of Biological Sciences, The George Washington University, 800 22nd Street NW, Suite 6000, Washington, DC 20052, USA

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<sup>1</sup>E-mail: stacy.farina@howard.edu

**Synopsis** Integration is an essential feature of complex biomechanical systems, with coordination and covariation occurring among and within structural components at time scales that vary from microseconds to deep evolutionary time. Integration has been suggested to both promote and constrain morphological evolution, and the effects of integration on the evolution of structure likely vary by system, clade, historical contingency, and time scale. In this introduction to the 2019 symposium “Multifunctional Structures and Multistructural Functions,” we discuss the role of integration among structures in the context of functional integration and multifunctionality. We highlight articles from this issue of *Integrative and Comparative Biology* that explore integration within and among kinematics, sensory and motor systems, physiological systems, developmental processes, morphometric dimensions, and biomechanical functions. From these myriad examples it is clear that integration can exist at multiple levels of organization that can interact with adjacent levels to result in complex patterns of structural and functional phenotypes. We conclude with a synthesis of major themes and potential future directions, particularly with respect to using multifunctionality, itself, as a trait in evolutionary analyses.

#### Introduction

Integration is a fundamental principle in organismal function (Pepper and Herron 2008). Coordination must occur among and within structural and physiological systems throughout the life of an organism to ensure its survival and contribution to the next generation. Morphological integration is a term that is broadly defined as any covariation, correlation, or coordination among structures at a broad range of time scales (Olson and Miller 1958; Cheverud 1996; Klingenberg 2008). For example, integration is produced and maintained by complex and often pleiotropic interactions among genes, developmental processes, functional performance, and selective forces (Olson and Miller 1958; Hulsey et al. 2005; Klingenberg 2008; Goswami and Polly 2010; Monteiro and Nogueira 2010; Parsons et al. 2011). This integration can be measured in morphology

(covariation among structures) and behavior (kinematic coordination) on time scales that range from microseconds (Camp 2019; Higham and Schmitz 2019; Kane et al. 2019), to ontogenetic time (Hernandez and Cohen 2019), to generational and ecological time scales (Friedman et al. 2019; Kane et al. 2019), and to macroevolutionary time scales (Evans et al. 2019; Farina et al. 2019; Felice et al. 2019; Hernandez and Cohen 2019; Kane et al. 2019; Pos et al. 2019; Stayton 2019). However, the influence of morphological integration on the evolution of form and function is complex and is only beginning to be understood.

With the development of new techniques and hypothesis testing frameworks, such as X-ray reconstruction of moving morphology (XROMM; Camp 2019), high resolution morphometric analyses (Felice et al. 2019), and multifunctional performance

landscapes (Stayton 2019), researchers are incorporating integration into studies of the evolution and function of complex biomechanical systems. Likewise, morphometric studies of shape integration are incorporating more explicit testing of function among integrated traits (Evans et al. 2019; Farina et al. 2019; Feilich and López-Fernández 2019; Felice et al. 2019; Hernandez and Cohen 2019). Integrated organismal structure and function can both limit and promote morphological diversification in different systems, and it is likely that early integration has a wide range of effects on morphological evolution (i.e., Evans et al. 2017; Hernandez and Cohen 2019). Investigations into patterns of morphological diversification and their underlying processes are beginning to disentangle the mechanisms by which integration can constrain and drive structural change. In many cases, function has been implicated in either driving integration or affecting the response of integration to alternative demands (Evans et al. 2019; Farina et al. 2019; Friedman et al. 2019; Hernandez and Cohen 2019; Higham and Schmitz 2019).

The constraint imposed by function on form has led many authors to use the term “functional integration,” but the meaning of this term has been inconsistent. In the field of development, functional integration typically refers to intraspecific or evolutionary covariation that can be explained by shared function (e.g., Zelditch and Carmichael 1989; Badyaev and Foresman 2004; Badyaev et al. 2005; Walker 2007, 2010). In the field of biomechanics, functional integration refers to the coordination of structures and the covariation of kinematics in performance of a function (Liem and Osse 1975; Schwenk and Wagner 2001; Collar et al. 2014; Cooper et al. 2017). Both forms of functional integration have been thought to limit morphological evolution, because disruption of integration can result in a reduction or loss of functionality (Collar et al. 2014), causing phenotypic stability to be maintained by selection on functional integration (Schwenk and Wagner 2001; Pepper and Herron 2008). However, if functional integration coincides with a major axis of genetic or developmental variation, this integration can drive functional anatomical systems to the furthest extents of morphological and performance space (Goswami et al. 2014; Marroig and Cheverud 2005; Kane and Higham 2015; Felice et al. 2018, 2019). Patterns such as mosaic evolution may also produce systems in which functional integration imposes constraint in some lineages or structures and relaxes constraint in others (Evans et al. 2019; Felice et al. 2019). Many of the

works in this volume suggest that, rather than either of these extremes, integration may have a broad range of effects on the evolution of morphological systems.

During the 2019 symposium “Multifunctional structures and multistructural functions: Functional coupling and integration in the evolution of biomechanical systems,” the proceedings of which are presented in this issue, we engaged in a significant conversation about the influence of integration in the performance and evolution of complex biomechanical systems. Speakers concluded their presentations with five or more minutes for questions, which led to in-depth discussions after every talk. Additionally, we held a 30 min panel discussion at the end of the symposium, in which four panelists (Drs Anja Goswami, Patricia Hernandez, Tristan Stayton, and Kory Evans) engaged the audience in a conversation about integration. Therefore, the insights described throughout this issue stem not only from our distinguished speakers but from the participants in all aspects of the symposium. This includes the symposium and panel discussion attendees, the speakers for the complimentary session (A.S. Dias, K.A.H. Smith, A.L. Camp, N.J. Gidmark, D. Krentzel, A.B. Lapsansky, and M.A. Wright), and the authors of the two complimentary articles in this issue (Camp 2019; Pos et al. 2019). Our graduate student social media contributors (Alexus Roberts, Kelsie Pos, and Katherine Corn) produced more than 60 tweets from the symposium and surrounding events, documenting the discussions and engaging with the community of Society for Integrative and Comparative Biology (SICB) meeting attendees and beyond. This article briefly covers many ideas that were discussed in our symposium and offers a synthetic overview of the role of integration in functional evolution that represents contributions from a large group of SICB attendees.

## Multifunctional structures and multistructural functions

As advances in technology improve our ability to examine organismal complexity, studies are increasingly revealing that most functions require the coordination of multiple structures and most organismal structures perform more than one function. In complex biomechanical systems, especially those that require precision and behavioral plasticity (Kane et al. 2019) or are dependent on sensory input to coordinate motor output (Higham and Schmitz 2019; Kane et al. 2019), multiple structures must work together in a highly coordinated manner to accomplish a task.

Although there can be multiple ways to achieve the same functional performance within an anatomical system (Wainwright et al. 2005; Kane et al. 2019), functional coordination and kinematic integration generally produce organismal function that is greater than the sum of individual parts (Mehta and Wainwright 2007; Kane and Higham 2015), requiring a more complex mapping of form and function. The true extent of functional integration is often underappreciated, even in the most well-studied biomechanical systems. For example, suction feeding in teleosts is a model system for functional integration in vertebrates, and yet the role of postcranial elements, although well-established, is often overlooked (Camp 2019). In fact, feeding in most vertebrates requires coordination of structures across most, if not all, of the body (Montuelle and Kane 2019). Therefore, we are only beginning to understand the role of multiple structures in feeding performance, specifically, as well as performance and function more generally.

Organisms are also phenomenal multitaskers, and their ability to use the same structures for multiple functions has allowed them to extend their physiological and behavioral repertoires without necessitating an increase in structural complexity (Evans et al. 2019; Farina et al. 2019; Stayton 2019), such as the number of parts, number of mobile joints between parts, or complexity in shape of single parts. The influence of multifunctionality on the evolution of complex biomechanical systems has been largely understood through the lens of “functional decoupling,” in which structural novelty or duplication creates an opportunity for a previously multifunctional structure to specialize on one function, while the new structure takes on one of its former functional roles or adds a new function altogether (Wainwright 2007; Friedman et al. 2019; Hernandez and Cohen 2019). The classical example of this in fishes is the evolution of pharyngognath in cichlids (Cichlidae) and wrasses (Labridae), in which the role of prey processing is assumed by the pharyngeal jaws, leaving the oral jaws to become specialized for prey capture (Liem 1973; Kaufman and Liem 1982; Wainwright 2006). This decoupling of prey capture and processing is considered a key innovation that led to the extensive functional and anatomical diversification in the jaws of fishes within these clades (Wainwright 2006, 2007). The idea that functional decoupling promotes morphological diversification implies that the opposite is true—that multifunctionality constrains the evolution of morphology. However, few studies have explicitly tested this (Tsuboi et al. 2015; Friedman et al. 2019), and

there is some evidence to the contrary. For example, developmental integration may have facilitated the origin of the kinethmoid in the skull of cypriniform fishes, thereby acting as a spark for new functions to evolve and diversify (Hernandez and Cohen 2019). Similarly, modularity of the hyoid or lower jaw from other integrated units of the skull may contribute to the diversification of feeding ecology while maintaining other functions such as protection of the brain, secondary sexual traits, and ventilation (Evans et al. 2019; Farina et al. 2019), despite the functional coupling that is prominent in fish skulls.

Ultimately, studies on the evolution of biomechanical systems must consider that the structures or functions under investigation may have been shaped by interacting and potentially asymmetrical demands (Evans et al. 2019; Farina et al. 2019; Higham and Schmitz 2019; Kane et al. 2019; Stayton 2019). However, multifunctionality should not be assumed to be a limiting factor of morphological diversification, even though this is true in some systems (Wainwright 2007; Tsuboi et al. 2015). Multifunctionality can promote morphological evolution in two primary ways: by disrupting evolutionarily stable functional systems (Felice et al. 2019) and by providing a catalyst for evolutionary novelty (Hernandez and Cohen 2019; Pos et al. 2019). Functional trade-offs that shape structures in opposing directions could impose limitations on potential morphological diversity (Ghalambor et al. 2003; Wainwright 2007), but the demands of a competing function could also disrupt the evolutionary stability of existing functional systems (particularly those with high integration) and release mechanical constraints on that system (Schwenk and Wagner 2001; Ghalambor et al. 2003; Friedman et al. 2019). When structural novelty arises and adds additional functionality to a system, it must be integrated with existing structures that can accommodate and facilitate the demands of the new function (Hernandez and Cohen 2019). The persistence of this novel structure and its evolving function can then lead to an increase in morphological, species, and trophic diversity.

## Perspectives: developmental integration

Developmental integration is occasionally presented as an alternative hypothesis to functional integration, but it may in fact be the base layer upon which integration at other levels can be applied (Hernandez and Cohen 2019). When patterns of integration do not appear to have functional consequences, these patterns are often attributed solely

to development or to ontogenetic growth patterns. When morphological integration is associated with functional performance, it can be maintained by selective pressures (Evans et al. 2019; Friedman et al. 2019; Kane et al. 2019; Pos et al. 2019; Stayton 2019), but integration attributed to development is considered a signal of historical constraint that limits morphological and functional diversity (Evans et al. 2019). However, many authors have determined that developmental integration has functional consequences and that natural selection acting on function can maintain these patterns of developmental integration (Cheverud 1996; Lieberman et al. 2000; Bastir 2008; Klingenberg 2008; Zelditch et al. 2009; Hernandez and Cohen 2019). In fact, developmental and functional integration represent coordination at varying levels of organismal hierarchy rather than conflicting evolutionary processes (Bastir 2008; Zelditch et al. 2009; Hernandez and Cohen 2019). Both development and function can be constrained by historical contingency and shaped by natural selection, and integration likely plays a role in both of these processes (Felice et al. 2019; Hernandez and Cohen 2019; Pos et al. 2019).

### Perspectives: ecomorphology and integration

Ecomorphological analysis permits hypothesis testing to match patterns of integration to environmental and functional diversity (Marroig and Cheverud 2005; Monteiro and Nogueira 2010; Santana et al. 2011; Feilich and López-Fernández 2019; Pos et al. 2019). Morphological integration can produce specialists as integrated traits are driven toward morphological extremes (Monteiro and Nogueira 2010; Santana et al. 2011; Evans et al. 2019; Hernandez and Cohen 2019), or it can produce a wide array of possible shapes for tackling similar ecological challenges due to many-to-one-mapping or extreme homoplasy (Wainwright 2006; Pos et al. 2019). Likewise, functional coordination can either produce specialists that must be highly coordinated to perform a specific behavior or generalists that have highly adaptable integrated systems, due to the ability of the integrated kinematics to respond to perturbation (Kane et al. 2019). As we work to understand the ecological consequences of integration, we find that these consequences are far more complex and context-dependent than previously assumed. For example, degree of integration can vary among individuals within a species due to sexual dimorphism, reproductive strategy, and social role (Friedman et al. 2019). Additionally, visual sensorimotor

integration has vastly different consequences for diurnal and nocturnal animals (Higham and Schmitz 2019). Even in a well-studied system such as suction feeding in fishes, the degree of integration between the body and head provides an underappreciated axis of variation as fishes use this system to match functional demands imposed by different types of prey (Camp 2019; Kane et al. 2019). As the ecological implications of various types of integration are tested, a certain degree of caution regarding such context is necessary (Feilich and López-Fernández 2019). Reducing the complexity of performance to a single functional metric can be just as problematic as reducing the morphological complexity of a highly integrated system to one morphometric dimension (Feilich and López-Fernández 2019; Stayton 2019). The environment is constantly changing, and integration can provide either flexibility or stability in the face of change, depending on a variety of genetic, developmental, functional, and evolutionary factors. Therefore, context and careful hypothesis testing are critical (Feilich and López-Fernández 2019).

### Perspectives: modularity and modulation

The term “modularity” generally refers to the tendency for structures to form units that show high internal covariation or coordination at the level of individuals or at evolutionary scales (Klingenberg 2008, 2014). Developmental modules are typically defined as groups of cells or structures with shared developmental origin and a high degree of coordination during ontogeny that produces internal covariation in morphometric analyses of adults. Likewise, functional modules are defined as structures or parts of structures with shared function and high covariation (Evans et al. 2019; Claverie and Patek 2013). In these cases, modules can be defined by measuring and comparing covariation within and among proposed organizational units, with the expectation that internal covariation will be substantially higher than covariation across units. However, “modularity” has a much wider range of definitions that can refer to any pattern of structures developing, functioning, or evolving independently of one another. Therefore, “modularity” can be seen either as a general lack of integration, as an explicitly defined metric of covariation among modules, or anywhere in between. Within this context, the ability to switch between discrete sets of behaviors based on context could be described as behavioral modularity. For example, fishes can switch between feeding modes based on prey type encountered (Ferry-Graham et al. 2001;

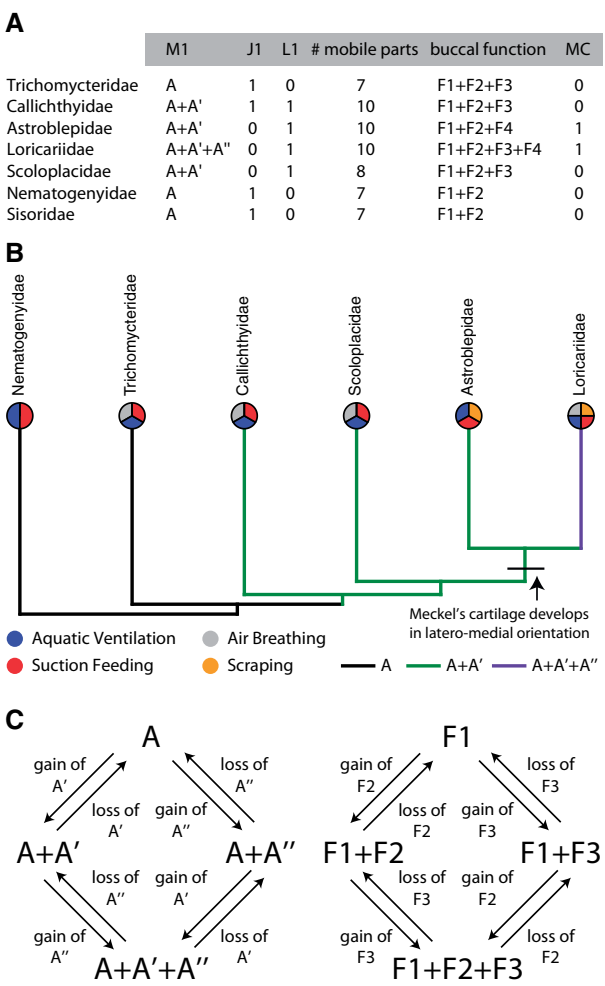


Van Wassenbergh and De Rechter 2011; Kane et al. 2019). This is instead referred to as modulation (meaning simply “change”) rather than referring to behavioral modes as integrated modules. The specific definition of “module” relative to the broad usage of “modularity” has resulted in ambiguous uses of the term “module,” often in the context of functionally coordinated units. We recommend using the term “unit” in place of “module,” if units are defined *a priori* before tests for within- and among-unit covariation, which many authors have already adopted (e.g., Schwenk 2001; Murren 2002; Badyaev and Foresman 2004; Labonne et al. 2014; Farina et al. 2019; Kane et al. 2019). Tests for covariation within and among mechanical or functional units may allow an author to elevate units to modules.

Recommendations: integration as a trait

Although the above discussion offers a wide array of considerations for studies of functional integration, incorporating all of the varied influences of integration into investigations of evolution of complex bio-mechanical systems remains difficult. One way to expand the current scope of such investigations is to leverage the increasing flexibility of phylogenetic comparative methods to test models of evolutionary associations among traits that encompass different types of morphological integration. Phylogenetic comparative methods rely on two types of data: phylogenies with information about relatedness among taxa and character matrices with the condition of each taxa. As robust phylogenetic trees for clades of interest become more readily available, additional emphasis can be placed on increasing the flexibility and utility of character matrices and models of character evolution.

Biomechanical traits have long been incorporated into evolutionary models as continuous characters (Arnold 1983; Westneat 1995; Ghalambor et al. 2003), but coding multifunctionality, mechanical decoupling, and kinematic and developmental integration as characters can open opportunities for testing hypotheses of structure–function evolution that have persisted in the literature. To demonstrate how this could be implemented, we assembled a character matrix based on a well-studied system (Loricarioid catfishes), using published functional and anatomical information for seven families (Schaefer and Lauder 1996; Adriaens et al. 2009; Fig. 1). We coded multifunctionality as a trait by defining four functions: F1 (aquatic ventilation), F2 (suction feeding), F3 (air breathing), and F4 (scraping). The single trait of “buccal function” (Fig. 1B, pie charts) could include



**Fig. 1** Multifunctionality as a character. We assembled a character matrix (**A**) based on a published information on Loricarioid catfishes (Schaefer and Lauder 1996; Adriaens et al. 2009), including three divisions of the adductor mandibulae (muscle 1 = M1), presence of a joint between the premaxilla and neurocranium (joint 1 = J1), and presence of a ligament between the interopercle and lower jaw (ligament 1 = L1). Multifunctionality of the buccal chamber was coded (**A**) and mapped onto the phylogeny (**B**) as if it were a polymorphic character state, with four functions: F1 (aquatic ventilation), F2 (suction feeding), F3 (air breathing), and F4 (scraping). We also included number of mobile parts and a developmental trait (MC = Meckel's cartilage orientation) to show the flexibility of the character matrix approach. Anything that could be coded as a character, including integration space and performance landscapes, could be included to test hypotheses about rate of transitions among states of multifunctionality and structural complexity (**C**) and model the relationships among multifunctionality, complexity, development, integration, and performance. Color available online only.

any number of these functions, and we mapped these onto a phylogeny as if they were polymorphic character states using *phytools* (Revell 2009). Also, Loricarioids are known for their successive increase in structural complexity of the skull (Schaefer and Lauder 1996), and we coded each structural unit as a

single trait (Fig. 1A: M1 = muscle one, adductor mandibulae; J1 = joint one, premaxillary joint; L1 = ligament one, interopercular ligament). In the case of the adductor mandibulae, we coded increasing structural complexity by designating the addition of new divisions of muscle A as A' and A''. We also included the total number of mobile parts of the buccal apparatus and a developmental trait (MC = Meckel's cartilage, Fig. 1A) to show the flexibility of the character matrix approach. Additional traits could include the position of a taxon in functional integration space (Kane and Higham 2015) or presence of modules in specific taxa. From this framework, models of trait evolution could be developed to (1) determine the likelihood and rate of transitions among states of multifunctionality and structural complexity (Fig. 1C), (2) test the relationship between total number of mobile parts and the evolutionary timing of multifunctionality or developmental events, and (3) test the hypothesis that more structural complexity leads to a broader functional repertoire, for example.

## Conclusion

Our symposium on multifunctional structures and multistructural functions brought together 16 speakers and members of the Society for Integrative and Comparative to discuss the role of multifunctionality on animal form and function. These discussions highlighted the broad applicability of integration and modularity, provided new mechanisms for testing questions about these ideas, and stimulated the formation of new hypotheses to be tested in future work. While broad generalizations can be made about the role of integration, context is critical for understanding the effects of multistructural or multifunctional systems. Specifically, integration likely occurs in layers within organismal hierarchy, such that some layers can be integrated while others are not, and integration at one level does not necessarily constrain integration at other levels. We also see that ecological demands can play a significant role in shaping both the integrated relationship as well as its underlying components and that often animals retain some degree of flexibility in integration to respond to these demands. From this work, we highlight four areas of synthesis and potential future directions: 1) the role of developmental integration on function, 2) the ecological consequences of integration and modularity, 3) the use and application of coordinated units as modules, and 4) the consideration of multifunctionality explicitly as a trait in evolutionary analyses. We hope that this

introduction, as well as the manuscripts within this issue, will provide researchers with new and exciting avenues for future research.

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