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COMMENTARY

# Joint mobility as a bridge between form and function

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## ABSTRACT

Joints enable nearly all vertebrate animal motion, from feeding to locomotion. However, despite well over a century of arthrological research, we still understand very little about how the structure of joints relates to the kinematics they exhibit in life. This Commentary discusses the value of joint mobility as a lens through which to study articular form and function. By independently exploring form–mobility and mobility–function relationships and integrating the insights gained, we can develop a deep understanding of the strength and causality of articular form–function relationships. In turn, we will better illuminate the basics of 'how joints work' and be well positioned to tackle comparative investigations of the diverse repertoire of vertebrate animal motion.

**KEY WORDS: Articular, Vertebrate, Range of motion, Kinematics, Form–function relationship, Functional morphology**

## Introduction

Slithering, sprinting, swimming, soaring – virtually all vertebrate animal motion relies on the joints that hold our skeletons together. As a result, vertebrate biologists have long investigated articular form (e.g. Bland-Sutton, 1897; Haines, 1942a,b; Hamrick, 1996a,b; Nowroozi et al., 2012; Parsons, 1899; Tsai and Holliday, 2015; Bailleul et al., 2017) and its development (e.g. Archer et al., 2003; Haines, 1947; Roddy et al., 2009) and articular function (e.g. Dial et al., 1991; Herbst et al., 2022a; Moon, 1999; Tsai et al., 2020) and its evolution (e.g. Aguilar et al., 2022; Bhullar et al., 2019; Brainerd and Patek, 1998; Cieri et al., 2020; Gridder-Porter and Rummel, 2022; Holliday and Witmer, 2008; Jenkins, 1973; Wilken et al., 2020). These endeavors are well chronicled in the past century of issues of the *Journal of Experimental Biology* (e.g. Anderson, 1993; Barclay, 1946; Brocklehurst et al., 2017; Brown, 1948; Congdon et al., 2012; Dawson et al., 2011; Fischer et al., 2002; Gál, 1993a,b; Gray, 1944; Handschuh et al., 2019; Herrel et al., 1999, 2000; Hutson and Hutson, 2012, 2013; Iijima et al., 2021; Jurestovsky et al., 2020; Kambic et al., 2014, 2015; Kargo et al., 2002; Konow and Bellwood, 2005; Lin et al., 2019; Long et al., 1997; Manter, 1938; Menegaz et al., 2015; Miyashita et al., 2020; Molnar et al., 2014; Oliver et al., 2016; Ravosa et al., 2007; Rubenson et al., 2007; Smith and Hylander, 1985; Werth and Ito, 2020; Wilga and Motta, 1998; Wilken et al., 2019).

However, despite such efforts, we still have a remarkably limited understanding of 'how joints work' at a fundamental level. Disentangling biological form and function is well known to be inherently challenging (Bock and von Wahlert, 1965; Gans, 1988; Koehl, 1996; Lauder, 1981; 1995; Russell, 1916; Vizcaíno and Bargo, 2021), making it unclear how much we can reasonably infer, for example, about the *in vivo* kinematics of joints from their structure. But determining the extent to which such inference is feasible is central to further advancing innumerable pursuits in organismal biology – from explaining the anatomical basis of adaptations, to attributing functional diversity to differences in morphology versus behavioral plasticity, to anticipating how animals will move and migrate through risky and ever-changing environments.

Here, I discuss the value of studying joint mobility – the set of all configurations that a joint can passively assume – in illuminating articular form–function relationships. I propose that joint mobility enables us to break down these relationships into two more tractable components (Fig. 1): (1) how specific differences in morphology correlate with differences in potential motion (the form–mobility relationship), and (2) how differences in potential motion correlate with differences in observed motion (the mobility–function relationship). In doing so, it bridges an otherwise insurmountable gap between static form and dynamic function, facilitating comparative biomechanical studies of extant and extinct vertebrates alike.

## The form–mobility relationship

Joints must create mobility between skeletal elements while maintaining enough stability to remain articulated. Too stable and they cannot move, too mobile and they fall apart. Over the past 500 million years of vertebrate evolution (Askary et al., 2016; Haines, 1942a), this balancing act has generated an extraordinary diversity of sizes and shapes of articular surfaces, arrangements of soft tissues that bind them, and motions prevented or permitted. Therefore, when exploring the form–mobility relationship, we have tandem objectives – to ask how articular structures prevent motion, and to take on the opposite perspective and ask how they allow it.

We can make progress towards these goals by teasing apart how different articular structures such as ligaments, cartilage, muscle and bone interact to shape mobility. Computational analyses of joint mobility offer opportunities to visualize how interactions between bony surfaces prevent certain joint configurations, formalize and test our assumptions about what characteristics of articulation make a joint configuration possible in life, and even experimentally modify morphology and assess the influence of introducing or eliminating structures (e.g. Brocklehurst et al., 2022; Demuth et al., 2020; Hammond et al., 2016; Herbst et al., 2022b; Jones et al., 2021; Fahn-Lai et al., 2018; Mallison, 2010a,b; Manafzadeh and Gatesy, 2021; Lee et al., 2018; Molnar et al., 2021; Nyakatura et al., 2015; Pierce et al., 2012; Regnault and Pierce, 2018; Richards et al., 2021; Wiseman et al., 2022; for a review, see Manafzadeh and Gatesy, 2022). To investigate the constraints imposed by articular soft tissues, we can supplement virtual analyses with laboratory measurements of mobility from intact (e.g. Akhbari et al., 2019; Hammond, 2014; Hammond et al., 2017; Manafzadeh, 2020;

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Journal of Experimental Biology (2023) 226, jeb245042. doi:10.1242/jeb.245042

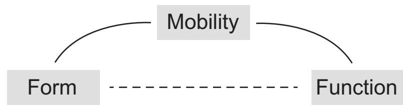


**Fig. 1. Joint mobility allows us to break down the investigation of complicated articular form–function relationships (dashed line) into more tractable studies of form–mobility and mobility–function relationships (solid lines).**

Manafzadeh et al., 2021) and serially dissected joints (e.g. Arnold et al., 2014; Cobley et al., 2013; Crisco et al., 1991; Hutson and Hutson, 2012, 2013, 2014, 2015a,b, 2018; Kambic et al., 2017a,b; Herbst et al., 2022c; Manafzadeh and Padian, 2018; Martin et al., 2008), bearing in mind the concomitant loss of physiological realism when reducing them to subsets of their parts.

Once measurements of mobility are gathered and related to morphology within individual joints, we can also view these data within the context of entire organisms and evaluate how anatomical connections between or among joints – another aspect of their form – may create coordinated, dynamic changes in mobility during life. Whereas posturally driven differences in the mobilities of joints linked by biarticular muscles may be relatively simple to characterize (e.g. Nonaka et al., 2002; Okada et al., 1996), those among joints contributing to complex multi-bar systems (e.g. Bhullar et al., 2016; Holliday and Witmer, 2008; Lemberg et al., 2021; Olsen et al., 2017) will require more involved, network-based consideration (see Olsen, 2019). As the relationship between form and mobility becomes clearer, analyzing our findings within a comparative framework will empower us to develop a mechanistic, predictive and broadly transferable understanding of how differences in joint anatomy directly cause differences in potential motion.

## The mobility–function relationship

The study of mobility–function relationships can be thought of, in some ways, as similar to that of ecological niche occupation (see Hutchinson, 1957; Vandermeer, 1972). Whereas joints have access to a large set of potential configurations prescribed by their morphology (analogous to a fundamental niche), they exploit only a small subset of these during any given behavior (analogous to a realized niche). By comparing mobility measurements with corresponding *in vivo* kinematic trajectories, we can begin to map out what subset of full potential motion is used during different behaviors. We can then ask how consistent this pattern is and what factors drive it – much as an ecologist might ask how variables such as predation and competition drive species distributions.

Because joints use interacting combinations of rotations in life (see Haering et al., 2014; Kambic et al., 2017a), analyses of mobility–function relationships will be most biologically meaningful when conducted with three or more degrees of freedom. Biplanar videoradiography studies [e.g. X-ray Reconstruction of Moving Morphology (XROMM) analyses; Brainerd et al., 2010; Gatesy et al., 2010] have led biomechanists to amass a wealth of six-degree-of-freedom *in vivo* kinematics from joints across the vertebrate tree (e.g. Bhullar et al., 2019; Brocklehurst et al., 2017; Cieri et al., 2020; Kambic et al., 2014; Lin et al., 2019; Maharaj et al., 2020; Menegaz et al., 2015; Miranda et al., 2013; Olsen et al., 2017), but because XROMM-based range of motion analysis is laborious and not yet amenable to automation (see Laurence-Chasen et al., 2020), comparably detailed mobility data for these joints remain scarce. That said, the few analyses conducted thus far (Herbst et al., 2022a; Kambic et al., 2017a; Manafzadeh et al., 2021) demonstrate feasibility and lay a foundation for future comparison with additional joints and taxa.

As we build up associated mobility and *in vivo* kinematic data for a broad variety of joints, we will be able to answer not only what subset of mobility is exploited in life, but also why this is the case. We can enhance our future datasets by integrating them with data collected about functional parameters such as joint stiffness (e.g. Johns and Wright, 1962; Jones et al., 2021; Herbst et al., 2022c; Molnar et al., 2014) or articular contact area (e.g. Ateshian et al., 1995; Bey et al., 2009; Jenkins and Camazine, 1977; Marai et al., 2004), augmenting our knowledge of each joint pose beyond a binary ‘possible’ or ‘impossible’. We will thus be better equipped to tackle questions such as what characteristics of articulation must be maintained during specific behaviors, or when joint motion is passively guided versus actively modulated. Ultimately, this work will reveal to what extent neuromuscular control is truly a concerning ‘wildcard’ (see Lauder, 1995) confounding our ability to reliably relate articular form and function.

## Reconnecting joint form and function

If we can predict potential motion from joint form, and we can predict which subset of that motion will be used during a given behavior, then it follows that we should be able to synthesize our findings to successfully predict observed kinematics directly from the structure of joints – perhaps one day even rendering our mobility-based ‘bridge’ (Fig. 1) obsolete. As we work towards this goal, we – the next century of comparative biomechanists – are faced with an incredibly exciting opportunity to not only draw correlations among form, mobility and function, but also to deeply and explicitly understand the strength and causality of these relationships. By striving to do so, we hold unprecedented potential to elucidate the enigmatic principles that underlie ‘how joints work’ – and in turn, to tackle future biomechanical analyses with an improved fundamental understanding of vertebrate animal motion.

**Acknowledgements**
I thank Stephen Gatesy for years of discussions that have shaped my views about how to study joints, Tyler Kartzinel for kindly lending the phrase ‘move and migrate through risky and ever-changing environments’, countless arthrologically inclined colleagues for their feedback on my work to date, the organizers of the Comparative Biomechanics Special Issue for the invitation to contribute this Commentary, and three anonymous reviewers for their constructive criticism.

**Competing interests**
The author declares no competing or financial interests.

**Funding**
The author was supported by a Gaylord Donnelley Postdoctoral Environmental Fellowship from the Yale Institute for Biospheric Studies.

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