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SYMPOSIA PAPER

Measuring Biological Function in Biomechanics: Observations and Consequences

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Abstract

Although functional reasoning is ubiquitous in biology, and philosophers have concentrated intensely on theorizing function naturalistically, the measurement of function has largely been ignored. Given its centrality in life science practices, there is good reason to scrutinize functional measurement in detail. I undertake a preliminary analysis of this issue by focusing on the measurement of function in the context of biomechanics to make several observations (e.g., functioning is a complex organismal property that cannot be reduced to a single measured variable) and then draw out novel consequences for debates about biological function and philosophy of science discussions of measurement.

1. Connecting function and measurement

Functional reasoning is ubiquitous in biology. Traditional philosophical debates have concentrated on formulating theories or concepts of function, especially with the aim of evaluating whether different naturalistic formulations are mutually exclusive or suggest pluralism (Garson 2018; Neander 1991). However, there has been little attention to how function is measured empirically. This is poignant given that practices of measurement related to function are central to life sciences across spatial and temporal scales, from cellular signaling to the functional morphology of fossils. When a controversy erupted around the claim by the ENCyclopedia Of DNA Elements (ENCODE) initiative that as much as 80 percent of the human genome was "functional" (ENCODE Consortium 2012), criticism concentrated on concepts of function (Doolittle 2013; Germain et al. 2014), with no attention to questions of measurement (but see Guttinger and Love 2026).

One aim of this article is to argue that connecting function and measurement explicitly can reconfigure long-standing debates about biological function. For example, philosophers of biology have argued that a desideratum for a theory of function is the ability to distinguish between nonfunction and malfunction (Garson 2016). Yet most discussions rely on appeals to disease conditions (for malfunction)

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without attention to how functional capacities are measured to make these determinations. Researchers often track quantitative differences of performance that indicate malfunction, such as the rate at which a virus is eliminated by the immune system. These measurements require close attention to multiple related variables beyond a particular measurand.

A second aim of this article is to suggest that paying attention to how function is measured has implications for literature on measurement in philosophy of science (Tal 2020). Much of this work has focused on fields such as metrology or psychometrics. To date, there have been few analyses of measurement in biology outside of medicine (but see Bocchi 2022, 2024; Montévil 2019). However, biologists have worried about measurement issues and whether applications of measurement theory solve specific problems encountered in their practices (Houle et al. 2011). Beyond expanding the measurement conversation to other scientific contexts, some life science fields in which measurement is prominent involve the coordination of resources from different sciences, such as the use of Newtonian mechanics to analyze functional capacities of animal morphology relevant to locomotion (Biewener and Patek 2018). This coordination bears on how models of the measurement process are formulated (Tal 2017b). Other salient issues include complex measurement aggregations for functionality and measuring variation in a variable rather than a primary value of interest (Bookstein and Schaefer 2009).

I begin with a brief rehearsal of the return of scientific measurement to philosophical attention before turning to an area of biology where functional measurement is paramount: biomechanics. I make three observations about measurement in this context: functioning is a complex organismal property, functional capacities are compensatory and plastic, and functional measurement involves combinations of measurement models. Then I draw out consequences from these observations for debates in philosophy of biology about function, including how whole organism functioning challenges an emphasis on the function of parts, and for the philosophy of science literature on measurement, such as the descriptive adequacy of distinctions between fundamental and derived measurement.

2. The return of measurement

Over the past decade, epistemological questions that arise in the context of scientific measurement practices have received substantial attention (Mari et al. 2023; Mößner and Nordmann 2017; Tal 2013). Under what conditions is measurement sufficiently accurate or precise? How does it contribute to knowledge in different domains of inquiry? How is measurement related to other concepts like observation, experimentation, or modeling? How are indirect measures or proxies utilized? Measurement is central to the production of scientific knowledge, yet it was a marginal topic in philosophy of science for the latter part of the twentieth century except in isolated instances, such as psychophysics (Savage 1970) or foundations for scientific methodology (Krantz et al. 1971). Questions of measurement loomed large in logical empiricism, especially with respect to the topic of operationalism (Chang 2021), which flourished in behaviorism within psychology (Feest 2005).

The situation has changed with the emergence of a broad body of work that emphasizes understanding science through its practices. New work in the

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"epistemology of measurement" (Mitchell et al. 2017) has explored these practices in detail, examining issues of instrument design and know-how, computer simulation, imaging technology, calibration, and their roles in the operationalization of scientific concepts and models (e.g., Chang 2004; Miyake 2013; Tal 2017a). The bulk of these analyses have focused on fields where measurement has received substantial attention from scientists: metrology and fundamental constants (Mari 2005; Tal 2011), particle physics (Perovic 2017), psychology and psychometrics (Borsboom 2005; Vessonen 2020), medicine (McClimans 2017; Root 2003), and the social and behavioral sciences (Alexandrova 2017; Boumans 2015). An important strand of recent work concentrates on proxy measures in historical sciences like paleoclimatology where access to a variable of interest is difficult if not impossible to attain (Watkins 2024; Wilson and Boudinot 2022).

The relative absence of analyses of measurement practices (as opposed to conceptual definitions) in biology is curious because they constitute a large swathe of contemporary science and comprehending similarities or differences with measurement in other sciences is of intrinsic philosophical interest.[1] Nor is the paucity of work on this topic due to disinterest among scientists. Biologists working on the quantitative analysis of form or shape ("morphometrics") have lamented the absence of sustained reflection on measurement methodology (Bookstein and Schaefer 2009). The adoption of automated methods for undertaking these measurements has only increased the urgency for this type of reflection (Porto et al. 2021). Quantitative geneticists have utilized the representational theory of measurement to diagnose pervasive errors (e.g., inappropriate transformations of data) that threaten to render the findings of studies meaningless (Houle et al. 2011). The treatment they recommend is philosophically oriented: "[I]n biology, the connection between concepts and measurements is often lost during the measurement process . . . awareness of measurement theory helps us to do better science by providing tools to ensure the meaningfulness of our work" (4–5).

One analysis devoted to measurement in biology concentrates on the importance of an overarching theory of the organism to govern these practices (Montévil 2019). The central premise of this analysis is that the objects of study in biology are fundamentally different from those in physical science. Biological objects are historically conditioned outcomes of developmental and evolutionary processes, which exhibit variability through space and time within different environmental contexts. Thus, the theoretical perspective relevant for practices of measurement must include principles of historicity, variation, and context. Even though biologists adopt forms of standardization to eliminate these effects, such as through artificial breeding to generate inbred strains or common conditions for culture and experimentation, they are never fully controlled for, and their presence requires strategies for choosing what variables to measure and how to compare the values ascertained at different moments of measurement. Montévil's solution is to start from his preferred theory of organisms that aims to incorporate these principles and thereby can appropriately inform measurement. However, this theory is contentious, which makes it difficult to concentrate specifically on measurement issues pertinent

[1] For example, dealing with the heterogeneity and potential incommensurability of different metrics seen for biodiversity measures in conservation biology (Bocchi 2022, 2024).

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to ascertaining functional capacities. A preferable place to probe these issues is where functional measurements are foregrounded, and theoretical disagreements are largely moot.

3. Measuring function in biomechanics: Observations and implications

"Biomechanics is the study of the structure, function and motion of biological systems using the methods of mechanics" (Hatze 1974, 189). It is understood as a kind of engineering in biology that covers a variety of concerns: dynamics (e.g., running or jumping); kinematics of mechanisms (e.g., how fishes protrude their jaws); properties of materials (e.g., bone); hydrostatics (e.g., buoyancy of aquatic animals); and fluid dynamics (Alexander 2005). These types of investigation conceptualize biological traits as configurations of functionality (e.g., a cranium complex of bone, muscle, and neuroarchitecture *for* mastication), drawing on the theoretical resources of Newtonian mechanics and adopting the orientation of mechanical engineering. One key area of biomechanics is animal locomotion (Biewener and Patek 2018), which involves the study of distinctive activities or movements related to different environments, the components and organization that generate locomotory capacities (e.g., muscles and tendons), and their underlying metabolic requirements. The quantitative measurement of variables relevant to both the organism and its environment are crucial for these investigations.

Physical dimensions of interest for measurement in these studies include energy (amounts, rates, efficiency), component forces (tendon force, pectoral fin lift), whole organism forces (ground reaction force, lift), loading (compression, torsion), material properties (rigidity, viscosity), and a variety of areas, lengths, masses, velocities, and angles. Complex measurement apparatuses are utilized to capture these dimensions. For example, force plates that rely on different kinds of sensor elements detect the component forces of individual appendages during walking, running, or jumping (Limam et al. 2021). Angles of impact are gleaned from high-speed videography (McHenry and Hedrick 2023). Additionally, media in which these activities take place (e.g., water vs. air) are evaluated for the amount of drag they engender on a body part or the whole organism (Lutek and Standen 2021). Many other physical dimensions are calculated from these measurements. For example, in studies of loading, the length of a body part is measured in a resting state versus a loaded state and then *strain* can be calculated from the change in length divided by the resting state length (Blob and Biewener 2001).

Several observations from these practices in biomechanics have conceptual implications for debates about function and the philosophy of measurement. First, functioning is a complex property of whole organisms that cannot be reduced to a single variable in measurement practices. Consider terrestrial locomotion. Relevant physical dimensions include body mass and weight, relative timing of limb support during a stride, different components of ground reaction force, body posture, stiffness of limb components, and different forms of loading on muscles, tendons, and bones. Overall functioning referred to as "locomotion" is a composite of these different physical dimensions, including compound properties calculated from individual measurements (e.g., effective mechanical advantage derived from relating ground forces and limb muscle forces). This can be situated in a causal-role account of

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function, where functional analysis aims to identify and characterize operational parts of a complex system and the roles they play to yield a system capacity (Cummins 1975). From the perspective of measuring terrestrial locomotion, this means the system in view is the whole organism and measurements of individual working parts must be aggregated in different ways to generate a measurement of overall locomotory function.

Second, systems that underlie functional capacities of organisms like locomotion are inherently compensatory and plastic (Fernández et al. 2012; Seebacher and James 2008). This means that the measurement of one system variable, such as a muscle, must account for what is going on with other muscles and working parts (e.g., tendons). Variations in values for measurements related to loading are likely to be both a direct consequence of movement in a medium and the compensatory behavior of other muscles that contribute to or modulate that movement. The primary upstroke muscle for birds in flight is the supracoracoideus; the primary downstroke muscle is the pectoralis (Tobalske and Biewener 2008). "Primary" indicates that neither muscle operates alone in contributing to flying behavior, but the relevant contributions vary. Additionally, these two muscles exhibit antagonistic activity in the flight stroke cycle. Thus, measurements are conditioned by the activity of other working parts, which also need to be measured and compared. Beyond compensation, functional capacities are plastic in the sense of being altered based on repetition or learning and therefore particular measurements can be potentially misleading about what is or is not required in a system to perform a function. Birds can learn to take off without the use of the supracoracoideus even though it is typically active in all modes of flight (Dial 1992).

Third, it is often not possible to derive values for variables of interest except by way of the measurement of other variables. In the context of inquiry into energetics, if a researcher wants to evaluate the efficiency of a locomotory pattern, then they need to secure values for the variables of work (energy output) and metabolic energy (energy input). Locomotory work accomplished by limbs can be measured by force plates and metabolic energy can be measured in terms of oxygen consumption. On the assumption of aerobic glycolysis, the amount of needed ATP (i.e., energy input) is derived from oxygen measurements (using a standardized rate: 20.1kJ/liter O_2). This measurement process involves proxies and inferential chains to get at the property of interest (i.e., efficiency). A proxy is utilized whenever a variable is not immediately accessible, forcing researchers to consult properties, entities, or processes that act as a stand-in for the target of interest (e.g., oxygen use as a stand-in for amount of needed ATP). An inferential chain is comprised of links between variables (whether proxies or not), often by way of equations, that conclude in a property of interest (e.g., efficiency as derived from work and metabolic energy). These proxies and inferential chains are also conditioned by the medium within which the measurements are undertaken.

The first observation (functioning is a complex property of organisms) implies that "functional measurements" in biomechanics are never directly of the function of interest. Whole organism locomotory capacities are built up out of separate measurements that must be combined into an account of overall functioning, similar to complex measurands in social science like well-being (Alexandrova 2017). However, in biomechanics there is little concern about the value-ladenness of

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component measures or how the phenomenon is conceptualized. Instead, the issue is striving for sufficient completeness in empirically tracking and coordinating what are already theoretically justified variables. For example, a study of pectoral fin lift might measure the oscillating movement of the pectoral fin through an impact on local water displacement, including the drag due to water density. However, the capacity to generate lift in the pectoral fin is affected by muscle architecture and energetics, so another study might focus on electromyographic recordings of pectoral fin abductors and adductors or oxygen consumption. Multiple types of functional measurement will be required to approximate how the whole organism manifests a locomotory capacity and incompleteness must be reckoned with constantly.

The second observation—compensation and plasticity—implies that isolating individual working parts that contribute to a functional capacity will be difficult because there may be no defined contribution a component makes to the capacity. This means researchers typically need to establish a reference standard and the measurement process will be a comparative endeavor that requires measuring multiple variables (e.g., different flight-related muscles) under different conditions (e.g., upstroke vs. downstroke; takeoff vs. landing) and with respect to different experiential regimes (e.g., naïve, mature, or trained flyers). Further comparisons involve different environmental conditions (e.g., temperature, wind speed) and different ecological circumstances (e.g., takeoff under duress from predator presence).

The third observation related to deriving values for variables of interest implies that functional measurement involves combinations of models rather than a single measurement model.[2] One type of combination involves different measurement methods to get at the same variable (e.g., force plates vs. pressure pads for ground reaction forces). Another combination involves measurement methods for different variables needed to build up relevant quantities for the system capacity. These combinations will be different depending on the variables of interest and the media in which the measurements are undertaken. Thus, there is no single model for the measurement process for locomotory function but rather multiple models of measurement that require independent calibration of indications and outcomes, as well as careful procedures for aggregation because of potentially conflicting assumptions. A variety of reference standards must be established to ensure that different proxies or inferential chains are not "misbehaving," which will be critical when measuring novel properties of functional systems that have not been established with existing models.[3]

4. Consequences for debates about biological function

The implications of these observations position us to see consequences for philosophical discussions of biological function and measurement. Starting with the former, there is a presumption in standard analyses of biological function that function ascription focuses on parts (hearts pump, jaws bite, eyes see). In selected

[2] Although model-based accounts of measurement conceptualize the modeling process expansively, they are primarily focused on a single model (see, e.g., Tal 2017a).

[3] Discussions about "cross-checking" in exploratory experimentation (e.g., Burian 1997) exhibit a strong parallel to these circumstances.

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effects accounts (Neander 1991), this connects to the explanatory nature of function ascriptions (some *X* exists because it did *Z* in the past). However, animal locomotion studies often ascribe "functioning" to whole systems; legs and fins do not locomote, though we can ask how they perform in relation to walking or swimming. Measurement is pertinent to parts, but the overall measure of functionality is typically of whole organisms. These functional ascriptions are not teleologically explanatory; we don't say "the fish exists because it swims." However, these functional ascriptions can still be explanatory in terms of causes and mechanisms. Functional measurement in biomechanics points to a distinct level of organization where the selected effects account is less obviously applicable.

Functional analysis in the sense of a causal role account of function is useful in interpreting the measurement process to discover system capacities. This involves identifying working parts, characterizing their operating behaviors, and validating their contributing roles. Although functional analysis has also traditionally emphasized parts rather than the organism, this is less threatening to the account. However, our observation about compensation and plasticity implies a distinct form of multiple realization with respect to system capacities (e.g., a major muscle may or may not be involved in a capacity), which makes characterizing operating behaviors of working parts and validating contributing roles to the system through measurement procedures demanding. Additionally, although functional analysis involves consideration of analytical context for function ascriptions, the causal role account has not grappled with the environment (i.e., not the system) in comprehending functionality, which is pertinent for measurement in biomechanics. Proponents of the causal role account have argued it is "without purpose" and escapes teleological concerns foregrounded in selected effect accounts (Amundson and Lauder 1994). Yet whole organism functioning studied in biomechanics is purposive. Animal locomotion is done "in order to" achieve something in a specified environment (migration, finding prey, escaping predators).

One reason Amundson and Lauder might have interpreted causal role accounts as nonteleological is that the categories of locomotion are not tied to specific selection pressures. Fish (whole organisms) swim to achieve many different things and in doing so use the same system capacity. Ascriptions of functioning in biomechanics are inherently multifunctional or "generic." Terrestrial running can be for escaping predators or chasing prey. Measurement procedures in biomechanics are conducive to discovering generic principles of functionality (e.g., efficient lift for vertebrate flight from feathered wings or interdigital skin flaps). These principles yield distinct kinds of generalizations with associated predictions—limb propulsion in terrestrial vertebrates, galloping speed in quadrupedal mammals, size constraints on swimming organisms—but have mostly escaped philosophical notice, though something analogous has been scrutinized in molecular systems biology (Green 2015).

One final area where debates about biological function might be reconfigured through functional measurement is the recurring issue of adaptationism. This theoretical commitment held by some biologists presumes organismal features, like patterns of animal locomotion, are optimized by long histories of natural selection. In addition to standard concerns about developmental constraints, phylogenetic history, and the causal impact of changing environments, the measurement of function adds a novel twist: safety factors (Blob et al. 2014). Measurement outcomes for functional

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capacities have shown that organisms are overbuilt. "Skeletons operate with safety margins—strengths that exceed their maximum likely loads by as much as three to fivefold, or even greater" (Biewener and Patek 2018, 30). The existence of safety factors raises the question of how to think about "unutilized" functional properties detectable using quantitative measurement. Much of the literature on ways organisms exhibit nonoptimized features conceptualize them as structural constraints on form as a consequence of the way organisms develop (Amundson 1994). Safety factors are a functional constraint on form (i.e., to avoid catastrophic failure), but these constraints have high energetic costs and are unlikely to be tested in one lifetime. Although there is evidence for evolutionary trends in the decrease of safety factors for individual skeletal elements of birds and mammals (Blob et al. 2014), this intensifies the evolutionary puzzle of how high safety factors originated as they appear to predate the invasion of land and terrestrial locomotion (i.e., they were present before being needed). At a minimum, the existence of safety factors in organismal design, detected through functional measurement, demands more attention.

5. Consequences for the philosophical study of measurement

Moving on to consequences for discussions of measurement, our observations about not measuring function directly and the indirect derivation of variables has bearing on distinguishing fundamental and "derived" measurement (Kyburg 1984; Tal 2020). The former is usually associated with the measurement of lengths, areas, and volumes that exhibit ordering (e.g., "longer than" behaves like "larger than"; transitivity and asymmetry) and concatenation (e.g., the conjoining of measurement operations—using a rigid rod for length determination—behaves structurally like addition; association and commutativity). The latter is characterized by utilizing patterns among magnitudes ascertained by fundamental measurement (e.g., density as the ratio of mass and volume). Although the distinction bears on functional measurement because variables of interest include those corresponding to these categories, it does not capture the indirectness of functional measurement that involves combinations of proxies and inferential chains where the final assessment of locomotory function is nothing like a derived measurement of temperature or density. How exactly to characterize functional measurements and whether a revised typology of categories is required remain open questions. Kyburg's (1984) notion of systematic measurement, which involves three or more quantities related theoretically (e.g., in thermodynamics), is pertinent but fails to capture the multistep inferential chains among individual operations underlying functional measurement.

Another consequence of these observations is that model-based accounts of measurement may require revisions in how criteria such as coherence and consistency are applied. The former criterion involves coherence between model assumptions and background theories about what is being measured; the latter involves consistency between measurement outcomes under different instrumental, environmental, and modeling conditions (Frigerio et al. 2010). Coherence is more difficult to achieve when multiple models are in play; even if individual models for quantities exhibit coherence, the combined aggregate relevant to determining function may not. Under what conditions are failures of coherence acceptable in

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measurement procedures we observe in biomechanics? Consistency also will be a challenge due to variations arising from compensation and plasticity. Measurement indications and outcomes will be variable for a single organism with respect to locomotory function and variable across different organisms where similar measurement procedures are undertaken. Consistency with some reference standard for locomotion function will always be a context-relative determination. Even though the objectivity of measurement might seem threatened in this circumstance, it is a natural consequence of the objects of measurement exhibiting historicity, variability, and contextuality (Montévil 2019).

A last consequence from these observations is the centrality and ubiquity of proxies in the epistemology of measurement. Although this has been analyzed in historical sciences like paleoclimatology where access to variables is challenging (Watkins 2024; Wilson and Boudinot 2022), its presence in sciences where the object of investigation is readily available has mostly been noted in medicine (Root 2003). Researchers in biomechanics utilize diverse proxies and inferential chains in measuring functionality not merely out of necessity but also because these can be combined creatively to generate distinctive types of insight (Guttinger and Love 2025). For example, a key concern in biomechanics is the discovery of higher-order engineering principles of functionality: "Which principles of design are shared by a racing antelope, a scurrying lizard or a running cockroach?" (Biewener and Patek 2018, 1). Measurement procedures differ for these taxa that locomote on different scales, but combinations of different proxies and chains of inference facilitate processes of abstraction that can yield explanatory principles like "a unified model for swimming, slithering, and walking" from geometric mechanics (Zhao et al. 2022).[4] These practices in biomechanics show that measurement is guided by a concern to infer distinctive generalizations about functionality. This exposes a wider range of standards for evaluating how and why function is measured, suggesting unexpected similarities between biology and physics.

6. Summary

The return of measurement in philosophy of science traveled alongside a renewed attention to scientific practices. Biology has been relatively absent from these analyses, though not because measurement is peripheral; the measurement of function is central, something overlooked in debates about biological function. By examining functional measurement in biomechanical studies of animal locomotion, we made three observations: functioning is a complex organismal property that cannot be reduced to a single measured variable; systems exhibiting functional capacities are compensatory and plastic; and deriving values for variables of interest using proxies and inferential chains implies that functional measurement involves combinations of measurement models.

From these observations, we isolated several consequences for debates about biological function and questions in philosophy of measurement. For debates about biological function, whole organism functioning in biomechanics challenges the

[4] Controversy about these principles constitutes a distinctive feature of discourse in biomechanics, such as debates about the principle of "symmorphosis" (Weibel et al. 1998).

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exclusive emphasis on parts, undercutting the explanatory rationale for selected effects accounts of function in these instances, with causal role accounts requiring more attention to compensation and plasticity, environmental context, and purposiveness in functional analysis. Generic functional ascriptions emerging from biomechanical analyses have been neglected thus far and adaptationism debates can be reinvigorated by exploring the nature of safety factors. For philosophy of measurement, we identified a need to revisit the descriptive adequacy of distinctions between fundamental and "derived" measurement, raised questions about how criteria like coherency and consistency are applied in multiple measurement models or conditions of compensation and plasticity, and highlighted the predominance of proxies whose motivation arises from seeking distinctive forms of generalization ("design principles"). Although this does not exhaust the possible consequences arising from functional measurement for philosophy of science generally or biological function specifically, the range of issues biomechanics alone brings to our attention argues compellingly that attention to functional measurement across biology will augment our philosophical perspectives on scientific measurement.

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