

Commentary

Stereotypy, flexibility and coordination: key concepts in behavioral functional morphology

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Summary

Animal movement and its muscular control are central topics in functional morphology. As experimentalists we often manipulate stimuli in a controlled setting or compare species to observe the degree of variation in movement and motor control of particular behaviors. Understanding and communicating the biological significance of these sources of variability requires a universal terminology that is presently lacking in the functional morphology literature. We suggest that ‘stereotypy’ be used to refer to the degree of variability observed in a behavior across trials under a given set of conditions. The ability of an organism to alter its behavior across experimental treatments is referred to as ‘flexibility’. We discuss how there has been a tendency to confound the phenomenon of a behavior exhibiting low variability, which we refer to as stereotyped, with inflexibility, or the inability to alter the behavior in response to a change in stimulus. The degree of stereotypy and flexibility in a behavior need not be correlated, nor need they have a common underlying basis. Coordination, a term used to describe the relationship between different body parts during movement, can be stereotyped and can show flexibility. Stereotypy of coordination can be assessed by the strength of correlations between movements of two body parts. The influence of coordination coherence on behavioral performance has rarely been considered, and could shed light on how taxa differ in their ability to perform behaviors. We suggest definitions of the terms stereotypy, flexibility and coordination, and provide examples of how and when these terms could be used when discussing behavioral changes in functional morphology.

Key words: behavioral integration, kinematics, motor pattern.

Introduction

Functional morphologists studying locomotion, feeding, respiration and other behaviors recognize a number of sources of variation in the movements and motor patterns that underlie these behaviors. Indeed, the patterns of variation in these functional traits and the sources of their variation are a major focus of this field. Discriminating different sources of variation plays a vital role in finding answers to a range of common research questions. Does the pattern of muscle activity or kinematics associated with prey capture differ among species (Deban and Marks, 2002; Mehta and Wainwright, 2007; Motta and Wilga, 2001; Reilly and Lauder, 1992; Wainwright, 1989; Wainwright et al., 1989)? Is the pattern of muscle activity observed during feeding more variable in one species than another (Ralston and Wainwright, 1997; Van Wassenbergh et al., 2006b)? Does prey-capture behavior change during ontogeny (Reilly, 1995; Richard and Wainwright, 1995; Van Wassenbergh et al., 2006a)? How are locomotor and prey-capture kinematics coordinated (Higham, 2007; Rice et al., 2008; Rice and Westneat, 2005)? How are the movements of different body parts coordinated during locomotion (Danos and Lauder, 2007; Shemmell et al., 2007)? Each of these questions is concerned with partitioning variation in behavioral traits; within and among individuals, among species, among treatment groups and among body parts.

While these studies have contributed to a deeper understanding of the nature and diversity of animal functional morphology, this literature exhibits inconsistencies in how these effects are

interpreted and in the terminology used to describe particular patterns of variation. For example, the term ‘stereotyped’ has been used in reference both to a behavior that shows low variation (Deban et al., 2001; Nishikawa, 2000), and to the behavior of an organism that does not vary in response to a treatment effect, such as changes in prey type (Matott et al., 2005; Wainwright and Lauder, 1986). In both of these cases, stereotyped refers to a pattern of low variance, but in the first case it refers to repeatability of the behavior within a specific set of treatment conditions, while the latter usage describes the failure of the animal to alter the behavior in response to a change in the treatment conditions. These different uses of the term ‘stereotyped’ can lead to significant confusion, because one can imagine that these levels of variation relate to different abilities of the organism that need not be related to one another. A highly repeatable kinematic pattern that shows very little variation under a given set of conditions could be considerably altered in response to some treatments. One such example was illustrated in a study by Ferry-Graham and colleagues with the cheeklined wrasse, *Oxycheilinus digrammus* (Ferry-Graham et al., 2001). This fish showed highly repeatable kinematics when feeding on a specific prey type, but the kinematics of prey capture were altered when feeding on different prey, with elusive prey eliciting faster movements and greater excursions of cranial elements.

The coordination of movements and motor patterns among body parts used for a specific behavioral output has long been recognized as a key aspect of locomotion, feeding and respiration (Weiss, 1950; von Holst, 1973; Hildebrand, 1980; Dickinson et al., 2000;

Table 1. A suggested terminology for different sources of variation in behavioral traits, such as kinematics or motor patterns, and the quantities that can be used to measure them

Feature	Source of variation	Parameter
Stereotypy	Among trials measured under the same set of conditions	Variance, coefficient of variation
Flexibility	Among treatments or alternative stimuli	Test of effect with ANOVA or regression
Coordination	Association between movements of different body parts	Correlation between variables

Ferry-Graham and Lauder, 2001). Assessment of how repeatable, or stereotyped, the coordination among body parts is during these behaviors can provide significant insight into the relative abilities of animals to control complex behaviors. The repeatability of a coordination pattern between two or more body parts in successive trials, under a given set of conditions, represents one facet of how tightly linked movements are during a particular behavior. This can be distinguished from changes to the pattern of coordination in the face of a treatment. Coordination and its relationship to performance are understudied in the comparative literature, although this topic has been explored in more depth in the human literature (Anderson and Sideaway, 1994; Egan et al., 2007; Post et al., 2000).

In this paper we discuss these commonly studied sources of variation in the behaviors studied by functional morphologists. We use this discussion to highlight some of the ambiguities in functional morphology and propose terminology towards a standardized approach to quantifying these sources of variation. Our ideas are illustrated with examples from prey-capture kinematics in fishes, although we intend our comments to apply generally to movement and motor pattern data associated with animal behaviors.

The field of animal behavior has a long history of defining and quantifying stereotypy and interpreting its significance (Adams, 1931; Altmann, 1965; Barlow, 1968; Barlow, 1977; Brown, 1975; Gerhardt, 1991). Some of the issues addressed in the present paper recall discussions in animal behavior that took place decades ago and in general functional morphologists have been slow to incorporate the notions and lexicon common to animal behavior, even though in many cases the issues are virtually identical. Where possible we attempt to identify these connections and highlight relevant insights from animal behavior that may prove valuable in functional morphology.

Functional morphologists usually quantify behaviors by measuring movements or motor patterns. Displacements and the relative position of body parts, or kinematics, are measured as a function of time, such as rotation of joints or the position of the body with respect to some reference. Most kinematic variables quantify either event timing or amplitude, or are a derivative of displacement data, such as velocities or accelerations of movement. Behaviors are also characterized at the level of motor patterns, by measuring activation patterns of muscles or nerves. For example, timing and amplitude of muscle activation are often measured from electromyograms. An individual cycle of the behavior under study is typically characterized by a set of these variables that define the relative timing and amplitude of major movements of the behavior or the relative timing and amplitude of activity of muscles that control the movements. It is standard practice to characterize the kinematics or motor pattern of the behavior by measuring the panel of variables for several cycles, thus producing an average value for each variable and a value for variance under those observational conditions. Examples of this protocol are abundant in both functional morphology (Dial et al., 2008; Irschick and Jayne, 1999; Wainwright and Lauder, 1986)

and behavior (Gerhardt, 1991; Stamps and Barlow, 1973; Stankowich, 2008; Wiley, 1973).

Stereotypy and flexibility

We define stereotypy as the extent of variation in a behavior under a given set of conditions. Stereotypy is thus measured on a continuous scale (Gerhardt, 1991) with the extremes being termed 'stereotyped' and 'variable'. A stereotyped behavior would be one that shows little variation from trial to trial, while a variable behavior would show inconsistency and hence greater variation (Table 1). Stereotypy can be quantified as the variance in the variables that are measured to characterize a behavior, but because variance is usually correlated with the mean value of a trait, we follow the tradition of animal behaviorists who recommend the use of the coefficient of variation (standard deviation as a percentage of the mean) (Barlow, 1977; Schleidt, 1974).

To compare the variability of a trait between two species one could measure the coefficient of variation of the trait in several individuals per species and compare the average coefficient of variation between species with an analysis of variance. Fig. 1 illustrates the variation in a kinematic trait measured during prey capture by two species of sunfish feeding on live shrimp. *Lepomis cyanellus* shows a more stereotyped pattern than *L. microlophus*, as evidenced by a smaller coefficient of variation: 0.19 vs 0.46. Transforming raw values into logarithms is another method that usually disassociates mean and variance and would allow direct comparisons of variance.

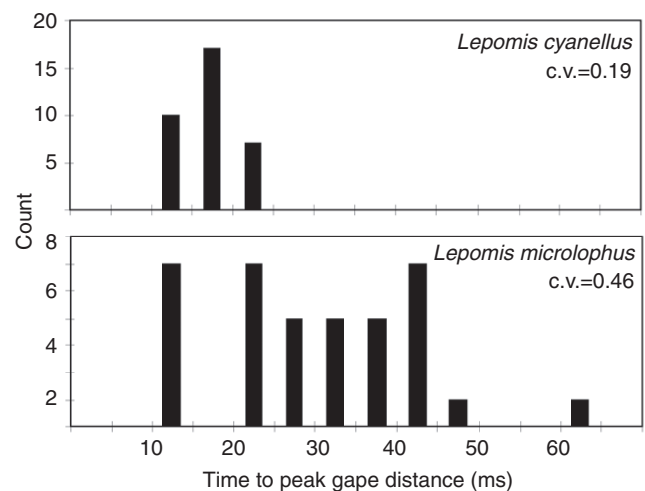


Fig. 1. Frequency histograms of time to peak gape distance, measured from videos of two species of centrarchid fishes, feeding on live shrimp, under the same set of laboratory conditions. From strike attempt to strike attempt *Lepomis cyanellus* shows a less variable kinematic pattern than *Lepomis microlophus*. This lower variability is reflected in a lower coefficient of variation (c.v.) in *L. cyanellus*. Under the terminology scheme suggested in this paper, *L. cyanellus* shows a more stereotyped kinematic pattern than *L. microlophus*.

Another point we stress here is that assessment of whether a particular behavior is stereotyped or not should be made in a comparative context. We do not believe that it is useful to arbitrarily choose a particular cut-off for the coefficient of variation to define 'stereotyped'. One reason for this is that insufficient data are currently available to gauge whether global generalizations would be useful, and also we suspect that levels of stereotypy will depend on the specific conditions under which behaviors are measured. We note that in his classic work on frog mating calls, Gerhardt initially felt that low and high variance components of calls could be readily categorized as 'static' or 'dynamic' (Gerhardt, 1991). However, after reviewing a wider range of frog calls, he subsequently concluded that variability in elements of frog calls was continuous and did not always fall clearly into static and dynamic categories (Gerhardt, 1991; Gerhardt and Huber, 2002).

We propose to restrict the use of the term 'stereotyped' to refer to behaviors with low variance in traits measured across replicates of the behavior under the same set of experimental conditions. This among-trial variability reflects a basic capacity of the organism to repeat the behavior consistently. Particularly in the case of repetitive and rhythmic behaviors, such as steady locomotion, stereotypy among cycles may strongly influence the overall effectiveness of the behavior (Adams, 1931; Alexander, 1980).

We further suggest that it will be helpful in future functional analyses to distinguish between among-trial variation and variation due to the ability of the animal to alter its behavior in response to different stimuli. We define 'flexibility' as the extent to which the behavior is altered in response to a change in stimulus. A behavior that shows no statistically significant change in response to a treatment would be described as 'inflexible' with respect to that stimulus, whilst a behavior that shows a relatively large change in response to the treatment would be described as 'flexible' (Table 1). Flexibility can be measured as the proportional change in the quantified elements of the behavior, but comparisons of the behavior in two or more treatments should be based on levels of variance within a treatment. For example, when comparing two behavioral variables, we may observe that their means are quite different in magnitude. However, if variance within each behavior is high these means may not be statistically different from one another. Published examples of tests for flexibility relate to a wide range of treatments, including the effect of an incline on footfall patterns (Garnier et al., 2008), the effect of obstacles on limb kinematics during running (Kohlsdorf and Biewener, 2006), the effect of temperature (de Vries and Wainwright, 2006), the effect of flight speed on wing kinematics (Tobalske et al., 2003), the effect of food attributes on feeding motor patterns (Ross et al., 2007; Sanderson, 1988; Wainwright, 1989), and the effect of body size (Van Wassenbergh et al., 2006a; Wainwright and Richard, 1995). Tests of flexibility involve comparisons of mean values under separate treatments and can be done with analysis of variance if the factor of interest is categorical, such as different prey in a feeding experiment, or substrate type in locomotion. Regression can be used when the factor of interest varies continuously.

We argue for the importance of distinguishing stereotypy from flexibility because the two need not have the same underlying cause and need not be mutually exclusive or correlated. All combinations of stereotypy and flexibility are realistic. An animal may show a highly variable behavior that is not altered across treatments, or a stereotyped behavior that is flexible. Researchers have even reported cases where choice of stimulus affects the level of stereotypy in the behavior. In one example, it was noted that pufferfish showed a more variable feeding behavior when feeding

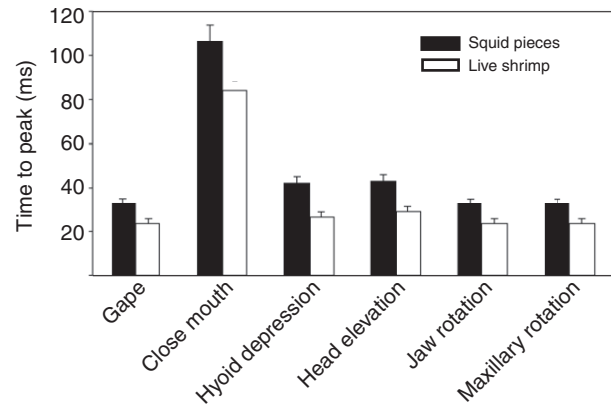


Fig. 2. Evidence of kinematic flexibility in a specimen of *Micropterus salmoides*. This fish modulates prey-capture kinematics in response to feeding on different prey.

on pieces of dead shrimp than when feeding on live prey (Ralston and Wainwright, 1997) (see also Fig. 2).

In the functional morphology literature, 'stereotyped' is often used to refer to what we term 'inflexible', or a lack of variation in a behavior with respect to a wide range of controlled experimental treatments (Matott et al., 2005; Sanderson, 1991; Van Wassenbergh et al., 2006b; Wainwright and Lauder, 1986). We feel it is advantageous to distinguish between among-trial variation and variation across stimuli because stereotypy and inflexibility can have different underlying causes.

It is interesting to note that, when determining levels of stereotypy, behaviorists have shown the same inconsistency seen among functional morphologists concerning whether to distinguish between among-trial variation (the source of our stereotypy) and variation due to the response to changes in stimuli (the source of our flexibility). Our proposal largely follows Barlow, who calculated stereotypy as the inverse of the coefficient of variation of a behavior, and who separately asked whether modal action patterns could be altered (Barlow, 1977). In contrast, when evaluating why some elements of frog mating calls showed high coefficients of variation, Gerhardt and Huber noted that 'Some of the high within-male variation in these properties is almost certainly attributable to purely environmental factors such as the calling behavior of neighbors and variability in the availability of energetic resources needed to fuel signaling' (Gerhardt and Huber, 2002). Altmann, who constructed his own metric of stereotypy for analyzing the sequence of behaviors in rhesus monkeys, lumped many possible environmental influences into the variation that was captured by his metric (Altmann, 1965). Thus, both Gerhardt and Altmann included variation due to alternative stimuli in their measures of stereotypy.

Causes of stereotypy and flexibility

A stereotyped behavior is one that is repeated with little variation from trial to trial. This control may be active, as when the individual has the ability to alter the behavior in response to sensory information, or passive, as when movements are limited mechanically (Westneat, 1990), intrinsic stabilizing mechanisms are involved (Nishikawa et al., 2007), or the neuromotor basis of the behavior is simple and not readily altered by sensory input (Brown, 1975). A high degree of control on the part of the individual is implied if a behavior is stereotyped and flexible (Wöhl and Schuster, 2007).

We note that the underlying cause of stereotypy and inflexibility may be the same in some situations. If a stereotyped behavior cannot be altered by sensory feedback and is therefore inflexible, it is likely that the root cause of stereotypy and inflexibility is the same. We predict that such behaviors will prove to be rare. There is a tendency to assume that stereotyped behaviors will also be inflexible. On close inspection, however, many candidate ‘modal action patterns’ have been shown to be stereotyped, but also flexible. Examples include the classic strut display of male sage grouse (Wiley, 1973) that has recently been shown to change in different contexts (G. Patricelli, personal communication), the Mauthner cell-mediated C-start escape response of fishes that is known to be altered in response to the nature of the stimulus (Canfield, 2003; Eaton, 1988; Tytell and Lauder, 2002), and prey-restraint behavior in early lineages of macrostomate snakes, which has also been shown to be altered in response to changes in prey characteristics (Mehta and Burghardt, 2008).

One should not assume that an absence of flexibility in an experiment is caused by an inability of the animal to alter the behavior. There are at least two other possible causes of inflexibility (Bout, 1998). First, it could be that the optimal or adaptive response is the same for all treatments being considered (Wainwright, 2002). In such a case the animal uses the same behavior with little modification because that particular behavior is well suited to all situations examined. A second possibility is that inflexibility is due to mechanical coupling between the elements involved in the behavior, physically limiting variation in the movements. In the case of mechanical coupling, it is still common to see flexibility in the rate of movement. But in these cases, stereotypy and inflexibility may be linked, both being caused by an inability of the animal to create variation in the behavior.

We note that while the degree of stereotypy and flexibility is likely to be significantly correlated (e.g. Horner and Jayne, 2008), it is unlikely to be identical. The pattern of nerve firing that is controlled by the central nervous system interacts with environmental factors and musculoskeletal mechanical properties to produce a kinematic pattern. Passive mechanical properties of the musculoskeletal system can have a significant impact on the kinematic output produced by motor input (Full et al., 2002; Nishikawa et al., 2007). Ultimately, we must directly measure levels of stereotypy and flexibility prior to determining mechanisms of regulation.

Integration and coordination

Animal movements primarily involve the coordinated actions of numerous muscles and motion at multiple joints. A major question about the nature of movement is the degree to which different skeletal elements and the activity of different muscles are integrated. During the behavior, how is motion in one body part related to movements in other parts? We propose use of the term ‘integration’ to describe the repeatability, or consistent nature of the phase or positional relationship between movements in two or more body parts, or the activity of two or more muscles. One measure of integration could be the correlation between two variables, measured over time throughout a trial and across multiple trials (Table 1). Examples of high and low levels of integration are illustrated in Fig. 3. In a highly integrated movement, the position of one body part can be accurately predicted by the position of a second body part. In Fig. 3A, depression of the hyoid bar is highly correlated with the opening of the mouth aperture during the expansion phase of prey capture in the largemouth bass, *Micropterus salmoides*. Not all aspects of cranial kinematics are as

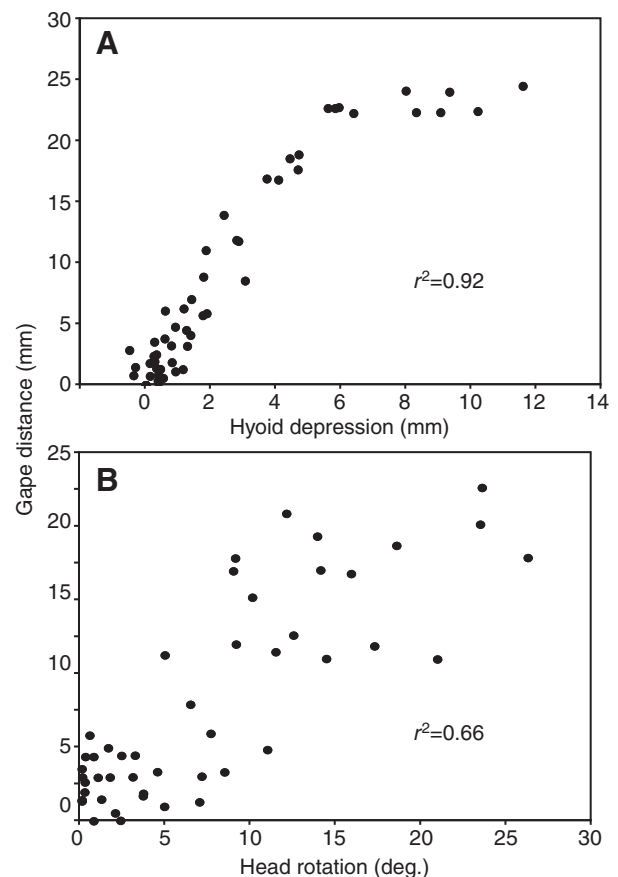


Fig. 3. Examples of tightly integrated kinematics (A) and a less integrated pattern (B). The data plotted represent five prey-capture sequences from a single individual *Micropterus salmoides* feeding on live shrimp prey. (A) The relationship between gape distance and hyoid depression was measured in 10 video frames over the course of the expansion phase of each prey-capture event. A quadratic relationship was fitted, with a relatively high coefficient of determination ($r^2=0.85$), indicating that hyoid depression and mouth opening are tightly integrated during prey capture in this fish. (B) The relationship between gape distance and the angle of head rotation during mouth closing after prey capture in the same feeding sequences analyzed for A. The much weaker coefficient of determination ($r^2=0.31$) indicates that after the time of peak mouth expansion, these kinematic variables are weakly integrated. In this paper we suggest that the repeatability of positional relationships between different structures during movements be assessed by correlation, or coefficient of determination, as a measure of how tightly integrated the movement is.

tightly integrated, and during the compression phase of prey capture in bass, cranial elevation and mouth closing show much less integration than do hyoid depression and mouth opening (Fig. 3B). We suggest that ‘integration’ should refer to the strength of the relationship between two kinematic or motor pattern variables.

The underlying causes of a highly integrated movement range from neuromotor control and regulation of structurally independent elements (Card and Dickinson, 2008) to mechanical coupling, as occurs in a structural linkage system (Westneat, 1990). In a four-bar linkage (Fig. 4), four skeletal elements are connected together in a loop that allows planar motion at each of the four joints connecting pairs of links (Muller, 1996). A four-bar linkage has only one degree of freedom: if one skeletal element moves there must be exact compensatory motion in each of the other three links. In such a system movements of the four links will be perfectly

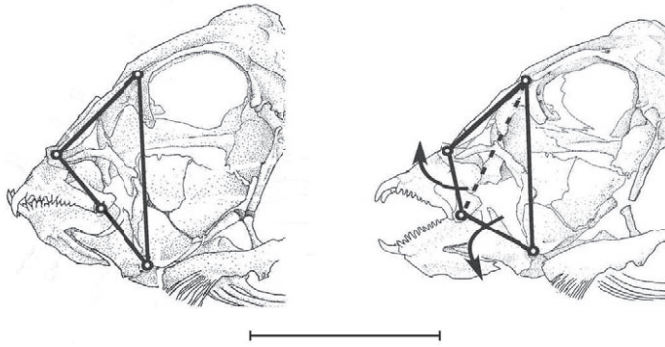


Fig. 4. The four-bar linkage in the oral jaws of *Xyrichtys martinicensis*. In a four-bar linkage four skeletal elements are connected together in a loop that allows planar motion at each of the four joints connecting pairs of links. In spite of its complexity, this system has only one degree of freedom. When one skeletal element moves there is exact compensatory motion in each of the other three links illustrated. A four-bar linkage would produce perfectly integrated movements. Scale bar=1.0 cm.

integrated. If the angle at one joint is known, all of the other angles can be determined. A highly integrated system has one degree of freedom and although the speed of movement of the system may vary from trial to trial, the tight coupling means that the relative timing of events is always the same (Patek et al., 2007; Westneat, 1990).

Integration can also be assessed between physiological (e.g. muscle function) and mechanical (e.g. joint angles) components of a system (Higham and Nelson, 2008). For example, distal limb muscles of many terrestrial vertebrates insert *via* long elastic elements (tendons), allowing a muscle to operate at a constant length (which may maximize force output) while the joint undergoes an excursion (e.g. Roberts et al., 1997). This enhanced performance can be viewed as being permitted by reduced integration between muscle function and limb kinematics.

An important question in functional morphology is what pattern of coordination results in the highest performance for the behavior under consideration. In the field of human motor learning, coordination has been defined as 'the relative movement between interacting body parts and the object to be intercepted during goal-directed behavior' (Newell, 1985). 'Coordination' has been used for some time in this literature to relate performance of a behavior to specific features of kinematics or the motor control of the task (Dessing et al., 2007). Once a specific metric of performance is defined, a group of trials can be evaluated and one can ask what kinematic or motor pattern results in the highest performance. For example, what pattern of muscle activity or limb and body kinematics results in the longest jumps by a frog or lizard? What kinematic pattern results in the strongest suction pressure in a suction-feeding fish (Sanford and Wainwright, 2002; Svanbäck et al., 2002)? In addressing a somewhat different issue, one could also ask whether high-performing individuals or species are characterized by a more tightly integrated pattern of kinematics or muscle activity.

While coordination is routinely documented in vertebrate functional morphology (Irschick and Jayne, 1999; Rice et al., 2008; Ross et al., 2007), the affect of coordination on performance has received much less attention (Toro et al., 2006; Astley and Jayne, 2007). Relatively little is known about what combinations of kinematics or motor activity result in high performance or whether high performance requires tight integration of kinematics, and yet

this should be a valuable avenue for investigation (Full et al., 2002; Holzman et al., 2007).

As in the case of stereotypy and flexibility, distinguishing strength of integration from the question of which pattern of integration maximizes performance will allow us to explore whether some highly integrated behaviors may not result in high performance. It is likely that performance is more a function of the pattern of integration, such as the relative timing of movements, rather than of the variance of that timing (Egan et al., 2007).

Understanding integration of movements may have important implications for how they are controlled at the level of the CNS. Tightly integrated movement across the three major leg joints in humans has been used to argue for a simple kinematic regulatory mechanism that modulates the magnitude of torque at only one joint (Shemmell et al., 2007). But, just as morphological innovation during evolution often proceeds by breaking trait correlations that constrain diversity in ancestors, it may be useful to think of behavioral innovations in terms of the mechanisms that allow coordination patterns to be altered during evolution (Liem, 1979). Patterns of coordination may vary among ecomorphs within diverse lineages (Rice, 2008). The mechanisms that underlie evolutionary shifts in integration may be structural, such as the origin of novel joints (Konow et al., 2008), or decoupling events (Westneat, 1991). Whether behavioral innovation is more often driven by breaking neural regulatory linkages or by structural changes in the skeletal system promises to be an important area of investigation. But, like answering other questions about the nature of behavioral variation, it will be necessary to appropriately attribute variation to its potential causes and, thus, a paradigm is needed that promotes the ability to make key distinctions.

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