Fluctuating Asymmetry (FA)

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Introduction

Developmental stability is referred to as an "ideal" form of an organism to respond against random perturbations during development under a set of conditions (Palmer and Strobeck 1986). As such, abrupt deviations from the ideal condition, when stability in development is disturbed, produce a range of forms that depart from normal phenotypes. Under normal conditions, those outcomes of stability are widely known in bilateral organisms. Even though bilaterally symmetrical organisms have been extensively used as a calibration point to assess deviations from the norm, these organisms also present developmental instability (DI), especially between the left and right sides of certain characters, and thus they have been of interest to evolutionary biologists.

Developmental instability (DI), also known as developmental noise, or treated as an outcome of that, implies subtle deviations from symmetry, which usually exhibit one of three types: fluctuating asymmetry (FA, imprecisely determined path during development); directional asymmetry (DA, general tendency in which one side shows greater development); and antisymmetry (AS, equal frequency of variation) (Fig. 1). These terms refer to patterns of variation in a particular characteristic displayed by a sample of individuals. Fluctuating asymmetry is the most studied and has become a measure of DI, especially because it is the easiest to visualize in populations due to differences in the left-right sides (L-R). However, it is a matter of debate which stressors trigger DI during ontogeny and whether genetics alone, or together with the environment, play a role in producing such variation in chirality. Despite extensive efforts to discover the development basis of FA, the underlying causes of heterogeneity are still unclear. Here, we will highlight the current state of knowledge on FA, measurements, and its applications in evolutionary biology.

The Definition of FA

Fluctuating asymmetry is characterized by small, random departures from the symmetrical form in

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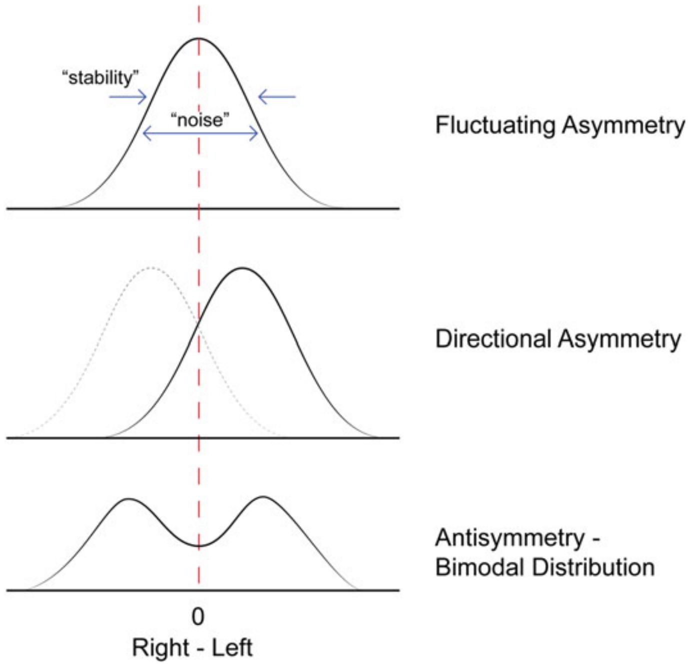
Fluctuating Asymmetry (FA), Fig. 1 Three most common potential distributions of the right-left means in bilateral organisms. Fluctuating asymmetry in a population exhibits a normal distribution of the difference between the sides with a mean of zero (R–L = 0)

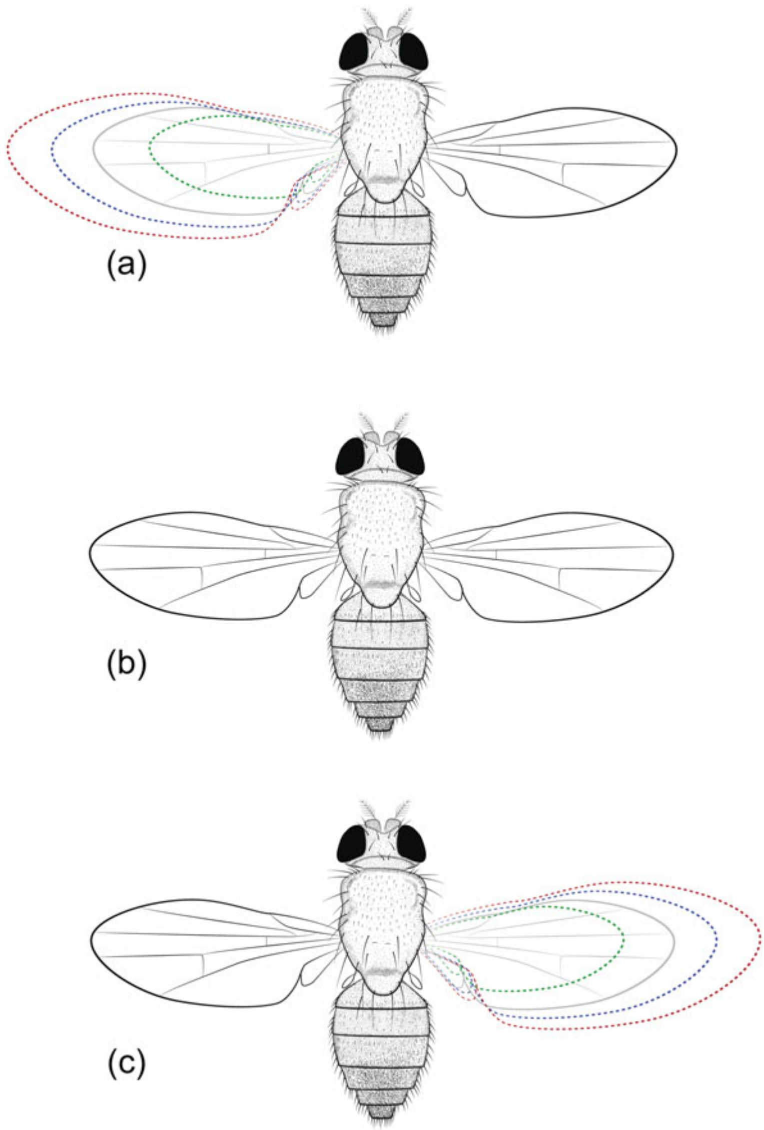


bilateral organisms. During DI, individuals are unable to overcome extrinsic (e.g., habitat fragmentation, thermal noise) and intrinsic (e.g., inbreeding depression, bottleneck event) stressors, exhibiting nonidentical forms on both sides of a given trait. Because phenotypes are not identical within populations, as FA implies imprecise pathways during development, FA can be used as a measure of developmental (in)stability, estimating the sensitivity of development from genetic and environmental stresses. Therefore, FA has been the subject of a lot of attention for generating valuable outcomes for assessing the biological effect of stress at the population level and its impacts on fitness and heritability (see Van Dongen 2006; Benítez et al. 2020).

The search for features notably under FA is quite simple: these traits will be asymmetrical on the right-left sides and can be measured separately, considering the right-minus-left in each individual in a population (Fig. 2). These measures reflect the usual normal distribution with a mean around zero, characterized by a leptokurtic (i.e., when the distribution has an excess of kurtosis, with tails larger than the normal distribution) curve in FA. Although it is well-known to affect the behavior of populations, particularly sexual behavior, and have genetic bases still to be discovered, FA does not have adaptive biases. Basically, this claim is underpinned by the idea that symmetrical traits are the ideal form and, thus, highly genetically controlled (Tomkins and Kotiaho 2002).

Measuring FA

Fluctuating asymmetry can be achieved as simply as measuring the size of a given bilateral trait in the left-right sides and assigning the difference between the absolute value of both afterwards, although other indices can also be used to assess this variation (e.g., morphometrics; see Palmer and Strobeck 2003). Therefore, more symmetrical traits are those whose difference is closer to zero. However, quantifying FA among individuals can be a troublesome task, as the magnitude of FA is usually the same as the measurement error (Palmer and Strobeck 1986). Measurement error reinforces variance in a sample, especially in mean absolute deviations, which often generate apocryphal associations (Graham et al. 2010). To



Fluctuating Asymmetry (FA), Fig. 2 Hypothetical scheme of a *Drosophila* showing R-L wing size variation: (**a**) right wing size variation; (**b**) symmetric form; (**c**) left wing size variation. In fluctuating asymmetry, it is expected that small deviations from symmetry in a sample of individuals should have a larger or smaller right side (**a**, positive asymmetry) or should have a larger or smaller left side (**b**, negative asymmetry). Measurements can be taken using morphometry methods (e.g., wing width versus wing height) to estimate the fluctuating asymmetry of a population by the average of the absolute differences between both sides

avoid spurious information, a statistical analysis must be included in FA observations, and the most widely used is the mixed model analysis of variance (ANOVA).

In this regard, most experts have repeatedly measured the same character on both sides to ensure accuracy in their analysis, also applied to estimate the extent of the variation during counting the focal character, which accounts for measurement error. These measurements must be taken under the same conditions (e.g., stereomicroscopy), guaranteeing the same manipulation in achieving the measures. Repeatability is of paramount importance in every trait that will be analyzed, mostly because it is the principal input for the statistical analysis for both measurement error (ME) and traits (ANOVA), which will indicate if the observed asymmetry is significantly different from ME and whether it reaches a normal distribution (Graham et al. 2010). A thorough statistical procedure is available and detailed in Palmer and Strobeck (2003).

Regarding the accuracy of FA as an estimator of DI, estimated DI is rather difficult to generalize to a population, especially because FA is usually measured from two sides of a given bilateral trait (i.e., with one degree of freedom), which reflects the DI of that individual (Leamy and Klingenberg 2005), and not the whole population, resulting in low precision as an estimator of DI variability. Therefore, to have confidence that differences in L-R sides in a population are due to FA, sampling variation should rely on many FA values. For this, FA and DI should be standardized by *hypothetical repeatability* (HR), an estimator that correlates how much of the difference observed by FA corresponds to differences in DI (Van Dongen 1998). However, even when estimating HR for a huge number of traits and values of FA, it is difficult to establish that high values of HR express high DI, mainly because different traits may be upon different selective pressures on its symmetry. Therefore, there is a common observation of low values of HR, stressing the difficulty in estimating the degree of DI in a trait.

More Common Than It Seems: The Evolutionary Significance of FA

Fluctuating asymmetry has been correlated with a number of evolutionarily relevant issues, such as sexual selection, mate choice, fitness, and heritability (Carter and Houle 2011; Ishihara and Miyatake 2020; Leung and Forbes 1996; Møller and Pomiankowski 1993). Most of these studies focus the attention on a particular aspect of FA at the population level, a feature that can be inferred by the degree of FA. In terms of sexual selection, for example, researchers have raised the idea that FA is a possible indicator of individual quality, a consequence of FA that directly affects individuals' behavior in natural populations. For instance, males with secondary sexual ornaments may be negatively affected by FA, as asymmetrical males indicate to potential mates that they are unable to cope with environmental stress during development, reflecting male quality (Møller and Zamora-Muñoz 1997). As such, females may benefit from choosing symmetrical males according to the "good gene" model of sexual selection.

Individual quality, especially in males, is thought to be sensitive to FA under the assumptions of three main hypotheses: (i) secondary sexual ornaments are costly to produce; therefore they are more sensitive, suffering more from environmental stress, decoupled from other highly costed, and more functional important, symmetric traits; (ii) selected traits are dependent on their expression, and the tiniest modification in that pathway triggers phenotypic deviations; (iii) symmetry is repeatedly observed in characters with a selective advantage, which makes it tempting to assume a genetic component underlying this pattern. Along with these, asymmetry in secondary sexual traits may be under recent directional selection (Møller and Swaddle 1997).

Convincing studies have demonstrated that females are biased toward choosing symmetrical males as mates, which raises the idea that females may have strengthened sensorial biases according to sexual selection models (i.e., sensory bias model). There is growing evidence that female mate choice shapes sexual selection, with empirical demonstration in birds, insects, and spiders. In insects, fireflies display a unique, and widespread, range of variation in both the left-right antennae, with cases up to 80% of asymmetry in a population (Nunes et al. 2020). Complex mate finding (i.e., using chemical components or light signals) may maintain unusual variation among taxa, which may benefit them from having extra antennomeres (i.e., more antennal surface). Another example is also reported in cerambycid beetles *Stenurella melanura* (Linnaeus 1758) in which males with symmetrical antennae were chosen more often than asymmetrical ones, reflecting that this trait has been sexually selected. However, these asymmetries characterized a sharp asymmetry between mated and unmated males, instead of slight deviations from the ideal form – which is a common form of FA (Møller and Zamora-Muñoz 1997).

Studies using tetrapods as a model system consistently show results in FA mean values among more functionally important traits in anurans and turtles (Didde and Rivera 2019; Rivera and Neely 2020). These findings agree with a growing current of thought that more useful and biologically important morphological traits may display lower degrees of FA. Especially in vertebrates, large differences in FA in limbs may decrease the performance of terrestrial animals (Trivers et al. 2013) and aerial organisms (Swaddle 1997), as well as aquatic tetrapods (Rivera and Neely 2020). This handful of examples highlight that different FA plays a different role and has evolved at different rates, according to the trait.

What Is the Role of Environment and Genetics in FA?

An organism's development is constantly under epigenetic phenomena (i.e., molecular alterations that occur on DNA but not within DNA sequencing, producing heritable phenotype changes), being subject to huge intrinsic perturbations. These perturbations give rise to the opportunity for unpredicted phenotypes, culminating in nondirectional departures of paired structures for perfect symmetry (i.e., fluctuating asymmetry). Environmental and genetic factors are the main drivers of FA, and their roles have been investigated in depth (Leamy and Klingenberg 2005; Mabrouk et al. 2020; Sandner 2020). Published evidence seeking signatures of both stressors upon individual development showed that FA arises whenever the environment presents higher concentrations of distinct contaminant exposure. In aquatic environments, ecotoxicological monitoring of several species of anurans and fish suggests that developmental instability increases as a result of exposure to pollutants (Seixas et al. 2016; Guo et al. 2017). As such, higher levels of FA are often found in these environments. These patterns also point to the importance of conservation policy, given that high rates of FA are found with chronic exposure to a range of pollutants, from metals to chemical components. Furthermore, these parameters are closely related to individual and environmental quality – polluted environments and higher levels of FA are suitable and reliable biomarkers for ecotoxicological studies, conservation, and prediction of FA (Leary and Allendorf 1989).

On the other hand, the role of genetics in shaping FA is still unclear and contentious. Some studies have found heritability in morphological characters (Carter and Houle 2011) while others have found no such relationship (Kruuk et al. 2003). In order to search for the role of genetics in developmental instability, researchers have focused on candidate genes (Batterham et al. 1996) and quantitative trait loci (Leamy et al. 1997, 1998). However, a consensus on whether the genetic architecture is conditional to certain characters to ensure symmetry in organisms' development awaits further investigation.

More generally, a better understanding on how the genetic pool affects the degree of FA under environmental stressors and the extent of phenotypic variation among populations is elusive. Heritable variation of FA has been reported for artificial selection of outbred populations in the fruit fly *Drosophila melanogaster* (Meigen 1830) (Carter and Houle 2011), although natural selection has not fixed all the extant phenotypes found during artificial selection. Noteworthy, according to these findings, natural selection tends to decrease levels of FA in evolutionarily relevant traits in all wild populations, such as locomotor appendages (e.g., legs, limbs, and wings). Therefore, it is assumed that FA (and DI) is deleterious to fitness.

Summary

Fluctuating asymmetry plays a pivotal role in mate choice, sexual selection, heritability, and conservation. To date, a broadly available literature portrays the importance of environment and genetics as a trigger of developmental instability, thus leading to higher degrees of FA in bilateral organisms. However, the mechanisms underlying FA remain to be investigated.

Cross-References

- ▶ Bilateral Symmetry
- ▶ Brain Asymmetry
- ▶ Radial Symmetry

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