© 2024. Published by The Company of Biologists Ltd | Development (2024) 151, dev203101. doi:10.1242/dev.203101

SPECIAL ISSUE
UNCOVERING DEVELOPMENTAL DIVERSITY

Assessment and the regulation of adaptive phenotypic plasticity

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ABSTRACT

Organisms can react to environmental variation by altering their phenotype, and such phenotypic plasticity is often adaptive. This plasticity contributes to the diversity of phenotypes across the tree of life. Generally, the production of these phenotypes must be preceded by assessment, where the individual acquires information about its environment and phenotype relative to that environment, and then determines if and how to respond with an alternative phenotype. The role of assessment in adaptive plasticity is, therefore, crucial. In this Review, we (1) highlight the need for explicitly considering the role of assessment in plasticity; (2) present two different models for how assessment and the facultative production of phenotypes are related; and (3) describe an overarching framework for how assessment evolves. In doing so, we articulate avenues of future work and suggest that explicitly considering the role of assessment in the evolution of plasticity is key to explaining how and when plasticity occurs. Moreover, we emphasize the need to understand the role of assessment in adaptive versus maladaptive plasticity, which is an issue that will become increasingly important in a rapidly changing world.

KEY WORDS: Developmental plasticity, Signal detection theory, Environmental cues, Facultative phenotypes

INTRODUCTION

Phenotypic plasticity is the ability of an organism to adjust its phenotype in direct response to changes in its environment (West-Eberhard, 2003). Such changes in phenotype can be profound, such as when the environment experienced during development alters an the morphology of an organism (Lofeu et al., 2021) or sex (Gemmell et al., 2019; Pla et al., 2021; Akashi et al., 2024). Alternatively, plastic phenotypic change can be subtle and potentially invisible to an outside observer, e.g. when a change in diet induces a shift in gene expression (Gilbert and Epel, 2015; Ferenc and Ikmi, 2023). Indeed, environmentally sensitive phenotypes are the rule rather than the exception, and understanding such developmental flexibility is crucial to understanding how living systems evolve and diversify. By allowing organisms to produce a phenotype that better matches current environmental conditions, plasticity is often adaptive (Nijhout, 2003; Yeh and Price, 2004; Kingsolver and Buckley, 2017; Riddell et al., 2018; Fox et al., 2019; but see below). For these reasons, plasticity is thought to play an important role in both ecology and evolution (Agrawal, 2001; Pfennig et al., 2010; Sultan, 2021; Hess et al., 2022; Leung et al., 2023; Uller et al., 2024), as well as in human health (Bateson et al., 2004).

The capacity to produce different phenotypes in response to the environment is itself a trait that can evolve (Moczek and Nijhout, 2003; Moczek et al., 2011; Chevin and Lande, 2015; Ehrenreich and Pfennig, 2016; Casasa et al., 2020; Campbell-Staton et al., 2021). Because the facultative expression (meaning phenotypic expression that is conditionally or environmentally dependent; i.e. is plastic) of traits that are ill-suited to their environment reduces an the evolutionary fitness of an organism, natural selection should favor either the evolutionary refinement of plasticity, so that it is fitness-enhancing, or, alternatively, the evolutionary loss of plasticity. Consequently, phenotypic plasticity is often assumed to be adaptive, and much work on plasticity has focused on whether – and how – organisms express adaptive environmentally induced phenotypes (Pigliucci, 2005; Nettle and Bateson, 2015; Pfennig, 2021).

Longstanding theory suggests adaptive plasticity will evolve only when organisms can detect features in their environment that reliably predict the fitness-enhancing phenotype in the new environment (DeWitt et al., 1998; Schlichting and Pigliucci, 1998; Moran, 1992; Langerhans and DeWitt, 2002; Nijhout, 2003; Chevin and Lande, 2015). In other words, theoretical and empirical work has highlighted the importance of environmental assessment in the expression and evolution of adaptive plasticity. By ‘environmental assessment,’ we mean that before a behavioral, developmental or physiological response is produced, an organism must first ‘detect’ and ‘evaluate’ cues from the environment and then determine whether to alter its phenotype in response to that environment. In short, to produce an adaptively plastic phenotype requires both a response (which is often readily observed) and assessment (which can be less readily observed). Thus, central to understanding the mechanisms of plasticity is the crucial process of environmental assessment.

In considering assessment, one must distinguish between environmental stimuli and cues. ‘Stimuli’ are aspects of the environment that alter phenotypes in ways that are not necessarily adaptive (Whitman and Agrawal, 2009). For example, some instances of plasticity might arise as an unavoidable consequence of fundamental laws of physics or chemistry, such as how numerous biological processes change with temperature (reviewed by Arroyo et al., 2022). With such ‘responsive plasticity’, assessment and response become inextricably linked. ‘Cues’, by contrast, are features of the environment that predict (or signify) the environment in a way that enables an organism to adopt a fitness-enhancing phenotype (Whitman and Agrawal, 2009). Examples of cues include photoperiod (if it reliably predicts future seasonal or temperature changes) and chemicals associated with predators (if they reliably predict the presence of a predator). As noted above, the theory holds that organisms should evolve mechanisms to detect and respond to environmental features that ‘anticipate’ the need for phenotypic change before a harmful (or beneficial) environmental

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factor appears. Thus, stimuli can become cues, and responsive plasticity can become 'anticipatory plasticity' that involves environmental assessment.

Note that assessment need not be cognitive or require actual 'thinking'. Indeed, even organisms lacking brains or nervous systems can make remarkable use of environmental cues, as exemplified by the slime mold *Physarum polycephalum*, which can integrate information about its environment to generate complex behavioral choices, all without a brain or even multiple cells (Boussard et al., 2021). Essentially, phenotypic plasticity can be considered a 'decision tree', whereby an organism, system or pathway can produce alternative outputs in response to different environmental inputs. The input is detected and evaluated, and one of the alternative outputs is produced. This process can be complex (as in many animals) or simple (as in plants and bacteria (Fig. 1).

Moreover, assessment is not restricted to evaluating the external environment of an organism. Organisms must often assess their internal environment and modify their phenotype based on their internal state. For example, many organisms express alternative behaviors or develop different features depending on their condition or age (Sunobe et al., 2015; Jernigan et al., 2021). Indeed, in many situations, organisms must detect their current phenotype relative to the prevailing environment to determine whether and how to respond to the external environment (e.g. Pfennig, 2007), with the result that facultative expression of a given trait depends on the interplay of both the internal and external environment of an organism.

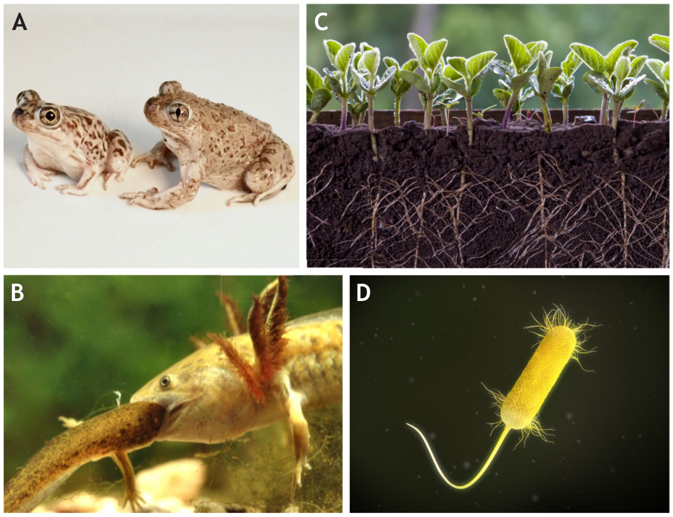

Fig. 1. Examples of diverse organisms performing impressive feats of assessment during adaptive behavioral or morphological plasticity. (A) Female plains spadefoot toads, *Spea bombifrons* (A, left), assess the depth of their breeding pond and their body condition, and switch to mating with males of another species, Mexican spadefoot toads, *S. multiplicata* (A, right) (see Pfennig, 2007; Chen and Pfennig, 2020). (B) Tiger salamander larvae, *Ambystoma mavortium* (B), are less likely to develop into a cannibal morph around kin than around non-kin (see Pfennig and Collins, 1993). (C) Many plants can assess nutrients and competitors when deploying their roots (see Cahill et al., 2010). Image reproduced, with permission, from Adobe Stock. (D) Many bacteria can gauge the density of bacterial cells in their immediate vicinity through a process known as 'quorum sensing' and switch on certain behaviors at high population densities. The bacterium *Pseudomonas aeruginosa* can even assess when interacting cells are more highly related (see Diggle et al., 2007). Image reproduced, with permission, from Adobe Stock.

As detailed below, assessment can determine whether phenotypic plasticity is expressed and enhances fitness (i.e. whether it is adaptive). Moreover, the mechanisms underlying assessment are potentially the targets of selection that dictate when and how plasticity evolves, so explaining how assessment evolves is crucial to understanding the broader process by which phenotypic plasticity evolves and contributes to the diversification of phenotypes. We address these issues by: (1) describing the role of assessment in adaptive plasticity; (2) developing two alternative frameworks for how assessment proceeds; and (3) discussing how assessment itself might evolve. We conclude by describing considerations for empirical studies that will further our understanding of how and when adaptive plasticity arises. Our conceptual framework does not depend on the specific form of inheritance (e.g. genetic versus epigenetic), on the mechanism by which assessment occurs or on the level of biological organization. Our goal is to provide a framework that applies whether one is examining complex phenotypes expressed at the level of an organism, the functioning of a developmental pathway or even the expression of a single gene.

The role of assessment role in the study and evolution of adaptive plasticity

Understanding the mechanisms by which plasticity is expressed and evolves requires considering assessment for two reasons. The first is logistical: if assessment is not considered, crucial mechanisms underlying the expression of plasticity could be missed or misconstrued. Specifically, as noted above, the facultative expression of a trait necessarily involves assessment of the environment (if only by minimally detecting that an environment has changed). Thus, organisms that express adaptive plasticity must generally be capable of both assessment and a phenotypic response. By contrast, an organism that possesses the capacity for alternative trait expression will not be identified in the first place if its capacity to assess its environment is limited. Thus, if an organism fails to assess its environment appropriately, it will appear to lack plasticity in the same way as an organism that has the capacity to assess its environment accurately but is incapable of responding to it. Nevertheless, the underlying mechanisms impacting the expression of plasticity differ between these two scenarios. Consequently, the targets on which selection can act (and how plasticity evolves) will also vary between these scenarios. Thus, because assessment is necessary for detecting plasticity, identifying and isolating the underlying mechanisms for either assessment or a facultative phenotypic response can be difficult empirically.

A second reason to explicitly consider the role of assessmen in plasticity is that assessment can determine when and how plasticity is adaptive. Although plasticity is often adaptive, this need not always be the case (Ghalambor et al., 2007; 2015; Van Buskirk and Steiner, 2009; Davidson et al., 2011). Maladaptive plasticity arises when the environment induces a change in phenotype that lowers fitness (Moran, 1992). For example, natural populations of a species with temperature-dependent sex determination, green sea turtles, *Chelonia mydas*, have experienced dramatic skews in sex ratio in response to increasing global temperatures. This has pushed adult sex ratios to be strongly female biased, potentially threatening population viability if some individuals cannot acquire mates (Jensen et al., 2018). This example presumably represents a breakdown of a previously adaptive assessment and response relationship. Under rapidly changing conditions, the relationship is potentially no longer fitness enhancing. This demonstrates the importance of assessment generally and how an adaptive assessment-response relationship can become explicitly maladaptive when environmental conditions change faster than assessment can evolve. We return to these issues in the section 'Evolution of assessment' below.

Assessment and phenotypic response: two alternative models

For adaptive plasticity to occur, a facultative shift in phenotype requires an accurate assessment of the prevailing internal and external environment of an organism. Selection is, therefore, expected to favor using internal or external cues that reliably predict the phenotype that maximizes fitness in the prevailing environment (reviewed by Snell-Rood and Ehlman, 2021). Beyond this broad framework for the evolution of assessment lies the problem of how information from the environment is transduced by the organism into the expression of an alternative phenotype. Two general models explain how organisms process and respond to environmental cues through plasticity (Fig. 2).

The distinct-stage model

Adaptive phenotypic plasticity can be presented as unfolding in two stages: assessment followed by a phenotypic response (e.g. West-Eberhard, 2003; Sultan, 2015; Pfennig, 2021). We define this framework as the distinct-stage model (DSM; Fig. 2A). Under the DSM, environmental cues are detected by the sensory, physiological or neural pathways of an organism. These cues then trigger subsequent downstream phenotypic shifts mediated by additional genetic, cellular, developmental and (neuro)physiological pathways. Thus, the DSM predicts that the mechanisms underlying plasticity occupy two sets: those involved in detecting the environmental cue(s) and those involved in producing a phenotypic response, given that detection of the cue(s) occurred. Indeed, the modular nature of developmental pathways may facilitate semi-independence in different stages of the expression of environmentally induced phenotypes (Snell-Rood et al., 2010).

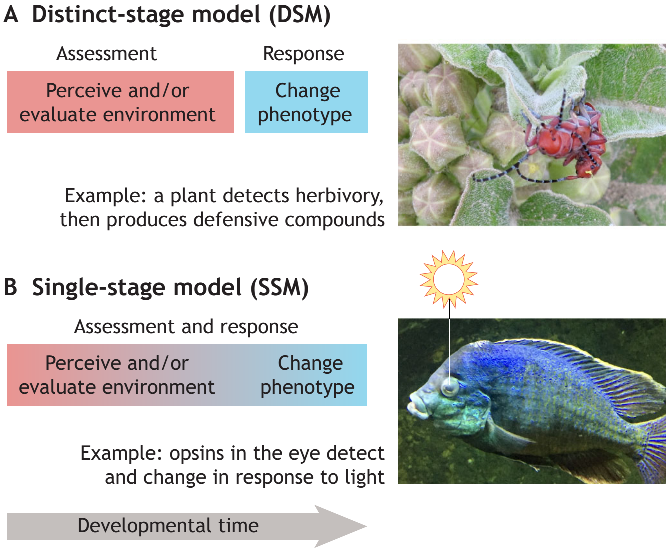

Fig. 2. Two alternative models of assessment and response in the expression of adaptive plasticity. (A) Under the distinct-stage model (DSM), the mechanisms underlying plasticity occupy two sets: those involved in the perception and/or evaluation of the environment, and those involved in changing the phenotype. (B) Under the single-stage model (SSM), the process of perceiving and/or evaluating the environment concomitantly changes the phenotype (and vice versa), suggesting assessment and response are the same. Also shown are possible real-life examples of each model; see also the main text.

Spadefoot toads potentially exemplify this two-stage model. In response to variation in their environment, spadefoot toads of the genus *Spea* express distinct larval phenotypes (a polyphenism). As in most anurans (frogs and toads), *Spea* tadpoles typically develop into an 'omnivore' morph, which eats detritus, algae and plankton. However, if they eat or are even exposed as embryos to live animal prey, such as fairy shrimp or other tadpoles (Pfennig, 1990; Levis et al., 2015; Harmon et al., 2023), some individuals express an alternative 'carnivore' morph. Such resource-use plasticity in *Spea* is favored because omnivores and carnivores are adapted to different environmental conditions (Pfennig, 1992; de la Serna Buzon et al., 2020).

Recent research on spadefoot toad tadpoles has taken advantage of the reversibility (and variation in ability to reverse) of the carnivore morph in different selective environments to probe the genetic and transcriptomic differences in individuals that differ in their capacity to assess new conditions and reverse developmental trajectories adaptively (Levis et al., 2020). By using this approach, Isdaner and colleagues (2024) identified four quantitative trait loci (QTL) associated with the phenotype and nine with adaptive plasticity (adaptive versus maladaptive environmental assessment), suggesting that environmental assessment and phenotypic response may be mediated by different genetic loci, as predicted by the DSM. Although natural experiments of this kind are uncommon, additional tests are needed to reveal whether and when the two components of plasticity are separate, as predicted under the DSM.

The single-stage model

An alternative to the DSM of assessment and response is that the assessment process concomitantly induces the facultative phenotypic response. Assessment and response are essentially the same under this model, which we define as the single-stage model (SSM; Fig. 2B). For example, in the cichlid *Metriaclima zebra*, the regionalized expression of different opsins in the retina is plastic and responds to both the spectra and orientation of light (Dalton et al., 2015). The environmental cue (light) is detected by opsins in the photoreceptors, the expression of which is the actual plastic phenotype in question. In this example, the assessment of light and the plastic expression of opsins are inextricably linked (see also Fogg et al., 2023). Thus, the phenotypic response cannot be separated into distinct assessment and response stages, as under the DSM (Fig. 2).

The frequency by which assessment and response can be characterized by the SSM framework remains unclear. Systems or pathways where responses are dictated by physical or chemical responses to environmental stimuli will often fall under this framework (recall the distinction between stimuli and cues described in the Introduction). Other types of responses are suggestive but remain unclear. For example, many animals can change color in response to different backgrounds. The caterpillars of one such species, *Biston betularia*, rapidly alter their skin color to match the twig on which they are resting (Noor et al., 2008). Such color plasticity enhances crypsis and, therefore, survival (Eacock et al., 2017). Interestingly, experimentally blindfolded caterpillars can change their skin color to match their background (Eacock et al., 2019), suggesting these caterpillars can determine colors with their skin. Similarly, 'blinded' squid can detect their background and change their skin to match it by turning on opsin genes in their skin

(Kingston et al., 2015). Without knowing how environmental cues or stimuli are transduced into a phenotypic response, it is difficult to say whether these constitute additional examples of a SSM framework, but systems such as these offer interesting opportunities to evaluate this framework.

Comparing the models

One could argue that the above distinction between the DSM and SSM frameworks is not useful, especially if it obfuscates rather than clarifies the relationship between assessment and response or our understanding of how plasticity evolves. However, the distinction becomes useful if, as described below, each has different conceptual and experimental implications.

When plasticity is mediated by distinct pathways of assessment and response, as in the DSM, the facultative expression of phenotypes can be evolutionarily ‘tuned’ via alterations of either of these sets of pathways. By contrast, under the SSM, refinement of plasticity by the selection might be expected to be derived almost entirely from changes to sensitivity to the inducing cue or stimulus instead of the resulting phenotype. Thus, plasticity might evolve according to the DSM when greater independence is needed between assessment and phenotypic response. Such might be the case when mechanisms involved in assessment are required for other processes (i.e. selection is buffering the system against pleiotropy) or if a facultative response depends on multiple environmental cues. By contrast, plasticity might more likely evolve via the SSM when such independence might be costly or reduce the efficacy of the phenotypic response. Moreover, SSM might be more likely when only a single cue is needed to induce a response or if a general response to an environmental stimulus is adaptive.

Notably, the two models are not mutually exclusive. The DSM and SSM might describe alternative levels of biological organization: e.g. what appears at the organismal level as DSM might consist of SSM-type systems at the gene expression, developmental, cellular, physiological or neural levels. Indeed, assessment and response might become distinct stages when selection favors increasing or greater coordination of multiple pathways operating according to the SSM.

Moreover, systems that operate according to a DSM framework might necessarily arise at the origins of cue use to induce a facultative response. As noted above, plasticity in response to an environmental stimulus is not necessarily fitness enhancing. If environmental stimuli promote maladaptive phenotypes, selection will favor the buffering of those systems that necessarily respond to environmental stimuli. Likewise, selection will favor using cues that predict the environment and the fitness-enhancing phenotype. If systems that function according to the SSM are primarily those that are responsive to stimuli (as opposed to cues), then those systems might be sequestered in a way that minimizes the likelihood of producing maladaptive phenotypes and/or are subject to modification via the use of cues. Regardless, the stage becomes set for the origins of more complex or modular systems that enable assessment to precede a response. Whether these dynamics explain the evolutionary origins of cue use and the organization of pathways underlying plastic traits is an exciting area that needs additional empirical work.

In considering the DSM and SSM, it is also vital to recognize that they simply describe the relationship between assessment and phenotypic response. As such, they do not necessarily make claims about the complexity or nature of mechanisms underlying plasticity. At first glance, the DSM suggests greater complexity, given the potential for multiple pathways to be involved across assessment and phenotypic response. However, complex gene-regulatory networks (GRNs) likely underlie many plastic traits (Pfennig and Ehrenreich, 2014; Schneider et al., 2014; Sommer, 2020; Ng and Kinjo, 2023), and these could function in a manner consistent with the SSM. Indeed, plasticity mediated by the SSM might be more complex than the DSM when effects across a given pathway are non-additive.

Empirical tests of these models in diverse taxa (and even in different plastic phenotypes within the same organism) will help elucidate these considerations and shed light on how the underlying mechanisms of assessment and response evolve and interact. Yet, as noted above, tests of these models and the hypotheses for how they evolve and impact plasticity encounter a methodological obstacle. Under the DSM, organisms can vary in plasticity either because they vary in their ability to assess their environment or because they vary in response to it. Although functionally equivalent, the pathways to the phenotypic outcomes are different. Empirical approaches that account for this problem are required to interrogate the underlying mechanisms that explain variation in plasticity.

A final issue is that plasticity across development can impact subsequent development and assessment. Indeed, it has previously been observed that plastic responses early in development might impact how assessment proceeds for plastic phenotypes later in development or adulthood (Moczek, 2015; Beaman et al., 2016; Burggren, 2020). This issue potentially pertains to systems as divergent as physiology and morphology to learning and behavioral innovation (Fischer et al., 2017; Mariette, 2024; Meillère et al., 2024; Tetrault et al., 2024). Understanding how early development subsequently impacts later processes and plasticity represents an exciting frontier for the field.

Evolution of assessment

Regardless of the underlying assessment mechanisms, all organisms face the crucial challenge of detecting – and determining a response to – cues in a complex, variable and noisy world. Consequently, organisms make mistakes in assessment that can result in the facultative expression of traits that reduce fitness (i.e. maladaptive plasticity) or the failure to respond facultatively when it is beneficial to do so. Such mistakes derive from two primary sources: (1) the use of cues that poorly predict which phenotype is adaptive for the environment (i.e. the use of unreliable cues); and (2) limits (both biological and environmental) imposed on accurately detecting a reliable cue in a noisy environment.

When cues are unreliable and the expression of plasticity costly [i.e. maladaptive (Langerhans and DeWitt, 2002)], selection should favor either the loss of sensitivity to the environment (i.e. the loss of plasticity) or the use of a reliable alternative cue. The latter potentially involves switching to new cues or even using multiple cues that generate complementary or redundant information that enhances the ability of an organism to accurately assess its environment (*sensu*; Candolin, 2003; Stoehr and Wojan, 2016; Potticary and Duckworth, 2020; Tibbetts et al., 2020). Furthermore, the degree to which a given cue reliably predicts the fitness-enhancing phenotype that should be adopted can vary over time and space (Mills et al., 2013; Kingsolver and Buckley, 2017). More studies are needed to understand how local adaptation in the pathways and mechanisms that detect cues during assessment contribute to diversity in plasticity.

Understanding if and how the evolution of differential cue use proceeds depending on cue reliability remains an area of inquiry for understanding the evolution of plasticity. As an aside, yet perhaps more crucially, conservation strategies might depend on revealing how global change impacts the responses of organisms to cues that vary in reliability. Generally, plasticity has been hypothesized to prevent extinction by buffering populations from the harmful effects of rapid environmental change while also facilitating adaptation to new environments (Riddell et al., 2018; Fox et al., 2019; Levis and Pfennig, 2020; Harmon and Pfennig, 2021; but see Hendry, 2016). However, plasticity might not be the imagined salvo for declining populations if increased environmental variability generates unreliability in environmental cues and, therefore, increased expression of maladaptive plasticity that further depresses the fitness of a population. Such might be the case with climate change, which is not only expected to alter environments, but also to alter variability in those environments (Bathiany et al., 2018; Bonamour et al., 2019; Turner et al., 2020). As more is known about how diverse species use cues from their environment in the facultative expression of traits, those studying plasticity could provide important insights into which species are better able to track global change than others via switching cues or using multiple cues. Such insights could be valuable for conservation efforts and protecting biodiversity, especially as plasticity impacts geographic range, physiological tolerance, sensitivity to stress and ecological and reproductive flexibility (Gilbert and Hadfield, 2022; Donelson et al., 2023). A further complication is that plasticity can sometimes facilitate adaptive evolution and, at other times, impede it (Price et al., 2003; Ghalambor et al., 2015; Muñoz, 2022). Establishing whether plasticity facilitates adaptive evolution and protects populations from extinction or impedes it and puts populations at greater risk will require identifying the underlying developmental, cellular, physiological and neural mechanisms involved in environmental assessment. Doing so will provide a general understanding of how organisms use environmental cues and the ease with which they can switch from less to more reliable environmental predictors. But, from a practical standpoint, the need to understand assessment and its role in adaptive versus maladaptive plasticity is an increasingly pressing issue, as an accelerating number of species face mismatches between cue reliability and their environments (Mills et al., 2013; Renner and Zohner, 2018; Zimova et al., 2022).

Even when organisms use reliable cues, they still face limits on their ability to detect them. Specifically, organisms could: (1) fail to detect those cues when they are present; and (2) mistakenly detect the presence of cues that are, in fact, absent. These potential mistakes derive from the combination of biological limits on the ability of an organism to detect and/or process signals, and the potential for cues (whether internal or external) to be present within a 'noisy' background of other cues and environmental stimuli. Hence, organisms face a 'signal detection' problem (detecting a salient cue from 'noise'), which has important implications that can shape the mechanisms used in detecting cues. Signal detection theory (SDT) provides a conceptual framework for understanding the evolution of detecting and responding to environmental cues across different levels of biological organization (Reeve, 1989; Wiley, 2006; McNamara and Trimmer, 2019; Scharf et al., 2020; Sumner and Sumner, 2020; Tibbetts et al., 2020).

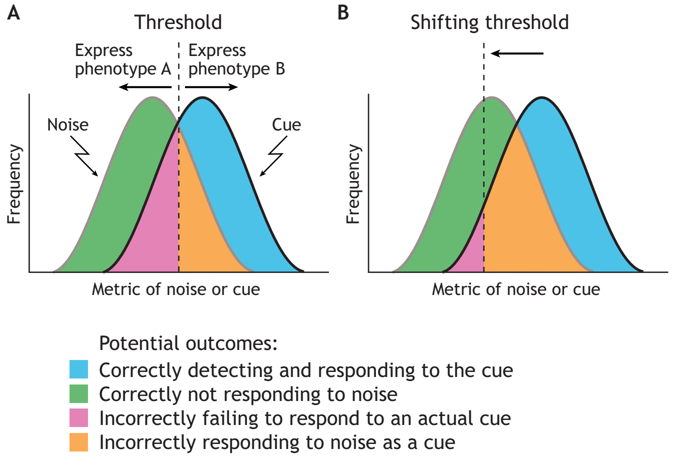

Fig. 3. Signal-detection theory applied to the expression of adaptive plasticity. (A) When assessing and responding adaptively to their environment, assessment systems must discriminate between cues (or stimuli; see text) and noise in the environment. The risk of correct assessment versus making mistakes depends on two factors. First, the risk of errors depends on the extent to which cues (or stimuli) overlap with other features of the environment (i.e. 'noise'), as indicated by the bell curves and their overlap. The more the curves overlap, the greater the risk of error in assessment and response. Second, there should be a threshold value of the strength of cues or stimuli (dashed line), above which the organism responds by switching from producing one phenotype (or range of phenotypes; in this case, phenotype A) to producing an alternative phenotype (or range of phenotypes; in this case, phenotype B). The optimal location of this threshold depends on the relative costs and benefits associated with the following: correctly detecting and responding to a cue that is, in fact, present (blue); correctly not responding to noise or the absence of the cue (green); incorrectly failing to respond to a cue that is truly present (pink); or incorrectly responding to a perceived cue that is truly absent (i.e. responding to noise as if the cue is present; orange). Selection should favor the evolution of a threshold that results in adaptive plasticity. Thus, the threshold should shift so that assessment is more (or less) sensitive to the presence of a cue (or stimulus), depending on the costs of the different types of errors. (B) For example, with predator-induced plasticity, failing to detect and respond to the cue of an actual predator is often costlier than responding to a perceived cue of a predator that is not actually present. In such cases, the optimal threshold should shift to a lower strength of cues (i.e. greater sensitivity) to minimize the likelihood of failing to respond to a cue that is truly present. For additional details, see main text. Modified from Pfennig (2021), where it was published under a CC-BY-NC-ND license (https://creativecommons.org/licenses/by-nc-nd/4.0/).

Originally developed for the problem of separating signal from noise in communications (Wiley, 2006), SDT posits a binary outcome by an organism: when it perceives a cue (whether present or not), it can either 'accept' the cue (i.e. respond to it) or 'reject' the cue (i.e. fail to respond to it). Thus, four outcomes follow, two of which constitute accurate assessment and two of which are mistakes in assessment (Fig. 3). Accurate assessment arises when an organism responds appropriately to a cue that is truly present and fails to respond to a cue that is truly absent. Mistakes occur when an organism fails to respond to a cue that is truly present or when the organism responds as if the cue is present but the cue is truly absent. The risk of errors depends on the sensitivity of the assessment system: oversensitivity results in organisms responding to the perceived presence of cues that are, in fact, absent (i.e. 'acceptance errors'), whereas under-sensitivity results in failure to respond to cues when they are present (i.e. 'rejection errors').

The optimal sensitivity to the presence of a cue can be characterized as a 'threshold', and the evolutionarily optimal threshold maximizes fitness by minimizing the more costly type of mistake (Reeve, 1989). Thresholds are expected to be more sensitive when the costs of failing to detect a cue (and, therefore, not altering a phenotype) are worse than the costs of detecting 'false' cues (Fig. 3). In other words, thresholds will evolve to be more sensitive when the facultative expression of a phenotype is relatively inexpensive in terms of fitness. By contrast, thresholds will be less sensitive when expressing an inappropriate alternative phenotype (maladaptive plasticity) is worse than not altering a phenotype in response to the environment.

This threshold perspective is congruent with a traditional perspective of phenotypic plasticity as having ‘switches’ or ‘decision points’, particularly during development (Abouheif and Wray, 2002; Nijhout, 1999 and 2003; Burggren, 2020). Evaluating whether developmental systems and, more generally, other mechanisms underlying plasticity evolve in this way is understudied. Moreover, the signal detection framework is often articulated as a single cue and/or threshold response problem. However, plastic phenotypes might be mediated by multiple cues at a given pathway or involve multiple pathways that are responding independently to different cues. How the signal detection problem plays out and impacts the evolution of assessment when multiple cues are used or complex systems are involved (that might or might not be independent of one another) remains an exciting area of inquiry. Thus, evaluating whether and how mechanisms evolve as expected under this framework would provide crucial insights into how plastic phenotypes are regulated and evolve.

Mechanistic considerations

Investigating assessment and plasticity is not always straightforward. Because assessment mechanisms are diverse and potentially specific to an organismal system or developmental, (neuro)physiological, cellular or genetic pathway, studies of assessment must necessarily be tailored to the specific trait and level of biological organization of interest. Nevertheless, three common issues exist for studies of assessment that should be considered in future work.

First, as described above, assessment can involve the evaluation of both external cues and the internal state of the organisms. Importantly, phenotypic responses to internal cues might impact phenotypic responses to external cues, and vice versa (e.g. Pfennig, 2007; Burmeister et al., 2020). For example, the regenerative acoel worm *Hofstenia miamia* can regrow any amputated body fragment and, conversely, amputated fragments can regenerate entire new bodies themselves (Srivastava et al., 2014). When injured, the worm must regenerate the correct missing structures. Doing so demands that an individual assess its internal condition and phenotype. In *H. miamia*, positional information during regeneration is provided through the expression of genes by muscle tissue (Raz et al., 2017). The positional information provided by the muscle is how the organism assesses its own state, which then enables the regeneration of the appropriate missing tissues.

Moreover, assessment of internal state can sometimes serve as an indirect method of assessing an important environmental variable. In plants, such as *Arabidopsis thaliana*, several developmental processes respond to photoperiod (Puterill et al., 1995). A classic example of this is in flowering, when the plant is directly sensing and responding to photoperiod to control the temporal expression of a phenotype (Yanovsky and Kay, 2002; Osnato et al., 2021). Growth is also sensitive to photoperiod, yet assessment for growth proceeds independently of assessment for flowering. Where assessment for flowering directly detects and integrates the cue (in this case, light), assessment for growth detects the internal state (Wang et al., 2024). Growth is sensitive to the expression of *MIPS1*, a gene encoding an enzyme necessary for myoinositol synthesis, which is induced during long days in response to metabolic byproducts of photosynthesis. Photoperiod for growth then is assessed indirectly via detection of the internal metabolic state of the organism.

Beyond accounting for the interplay of the internal and external environments in assessment, a second issue to consider in studies of plasticity is that social cues can influence plastic developmental phenotypes (Fischer et al., 2017; Jernigan et al., 2021; Lucon-Xiccato et al., 2022) and some examples of this may appear simple on the surface (Fig. 1C,D). How social conditions influence plastic phenotypes is perhaps best studied in insects (Corona et al., 2016). For example, desert locusts, *Schistocerca gregaria*, exhibit dramatic phase plasticity in response to population density, an environmental parameter that likely impacts the expression of hundreds of genes (Foquet et al., 2021). Despite the frequency of this phenomenon, piecing together the mechanisms of assessing these conditions is not always easy, especially in animals with complex social environments. Importantly, elements of plastic responses (and their underlying mechanisms) might be missed or inaccurately measured if experimental designs fail to include appropriate social stimuli (e.g. Calabrese and Pfennig, 2022).

A third major consideration in investigating the role of assessment in plasticity is the distinction between the inducing and selective environments. As noted in the Introduction, many species engage in anticipatory plasticity, where cues are used to predict the phenotype that an individual should adopt for the future. Classic examples of such plasticity are seasonal polymorphisms whereby organisms use cues from the current environment to predict which phenotype to adopt in the future (Mills et al., 2013; Osnato et al., 2021; Zimova et al., 2022). Likewise, *Drosophila* can express plasticity in adult reproductive morphology that depends on larval density they experienced during development (Bretman et al., 2016). Thus, assessment and response might be separated across different life stages, further complicating experimental designs aimed at identifying the pathways involved in assessment and response.

Conclusions

The evolution of plasticity generally requires identifying the underlying mechanisms by which organisms transduce information from the environment into a phenotypic response. Major headway in this realm will come from explicitly considering the role of assessment in the facultative expression of phenotypes and identifying the underlying genetic, developmental, cellular, neural and physiological systems that enable assessment. Doing so will thereby explain how these mechanisms foster – or limit – the way in which plastic phenotypes are expressed, adaptively coordinated and evolve.

Acknowledgements
We thank the three anonymous reviewers for their valuable comments that greatly improved the paper.

Competing interests
The authors declare no competing or financial interests.

Funding
Our research on plasticity is supported by grants from the National Science Foundation (DGE-2439854 to K.A.P.H., IOS-2217635 to K.S.P., and IOS-2306276 to D.W.P. and K.S.P.).

Special Issue
This article is part of the Special Issue ‘Uncovering developmental diversity’, edited by Cassandra Extavour, Liam Dolan and Karen Sears. See related articles at https://journals.biologists.com/dev/issue/151/20.

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