



Integration of plasticity research across disciplines

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Plasticity is studied across the social and biological sciences, but communication between disciplines is hindered by differences in the concepts used to do so. For instance, the distinction between expectant and dependent plasticity is widely used in psychology, but rarely used in evolutionary biology. As a consequence, researchers are less likely to benefit from each other's theories, methods, and findings. This paper discusses three challenges to the generality of the distinction: (1) organisms without neurons, (2) organisms that have multiple sensitive periods with flexible timing, and (3) variation in experience across individuals and populations. Although we hope that one day all disciplines will share a common, generalizable taxonomy of forms of plasticity, until then, we propose that psychologists continue using the distinction for traits and species where it applies, but also take low-cost measures to improve its connections with evolutionary biology. To this end, we provide five actionable recommendations.

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Introduction

Plasticity, the ability to adapt to environmental conditions, is studied across the biological and social sciences. However, different disciplines use different concepts to study plasticity. This diversity may be justified: researchers should use those concepts that are most productive for their particular subject matter. However, if researchers working on the same topic speak different languages, they are less likely to benefit from each other's theories and findings. This reduces scope for interdisciplinary research and hinders the integration of plasticity research across disciplines. Researchers miss out on theories that

illuminate their data and predict new observations; on methods that separate factors that are currently confounded in their studies; and on mechanisms in other species that provide insight into mechanisms in the species they study (for a shining example of recent integration, see Ref. [1^{**}]).

Here, we focus on a distinction that is widely used to study sensitive and critical periods in psychology, but rarely used in evolutionary biology: that between *expectant plasticity* and *experience-dependent plasticity* [2^{**},3,4^{*}]. Expectant systems process a specific type of information within a particular time period or life stage; a 'critical period'. However, some degree of plasticity may exist outside of this developmental window as well; in that case, the period is described as 'sensitive' rather than 'critical' [2^{**},3,4^{*}]. Dependent systems process experiences that are unique to each individual, as opposed to species-typical. Changes in these systems are thought to be gradual and reversible based on later experiences. Dependent systems do not have critical periods, even if their ability to respond to inputs may vary to some extent across ontogeny [5], as we discuss later.

In this paper, we discuss three challenges to the generality of the distinction between expectant and dependent plasticity [6^{**}]. In essence, there are types of plasticity that do not fit either category. Psychologists have not claimed that two types of plasticity apply to all species. However, they are naturally interested in integrating plasticity research across disciplines (e.g. Ref. [7]), and therefore need to be aware of these limitations.

The distinction between expectant and dependent plasticity is productive in psychology (e.g. Refs. [8–13]). It would thus be unhelpful to suggest that psychologists simply adopt the concepts used in evolutionary biology. Rather, we will propose that they take low-cost measures to improve connections with evolutionary biology. To this end, we provide five actionable recommendations. By strengthening ties between disciplines, these small steps could set the stage for the broader, longer-term goal of a common, generalizable taxonomy of forms of plasticity shared by all disciplines.

Two types of plasticity

Expectant systems are thought to evolve when all members of a species have a particular experience (e.g. encountering a parent) at the same time in ontogeny (e.g. when leaving the egg). In such cases, natural selection may favor neural systems to 'expect' this information, implemented through specific brain circuits showing

heightened neuroplasticity. When an organism encounters the relevant experience, major and rapid changes occur in the brain, which are difficult or impossible to reverse based on subsequent experience (Table 1). Consider filial imprinting: once a chick has imprinted on its mother, it will lose the ability to form parent-offspring attachment with other adults [14]. If the system is deprived of this input (e.g. visual animals being reared in the dark), it may lose the capacity to develop normally [15].

Dependent systems, by contrast, process a broad range of information [2,3,4]. These systems form and prune new synaptic connections in response to specific situations, and which occur over the course of individual lives, as opposed to at a specific time. Nonetheless, the degree of plasticity of dependent systems may vary across ontogeny. For instance, if a given object or event is especially common or relevant, neural systems may become specialized, or fine-tuned, for processing it (e.g. efficiently processing the features of phonemes or faces), at a cost to their ability to process other types of stimuli [16]. Such specialization processes are typically gradual and reversible based on later experiences (Table 1). Accordingly, dependent systems tend to retain the capacity to recover from deprivation.

Despite their differences, expectant and dependent plasticity may co-occur in a single system. For instance, a system may ‘expect’ linguistic communication of a certain general type to exist, but use dependent plasticity to acquire details of the particular language (e.g. learning irregular forms).

The distinction also provides a heuristic for research by suggesting that certain features of plasticity tend to go together. For instance, sensitivity to a specific input at a particular time is likely followed by major and rapid changes in the brain. Understanding such associations is key from an applied perspective. Expectant systems have windows of vulnerability and opportunity during which interventions have the most impact. For some traits in some species, researchers are able to modify the timing and duration of such windows, and to ‘reopen’ windows that had already ‘closed’, through pharmacological or

experiential manipulation. Such work has the potential to inform interventions that help to erase neural signatures of psychosocial trauma [17] and physical impairment [18].

The distinction between expectant and dependent plasticity has advanced insight into the mechanisms of plasticity [15,18,19]. One might therefore be surprised to learn this distinction is rarely used in evolutionary biology (for an exception, see Ref. [20]). This is likely because there are challenges to applying the distinction across the full tree of life. As we will see, some of these challenges are more easily resolved than others.

Organisms without neurons

Plants do not have neurons. Nor do some animals (e.g. sponges, sea urchins). However, these organisms do have systems of plasticity that produce critical and sensitive periods in development [21–24]. The distinction between expectant and dependent plasticity does not apply to these organisms, however, if we view neural mechanisms as essential features. This leads to missing opportunities for integration. For instance, the adaptive reasons for sensitive periods in brainy and brainless organisms may be similar, and there might be similarities in their functioning. For instance, plasticity may decline once organisms have acquired enough information about the current conditions [6,25,26].

Evolutionary biologists often define ‘sensitive periods’ in a way that decouples function and mechanism, as a time period or life stage in which experience shapes a trait to a larger extent than the same experience does in other developmental stages [25]. This definition does not specify physiological mechanisms, which vary between species [6,25]. It also includes sensitive and critical periods in morphological development. Such periods may involve physiological reorganization, which is not necessarily neural, triggered by specific experiences occurring at particular times (e.g. predator-induced defenses in prey species, such as growth of neck spines in *Daphnia* [27]).

In sum: critical and sensitive periods in non-neural systems may have features in common with expectant systems, but the distinction between expectant and

Table 1

The features of experience-expectant and experience-dependent plasticity, as they are typically represented in the literature. There are minor variations in the way these terms are used in different publications

	Experience-expectant plasticity	Experience-dependent plasticity
Evolution	Species-typical experience Particular type of information Time limited	Individual-specific experience Variety of information types At all points in ontogeny
Development	Heightened neuroplasticity Major, rapid changes to brain Hard to reverse	Non-heightened neuroplasticity Gradual formation of synapses Easier to reverse

dependent plasticity does not capture these systems. This issue, however, can be resolved easily: we may consider neural mechanisms a ‘nonessential feature’ that only applies when we are dealing with neural systems. In [Table 1](#), this would require two simple changes: replacing ‘neuroplasticity’ with ‘plasticity’ in row four (so it reads: ‘heightened plasticity’ and ‘non-heightened plasticity’), and replacing ‘brain’ and ‘synapses’ with ‘phenotypes’ in row five (so it reads: ‘major, rapid changes to phenotypes’ and ‘gradual formation of phenotypes’).

Multiple sensitive periods with flexible timing

The next time you peek into an aquarium, you are likely to see goby fish. These fish have small-to-medium sized ray fins, large heads, and tapered bodies. In nature, goby fish live in freshwater, brackish, and marine environments, where they display amazing abilities. Specifically, they are able to change sex. Goby fish live in groups of females (harem) with a single dominant male. If this male is lost from the group (e.g. dies, gets badly injured), one of the adult females (usually the largest) changes her sex to become male of the group. This sex change involves major coordinated changes across multiple biological systems, including anatomical, neuroendocrine, and behavioral axes [28]. There are other factors that can induce sex change in goby fish (e.g. reaching a critical age or size), and also other animals capable of changing sex (e.g. amphibians [29]). Sex reversals have some features that we think of as ‘experience-expectant’, but other features that do not fit this category, and which fit better with ‘experience-dependent’.

First, in contrast to expectant plasticity, sex change may occur at nearly all points in development [28,30]. It is induced by a specific event rather than a given ontogenetic stage. The loss of a dominant male may occur at any time (e.g. due to predation or infection). Therefore, the system has evolved to ‘expect’ the loss of a dominant male, responding to this specific cue with a major phenotypic reorganization, but the developmental timing of this response is flexible. This raises the question whether other animals — which experience fitness-relevant changes to their contexts at unpredictable intervals that can reliably be detected — are also able to have multiple sensitive periods with flexible timing.

Second, in contrast to expectant plasticity, individuals may change their sex multiple times during their lifetimes [31,32]. Such bidirectional sex change shows the effects of a sex change may not be lasting. Todd *et al.* [28] note: “Sexual fate is no longer seen as an irreversible deterministic switch set during early embryonic development but as an ongoing battle for primacy between male and female developmental trajectories. That sexual fate is not final and must be actively maintained via continuous suppression of the opposing sexual network creates the potential for flexibility into adulthood” (p. 223). Some other features

of sex change, however, do fit expectant plasticity. For instance, sex change is triggered by a specific cue (e.g. changes in social structure, and in some species, reaching a critical age or size), rather than extensive exposures, and involves a major reorganization of the phenotype.

In sum: sex reversal has some properties of expectant plasticity (e.g. a specific cue triggers a major reorganization of the phenotype), and others of dependent plasticity (e.g. reversals can occur at nearly all points in development and multiple times over the life course in sequentially hermaphroditic fish). Other properties do not fit either type of plasticity. For instance, in the absence of the cue, loss of a dominant male, the system develops into a female, rather than breaking down (as an expectant system might), or becoming recruited by other inputs (as a dependent system might). We think these challenges are difficult to resolve. This would require dropping or modifying several essential properties of expectant systems (in [Table 1](#), rows three and six).

Variation in experience across individuals and populations

Expectant plasticity is thought to result from experience shared by all members of a species ([Table 1](#)). However, different populations of the same species often vary in their levels of plasticity. Consider soapberry bugs. Males from Oklahoma are able to adjust their level of mate guarding adaptively based on the sex ratio they experienced earlier in their lives [33]. If there are many females, they guard their mates less; it is easier to find a new mate and their mate is unlikely to find a new male. Males from Florida, by contrast, are not able to adjust their level of mate guarding. They have not evolved to ‘expect’ variation in the local sex ratio. Over evolutionary time, the Oklahoma population has been exposed to rapid fluctuations in the local sex ratio (due to thunderstorms, which are more likely to kill females), but the Florida population has not. As there is barely gene flow between these populations, their differences in plasticity remain stable over time [34].

Thus, expectant plasticity does not need to be shared by all, or even by most, members of a species. This challenge is easily resolved by viewing expectant plasticity as a feature of populations (i.e. a number of organisms of the same species who live in the same geographical range and are capable of interbreeding), rather than species. In [Table 1](#), this requires a minor change: changing the left column of row one from ‘species-typical experience’ to ‘population-typical experience’.

Even within a single population, not all individuals need to be exposed to a given experience for expectant plasticity to evolve. It is sufficient for a proportion of the population to have the experience in each generation [35,36]. For instance, some individuals may never be exposed to a predator. However, because the costs of

getting killed are high, the entire population might evolve to ‘expect’ predators. This issue blurs the distinction species-typical (or population-typical) experiences and individual-specific experience. It can be resolved either by dropping the first row from [Table 1](#), or by revising it to stating that plasticity is expectant if all individuals in a population are able to developmentally adapt to (rather than have) the relevant experience. This solution is imperfect, too, because in some conditions natural selection might favor populations in which some individuals are plastic, in an expectant way, and others not. On the positive side, this challenge illustrates scope for synergy: theories from evolutionary biology may shed light on individual differences in plasticity within human populations (Ref. [37*]; for a formal model, see Ref. [38]; for statistical challenges to documenting ‘differential susceptibility’, see Ref. [39]).

Conclusion

We have argued that the distinction between expectant and dependent plasticity does not apply across the full tree of life. We have shown that there are many organisms that show only some of the properties of expectant plasticity, but not other features; or which have a mixture of the two types of plasticity; or, which fit neither type. The distinction is a useful heuristic for traits in species where it applies, but is limited in scope. This is not, however, how it is usually depicted in the literature.

So how do we proceed? Although we hope that one day all disciplines will share a common, generalizable taxonomy of forms of plasticity, until then, we propose that psychologists keep using the distinction when it fits a particular trait (e.g. filial or sexual imprinting) in a particular species (e.g. humans, rodents). However, in cases where it does not fit well, such as when considering hypotheses that might apply across the full tree of life, researchers could use constructs from evolutionary biology. For instance, they could define a ‘sensitive period’ as a window in which experience shapes a trait to a larger extent than the same experience does in other windows [25]. By decoupling function and mechanism, such a broad definition fosters the discovery of general principles in plasticity; for instance, based on the benefits and costs of being more or less plastic at different life stages, as a function of environmental conditions [40–42].

Using a broader definition of sensitive periods, however, will not be enough to ensure that research by psychologists is disseminated into evolutionary biology. To this end, we list five actionable recommendations. This list is not exhaustive, but it provides a start. Psychologists could:

- Include a section in their papers that uses broader terminology (e.g. phenotypic plasticity), and which highlights links to other organisms and other disciplines;

- Invite evolutionary biologists to present at psychology conferences (e.g. a keynote on sensitive and critical periods by a researcher studying non-human animals rarely represented at psychology conferences, such as insects or fish);
- Present their research at meetings attended by evolutionary biologists, as they are just as interested in humans as they are in other animals;
- Write a review paper for an interdisciplinary journal read by both communities (e.g. *Proceedings of the Royal Society B, Evolution and Human Behavior*);
- Tag organizations for evolutionary biologists when disseminating research on social media (e.g. on Twitter: @EES_update, @BehavEcolPapers, @EvolHumBehav).

Of course, it would be possible to compile a similar list for evolutionary biologists, which could help dissemination and understanding of ideas and findings from that field into psychology. In the future, we should strive for infrastructure that bridges not only psychology and evolutionary biology, but which also connects these fields to the other sciences, advancing consilience, i.e. the integration of all sciences. Our paper offers a small step in this direction.

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