
12 The Special Case of Behavioral Plasticity?

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CONTENTS

12.1 Introduction	301
12.2 Is Behavior More Plastic Than Other Traits?	302
12.3 Diversity of Behavioral Mechanisms across Life	305
12.3.1 Organism-Level Coordination of Response to Stimulus	305
12.3.2 Origin of Nervous Systems: Implications for Behavioral Plasticity ...	307
12.3.3 Storage of Information for Later Use: Learning and Memory	309
12.3.3.1 Evidence for Memory Mechanisms across Taxa	309
12.3.3.2 Evidence for Learning Mechanisms across Taxa	311
12.4 Behavior and Evolutionary Dynamics: A Systems Approach	312
12.5 Concluding Remarks	318
References	319

12.1 INTRODUCTION

Is behavior special? This question has often had a dual meaning in evolutionary biology. Not only does it ask whether behavioral expression is different from other traits, but it also asks whether behavior plays a distinct role in the process of evolution. These two sub-questions are related because it is from the unique expression of behavior that its outsized role in evolution is supposed to derive.

Historically, there have been several ideas about why behavioral traits might differ from other aspects of the phenotype in influencing evolutionary change (see Bateson 1988; Wcislo 1989 for reviews). One general argument is that behavior, because it is more plastic than other traits, should be at the forefront of responses to environmental change (Baldwin 1896; West-Eberhard 2003). This idea emphasizes the ‘flexibility’ of behavioral responses (see Box 12.1 for distinctions between types of ‘plasticity’) and suggests that this unique aspect of behavior enables organisms to respond quickly when encountering a novel environment, survive in difficult circumstances, and essentially buy time for evolutionary changes in other traits (see Diamond and Martin 2021; Levis and Pfennig 2021; Pfennig 2021 in this volume). A second argument is that particular types of behavior play a unique role in evolution. These include habitat choice because it determines the selective environment

(Waddington 1959; Bateson 1988; Huey et al. 2003), learned behaviors that allow swift and adaptive responses to environmental change (Plotkin 1988a; Dukas 2013), and social behaviors that generate their own unique evolutionary dynamics (West-Eberhard 1983; Dunbar 1988; Davison and Michod 2021). In turn, these different perspectives have led to a debate about whether behavior primarily drives or inhibits evolution (Huey et al. 2003; Sol et al. 2005; Duckworth 2009; Munoz and Losos 2018; see also Pfennig 2021). In this chapter, we suggest that the perpetual search for “the role of behavior in evolution,” reflects a general dissatisfaction with a static view of evolution (see Box 12.1)—a view on which we elaborate below. We argue that past perspectives on the role of behavior in evolution—whether viewing behavior as a driving or inhibiting force in evolution—can be reconciled through a systems approach in which the interactions of organisms and feedbacks between behavior, development, and natural selection are key to understanding mechanisms of evolution.

Before we elaborate on this perspective, we first discuss two major assumptions that have been implicit to this debate and have, to a large extent, hampered progress. The first assumption is that behavior is generally more plastic than other traits (West-Eberhard 2003). We argue that the range of plasticity and flexibility of behavioral traits cannot be generally described as more or less plastic than any other physiological or morphological trait. We suggest that this assumption has persisted because much of evolutionary theory has focused on the static expression of structural traits even though, across taxa, dynamic trait expression is the norm (Nijhout 2003; Sultan 2021). The second assumption is that any unique role of behavior in evolution can apply only to animals, and perhaps is even limited more stringently to animals with higher cognitive abilities (Plotkin 1988a). If this assumption were true, it would make the role of behavior in evolution relevant to only a small subset of the diversity of life on earth. To assess this assumption, we provide an overview of behavioral mechanisms across life, from protists and fungi to plants and animals, showing that there are ubiquitous principles of behavioral response across disparate taxa despite a diversity of mechanisms underlying these responses. Finally, after establishing that these assumptions are unwarranted, we suggest that the persistent fascination with the role of behavior in evolution reflects a need to integrate static and dynamic perspectives (Box 12.1) to better understand evolutionary dynamics.

12.2 IS BEHAVIOR MORE PLASTIC THAN OTHER TRAITS?

When biologists use the term ‘behavior’ it often evokes images of complex cognitive feats in animals, but it is really a more general term used across scientific disciplines to describe the movement and action (or inaction) of matter. Scientists apply this term to many different systems ranging from the movement of molecules across a concentration gradient to wave action on a sandy shore to a pair of breeding birds feeding their nestlings.

In organismal biology and evolution, the same general principle applies—behavior refers to movement or action—but, at this scale, it also refers to what an organism does. Behavioral traits are generally considered inherently flexible and reversible in expression, differing from physiological traits in that they are expressed at the level

BOX 12.1 GLOSSARY OF TERMS

- **Behavior:** *Across scientific disciplines:* the action of matter. *In evolution and ecology:* action (or inaction) that operates at a whole-organism level and so is visible to an external observer. This latter requirement is what differentiates behavior from physiology as well as thinking, the latter two being dynamic processes that occur at a lower scale.
- **Behavioral Flexibility:** A type of behavioral plasticity that occurs within an individual and is typically reversible. It differs from developmental plasticity in that behavioral changes occur post-maturity.
- **Developmental Plasticity:** A type of plasticity that occurs when the same genotype is capable of producing phenotypic variation as a result of variation in the environment during ontogeny. Developmental plasticity differs from phenotypic flexibility in that it is not reversible and refers to phenotypes that become fixed after maturity is reached.
- **Learning:** Acquisition of information about the environment through experience or observation, often resulting in modification of behavior.
- **Memory:** The storage of information about past events that can be accessed in the future to affect a behavioral response. Can be short-term and unstable or long-term and stable.
- **Niche Construction:** Modification of the environment by an organism. Can be active or passive.
- **Personality:** Consistent differences among individuals in behavior across time and/or contexts. Often measured as repeatability: an assessment of the relative among- and within-individual variance in a behavior. A low within-individual variance coupled with high among-individual variance means a behavior is highly repeatable.
- **Robustness:** The ability to maintain a steady phenotypic state in the face of environmental or genetic variation.
- **Static versus Dynamic Perspectives of Evolution:** Static perspective focuses on delineating patterns of variation in traits, fitness, and genomes and uses approaches such as measurement of selection, statistical partitioning of trait variation, and comparative studies. Dynamic perspective focuses on the underlying mechanisms that lead to these patterns and investigates the physiological, genetic, and behavioral bases of differences in reproductive success, how specific genes and environmental conditions interact to produce variation in traits, and the ecological interactions that underlie patterns of diversification and evolutionary change. The two approaches are complementary and one approach is incomplete without the other.
- **Systems Approach to Evolution:** A holistic approach to studying evolutionary dynamics. Views organisms and environments as complex systems and emphasizes feedbacks, nonlinear dynamics, and networks of interactions across scales.

of the whole organism. Their dynamic expression has contributed to the reputation of behavior for being highly plastic; however, while all behaviors are reversible in expression, many are also often stable in their level of expression across time and contexts (Sih et al. 2004; Duckworth 2009, 2015). Certain ‘personality’ traits, such as aggression, show particularly high repeatability (Bell et al. 2009; Duckworth 2014). Yet, even these relatively stable behavioral traits can be plastic, as their expression is often also influenced by environmental variation in adulthood or during development (Komers 1997; Stamps 2016). Therefore, behavioral plasticity encompasses a broad range of different types of behavior and timescales of expression from rapid actions to personality traits, and from the change in the level of expression of a behavior during an individual’s life (known as behavioral flexibility) to maternally induced fixed behavioral phenotypes (Bonduriansky 2021 in this volume) that are determined early in ontogeny (known as ‘developmental plasticity’; see Box 12.1).

Many morphological traits also span the range from stable to flexible and can even change on timescales similar to behavioral traits (Piersma and Van Gils 2011; see also Pfennig 2021 in this volume). Examples include the rapid increases in the gut size of snakes within minutes of feeding (Starck and Beese 2002), skin pigmentation changes within hours of sun exposure in mammals (Gilchrest et al. 1996), and muscle size changes within days to weeks in response to changes in use (see Piersma and Van Gils 2011 for review). Diverse multicellular organisms from plants and fungi, to cartilaginous fish, annelid worms, and echinoderms show indeterminate or flexible growth throughout life (Sebens 1987; Aizen et al. 2019). Moreover, all traits, even relatively stable skeletal traits, are dynamic during development and, during this time, are often more sensitive to environmental variation. Flexible responses to environmental variation are the default state for traits as the biochemical reactions and interactions that occur at the cellular level are affected by changes in temperature, pH, ion, and nutrient balance (Nijhout 2003). Thus, insensitivity of traits to environmental variation is a derived evolutionary state, as are adaptive plastic responses that are triggered by aspects of environmental variation that induce specific and directed phenotypic changes.

These observations emphasize that, even though it is often easier to focus on ‘static’ measures of traits (e.g., mean expression), all traits are ‘dynamic’ in their expression during ontogeny and many remain flexible in adulthood. However, because behavioral traits are ephemeral in their expression, they are more difficult to measure compared to traits that are relatively unchanging in adulthood, like structural size. This is undoubtedly the reason that such structural size traits (e.g., in determinate growers) are the focus of many evolutionary models even though across life they represent a minority of traits (Sebens 1987; Aizen et al. 2019). Heightened awareness of this issue has led to the development of new methodologies to measure and analyze dynamic traits in evolutionary and quantitative genetic frameworks (Wu and Lin 2006; Gomulkiewicz et al. 2018). The historical emphasis on static traits likely led to assumptions that behavior is more plastic than other traits even though, in reality, dynamic morphologies that are flexible in expression are relatively common. Thus, making broad statements about differences in plasticity between behavioral and morphological traits is misleading and unproductive. This doesn’t mean that there are no differences in plasticity between specific traits, but these types of comparisons always have to be made on a trait by trait basis and cannot apply to a class of traits as a whole.

A final point is that, even though the expression of behavior is ephemeral at the whole-organism level, variation in its expression is underlain by physical components of the neuroendocrine system. Thus, behavioral traits are subject to the same sorts of constraints as any other morphological trait (Duckworth 2018; Duckworth et al. 2018). This is why we observe a range of flexibility in behavioral traits from imprinted preferences to open-ended ‘learning’ to relatively stable personality variation. All traits fall along a spectrum of flexible to stable in adulthood and it is often flexibility at one level that enables stable expression at a higher level. For example, organismal homeostasis emerges due to a myriad of physiological interactions and responses that constantly monitor and react to changing environmental conditions (Nijhout and Reed 2014). In turn, some stable structures are necessary to maintain organismal integration and to enable flexibility at a higher level. After all, it is the relatively stable structure of the skeletal system in vertebrates that enables an animal to walk, run, and do other flexible activities. Thus, organismal phenotypes are necessarily a mosaic of flexible and stable components and it is the integration of these components across levels that enables functioning organisms. Most importantly, because all traits span the range of flexibility, it is not fruitful to make assumptions about the plasticity of a group of organisms or an entire class of traits; the extent of plasticity and flexibility can only be assessed and compared on a trait by trait basis.

12.3 DIVERSITY OF BEHAVIORAL MECHANISMS ACROSS LIFE

Past discussions of the causal role of behavior in evolution have generally focused on animals (Wcislo 1989; Huey et al. 2003; Losos et al. 2004) and in some cases, even more stringently on animals with higher cognitive abilities (Sol et al. 2005). But, at the same time, some authors have presented a broader case for the role of behavior in evolution analogizing various types of behavioral responses in animals to responses observed in plants (West-Eberhard 1983; Huey et al. 2002). In the introduction to his edited volume, *The Role of Behavior in Evolution*, Plotkin (1988a, p. 9) points out the tension between these views:

...whether behavior that is a consequence of a choosing intelligence has a role in evolution that is different from the role of behavior that is not a consequence of a choosing intelligence is a question that is left open in this book.

By ‘choosing intelligence’ Plotkin is differentiating between organisms that show higher-level cognitive behavior and organisms that only show stimulus-response type behavior. In the next section, we explicitly pick up where Plotkin’s book left off to address the ways that behavioral mechanisms are similar and different across different taxa before turning to the implications of these similarities and differences for understanding behavior’s role in evolution.

12.3.1 ORGANISM-LEVEL COORDINATION OF RESPONSE TO STIMULUS

To mount an appropriate behavioral response to a constantly changing environment, all organisms need an effective system of internal communication. While the specific

mechanisms differ among taxa, all involve similar functional components: a sensor, a system of internal communication and integration, and an external response at the whole-organism level. These response systems can be complex even in groups which are not typically considered consciously aware. For example, like animals, plants use an array of sensory systems to distinguish between up and down, between self and non-self; to sense light, heat, moisture, and nutrient content; and to either detect objects impassible to growing roots or vibrations from potential predators (Svistonoff et al. 2007; Bisseling and Scheres 2014; Lopez et al. 2014; Mescher and Moraes 2015; Assmann and Jegla 2016). They use these sensory systems to coordinate behavioral responses by directing movement and growth as well as upregulating defense mechanisms across the entire plant (Silvertown and Gordon 1989).

Chemical signals coordinate responses to stimuli either across cells, for multicellular organisms, or within cells but between different cellular structures, for unicellular organisms. The structures of many of these molecules are highly evolutionarily conserved, although they show a diversity of functions across clades. For instance, many hormones that are used as neurotransmitters in animals, such as glutamate (Forde and Lea 2007), dopamine (Guidotti et al. 2013), acetylcholine (Bamel et al. 2016), and GABA (Michaeli and Fromm 2015), are expressed across the diversity of life, from bacteria and fungi to plants (Kawashima et al. 2007). Thus, many of the chemical signals that we associate with eliciting behavioral responses in animals are ubiquitous and evolutionarily conserved across taxa.

For single-celled organisms, the line between physiology and organismal behavior becomes blurred, as the individual cell is also the entire organism. Despite this, behavioral responses in single-celled organisms involve the same basic components as in multicellular organisms: integration and transmission of information gathered by sensory receptors into directed movement using a motor structure. This type of system is so important it has evolved independently across multiple disparate groups, with flagella evolving in Prokaryotes, cilia in Eukaryotes, and archaella in Archaea (Albers and Jarrell 2018). The two-component signaling system in bacteria illustrates the basic principle of how these systems work. Upon detecting a stimulus, transmembrane receptors coupled with histidine-kinase proteins become methylated, which drives phosphorylation of response regulator proteins. These altered proteins then initiate the transcription of specific genes, whose products subsequently enable the components of the behavioral response for as long as the phosphorylation persists (Armitage 1992; Hazelbauer et al. 2008). This and other similar systems are responsible for variable taxis responses to light, chemical gradients, nutrient availability, and even voltage (Schweinitzer and Josenhans 2010).

Although organisms outside of Animalia lack neurons, the ability to coordinate components of behavioral responses is ubiquitous across life. This can mean chemical signaling as shown above, but interestingly also includes electrical signaling. Bioelectricity is used in many essential metabolic cellular processes (Cohen and Venkatachalam 2014) and the first action potentials and sodium and calcium ion channels likely began in Eukaryotes with the evolution of cilia (Brunet and Arendt 2016). Moreover, electrical potentials generated by a plant can propagate across its entire structure to transmit information and regulate responses (Fromm and Lautner

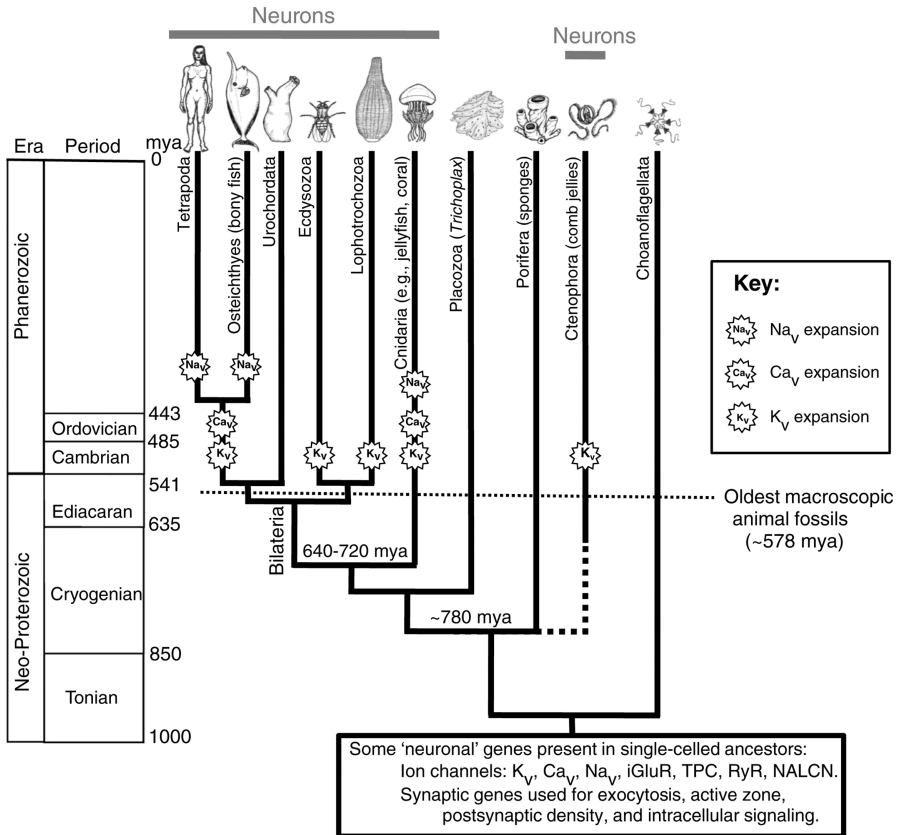
2006; Volkov et al. 2010). Similar to neural axons, long-distance electrical signaling is facilitated by phloem cells that preserve signal strength. It is thought that information about the specific stimulus type might even be encoded through variation in the shape, magnitude, method, and frequency of different types of electrical potentials (Canales et al. 2017). Similarly, fungi also have slow-wave electrical potentials within the hyphae and fruiting bodies (Adamatsky 2018) which change in frequency in nuanced ways in response to stimuli received by diverse sensory receptors (Xu et al. 2017). This enables the fungi to perceive changes in nutritional availability or detect dangers such as predation or fire (Olsson and Hansson 1995). Thus, the ability to transmit an electrical signal in response to a stimulus to direct a behavioral response is widespread across life even in the absence of neurons. These similarities in information acquisition across diverse taxa raise the question: What are the unique aspects of behavioral plasticity in animals?

12.3.2 ORIGIN OF NERVOUS SYSTEMS: IMPLICATIONS FOR BEHAVIORAL PLASTICITY

Beyond basic stimulus-response systems, there are multiple transitions in the complexity of mechanisms that enable higher-level behavioral responses, with the most obvious being the evolution of neurons and the nervous system in animals. Neurons emerged early in the evolution of animals with only poripherans (sponges), and placozoans (simple free-living multicellular organisms) lacking a nervous system (Figure 12.1). The earliest neural network was likely a nerve net much like that present today in cnidarians (jellyfish, corals, and sea anemones) and ctenophorans (comb jellies) (Arendt et al. 2016).

Much is still unknown about the origins of both neurons and neural organization largely because there is debate on whether ctenophores diverged before (Ryan and Chiodin 2015) or after (Moroz et al. 2014; Kristan 2016) poripherans and placozoans (Figure 12.1). Depending on where Ctenophora is placed on the evolutionary tree, it is possible that neurons either arose once and were lost in some groups or arose multiple times. Disentangling these possibilities would provide insight into the factors that lead to the evolution of neurons as the method of intercellular communication and coordination, as opposed to other mechanisms in non-neural animals, such as calcium signaling in sponges (Leys 2015) or small intercellular peptides in placozoans (Varoqueaux et al. 2018).

One of the unique contributions of the neural system to behavior is the dimensionality and complexity of behavioral response that such a system can support, but these attributes are not necessarily important in explaining its origin. Instead, it seems likely that neurons evolved primarily to coordinate motor responses across an increasingly complex organism (Bucher and Anderson 2015). Groups that do not possess a neural system either are mobile but small and simple in body form (e.g., Placozoa, Protozoa, and Archaea), or are sessile (sponges, plants, and fungi). In animals, the taxa which lack neurons also lack striated muscles (Steinmetz et al. 2012; Moroz et al. 2014). This suggests that neurons are necessary to coordinate complicated movement involving many separate muscles (Kaijzer 2015). Other organisms



Current Biology

FIGURE 12.1 Phylogeny of Animalia showing approximate timing of major transitions in the evolution of neurons. Black circles with serrated edges indicate the hypothesized order of appearance of various types of voltage-gated channels. Cells with a combination of Ca_v and K_v channels could generate action potentials, which expanded intercellular communication capabilities. The addition of Na_v channels increased the speed of transmission making rapid movements possible. (Reprinted with permission from Kristan, W. B. 2016. Early evolution of neurons. *Curr. Biol.* 26:949–954.)

are capable of sophisticated movement without a nervous system, but still arguably not in the range available to neural animals.

While there is clearly an association with motor capabilities across this broad scale, once neurons evolve, if movement is lost, this does not necessarily lead to a corresponding loss of the nervous system. For instance, the adult forms of tunicates do not lose their nervous system despite metamorphosis to a sessile state. Although sections devoted to motor processes are lost, the cerebral ganglion and neural gland remain and, in fact, the adult tunicate has a larger ganglion than the mobile juvenile (Mackie and Burighel 2005). Evolutionary losses of the nervous system may be rare

or impossible because, once evolved, it becomes an essential regulator of so many fundamental bodily systems. These observations suggest that the nervous system evolved initially to coordinate complex motor behavior, but subsequently was co-opted for many more functions. Most importantly, evolution of a nervous system is often thought to underlie the extraordinary capacity of animals for ‘memory’ and learning, topics which we explore in the next sections.

12.3.3 STORAGE OF INFORMATION FOR LATER USE: LEARNING AND MEMORY

The ubiquity and repeated evolution of various signaling systems across the tree of life highlight the importance of being able to mount an appropriate and coordinated response to the environment for all organisms. These signaling systems can affect a transient and reversible change in behavior, or they can catalyze longer-lasting changes. Also shared across life is the ability to consolidate information about the environment, store this information stably over long periods of time, and retrieve it later to carry out a behavioral response that differs from the original behavioral response. Storage and recall of information, and the ability to modify behavior as a result of this information, are the fundamental components of learning and memory. Although learning and memory are not necessarily behaviors themselves, they have persistent effects on behavioral flexibility as they enable organisms to reversibly modify their behavior in response to changing environmental conditions.

12.3.3.1 Evidence of Memory Mechanisms across Taxa

There are different types of memory storage and information processing across animals, some of which are analogous to information processing of non-neural organisms and some of which are much more sophisticated and complex. Information gathered by the nervous system can be used temporarily and then discarded, or consolidated into a stable form that can be drawn from repeatedly to guide adaptive behavior (Atkinson and Shrifin 1968). The most transient form of memory is sensory memory, which consists of what is currently being seen or heard and is gathered by sensory systems and then discarded within seconds (Tripathy and Ögmen 2018). The sheer quantity of sensory information is such that much of it is filtered and actively disregarded before it reaches conscious awareness (Cromwell et al. 2008). This type of transient information storage shares many parallels with mechanisms of information storage in non-neural taxa. For example, bacteria often use a nanobrain organelle that is composed of an interconnected network of the signaling and response regulator proteins, which serve as a temporary ‘memory’ of immediate past encounters of molecule concentrations to compare to current sensory protein inputs. These clusters of sensory receptors can result in surprisingly sophisticated behavioral responses such as changing flagella patterns in response to multiple simultaneously changing environmental conditions (Hazelbauer et al. 2008). Because of this, they have been compared to our own neural networks (Lyon 2015).

In animals, new experiences that are kept longer than sensory memories are stored as short-term memory, which can be recalled over brief periods of time. While most short-term memories are quickly forgotten, some of this new information transitions to long-term memories which are stable and can last a lifetime. Even though

single-celled organisms are not able to take advantage of the specialized interconnected cells devoted to the task of information storage that neural organisms have, they are able to store information over long time periods through other mechanisms. For example, one of the most well-known examples of such information storage is the epigenetic modification of DNA employed by bacteria as a memory of past infections: CRISPR (i.e., Clusters of Regularly Interspaced Short Palindromic Repeats). Fragments of DNA from viruses are placed between these repeats and used like an immune response to provide a memory of past infections enabling bacteria to defend against future encounters with the same virus (Barrangou et al. 2007). Despite lacking multiple cells, by using modifications to their own DNA and proteins, bacteria are able to store useful information for long periods of time and, in essence, remember natural enemies in a way that modifies their behavior toward them in subsequent encounters.

While the presence of a central nervous system can allow for the storage of more complex and information-rich memories, the CRISPR example suggests that all organisms have the basic components of long-term information storage on some level. Indeed, cellular differentiation during development involves changes in epigenetic regulatory mechanisms, which encode cellular fates and which are stably stored over time. Epigenetic mechanisms are also involved in neural memory formation (Levenson and Sweatt 2005; Heyward and Sweatt 2015; Kim and Kaang 2017). The question remains whether these types of mechanisms are used similarly across life for storage of information about past environmental experiences to influence future behavior (Thellier and Luttge 2013).

One major difference between neural and non-neural multicellular organisms (e.g., plants) is that, in the latter, there is no known central location or dedicated cell type where information is stored. Instead, in non-neural organisms, information seems likely to be recorded at a more general level in cells throughout the organism. However, one intriguing proposal, first mentioned by Darwin in *The Power of Movement in Plants*, is that actively dividing meristems and root tips might be important specific locations for information storage and retrieval, as they are places where the direction of growth is determined. Darwin (1872, p. 338) presaged current research in this area when he wrote:

It is hardly an exaggeration to say that the tip of the radicle thus endowed, and having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals; the brain being seated within the anterior end of the body, receiving impressions from the sense-organs, and directing the several movements.

Since Darwin, a number of studies have investigated the ability of plants to exhibit the capacity for learning and memory. However, research into mechanisms of learning and memory in plants has been sporadic due, in part, to a series of pseudoscientific books published in the 1970s claiming plants possessed psychic abilities (discussed in Mescher and Moraes 2015). Since then, the field has been divided between groups claiming intelligence and consciousness in plants, and those who believe that plants are incapable of any type of behavior or memory (Struik et al. 2008). The extreme views on both sides of this debate have severely stunted research in this field and empirical studies demonstrating plant mechanisms of learning and memory are few.

Despite these difficulties, evidence for a form of memory has been shown in *Bidens pilosus*, where pricking a leaf of a young plant results in directed growth of new buds days to weeks later (Thellier et al. 1982). This ability to store information has been replicated in other species of plants, has been reported to last for several weeks, and is initially sensitive to being ‘overwritten’ by subsequent events (Verdus et al. 2002). Like mechanisms of information storage in other groups, stored information in plants is likely facilitated through epigenetic modification of genes (Cazzonelli et al. 2014) or sustained changes in levels of signaling metabolites and transcription factors; however, the specific mechanisms and their prevalence are still unresolved (Crisp et al. 2016).

12.3.3.2 Evidence for Learning Mechanisms across Taxa

Learning can be a strong instigator of behavioral changes because it enables organisms to assess and respond to changes in the quality of an environmental stimulus. At the most basic level, it requires preservation of some information about the past state of that stimulus so a comparison can be made. Organisms then assess whether a change in stimulus is positive or negative and modify behavior accordingly. Habituation and sensitization are simple forms of learning that involve changes in the magnitude of a behavioral response due to repeated exposure to a stimulus. A stimulus that is consistently neutral can result in habituation and lack of response, whereas a stimulus that is consistently positive or negative can result in sensitization and an increased response magnitude. Sensitization and habituation seem to be a common form of learned behavior even in simple organisms. For example, despite lacking neurons, the slime mold (*Physarum polycephalum*) can become habituated to a mild adverse stimulus (caffeine) when presented with the stimulus successively over time (Boisseau et al. 2016).

One potential example of habituation can also be found in the sensitive plant (*Mimosa pudica*) which is known for folding in its leaves rapidly when triggered by vibrations or contact, an energetically expensive defense mechanism against herbivory. Repeatedly dropping the plant or otherwise triggering this response leads to habituation such that further similar stimulation no longer results in any response at all (Gagliano et al. 2014). This habituation persists even after a month, and so is independent of fatigue. Moreover, it is environmentally contingent as plants located in full sun and with access to more energy continue to exhibit the behavior despite repeated dropping, whereas shaded plants become habituated more easily (ibid).

Habituation and sensitization are types of learning in response to a stimulus currently present. Associative learning is another, more complex type that enables proactive responses in that an organism uses information about past environmental contexts and associated stimuli to change behavior in a way that maximizes benefit in a predicted future context and time. This ability is present in animals but is less well studied in other organisms because it was long thought to require a central nervous system. However, slime molds, once again, provide an example. When exposed to unfavorable conditions generated at a constant interval, they slowed down movement shortly before the next unfavorable period began, even when the unfavorable conditions were suddenly stopped (Saigusa et al. 2008). This response indicated that

slime molds not only have a mechanism to track the passage of time, but they also possess a mechanism for storage and retrieval of information of past events that influences behavior independently of present stimulus cues. So far there is only one study showing associative learning in plants. In it, pea plants (*Pisum sativum*) were conditioned to associate the presence of an unrelated stimulus (a fan) in a maze task as a cue for the presence of light. In subsequent trials, the plants grew toward the fan in the absence of light, even when the fan was moved to another location (Gagliano et al. 2016). Despite the limited examples in non-neural organisms, it seems that, if there are mechanisms for conditional information storage across life (such as epigenetic information retention) associative learning should evolve. For all organisms, the ability to adjust behavior in an anticipatory fashion based on prior experiences should have strong fitness consequences. Learning enables organisms to lessen a costly response to a stimulus that is harmless and mobilize defenses more rapidly to a repeatedly experienced harmful stimulus. However, it is currently unclear whether such learning abilities in non-neural organisms are due to true rarity or simply to a dearth of studies testing for them.

In neural organisms, centralized information storage in the brain has facilitated the development of complex neural networks and a high degree of specialization in the function of specific neurons and brain regions. In contrast, non-neural organisms lack the connected organization of a centralized nervous system that enables complex information assimilation, retrieval, and its recombination in novel ways. Essentially, non-neural organisms may have rudimentary learning and memory capabilities but lack the combinatorial power that underlies thought and reasoning. Such an ability to recombine information in novel ways is the basis for behavioral innovation and problem-solving, both of which have received much attention for their proposed role in evolution. While many of the basic mechanisms that underlie coordination of behavioral response and information acquisition are ubiquitous across taxa, evidence of problem-solving and innovation are so far limited to animals with brains. Thus, if basic elements of organismal response and information recall underlie the role of behavior in evolution then this role applies to all organisms. If, however, its role is confined to only organisms with complex cognition then its importance is limited to organisms with a brain and perhaps even to higher vertebrates. In the next section, we argue that even the most basic of behavioral responses influence evolutionary dynamics; however, we propose that characterizing how different levels of behavioral complexity affect evolutionary dynamics is the core question of the field.

12.4 BEHAVIOR AND EVOLUTIONARY DYNAMICS: A SYSTEMS APPROACH

Over the last century, there have been many proponents of the idea that behavior plays a special role in evolution (e.g., Wyles et al. 1983; Huey et al. 2003; Duckworth 2006; Munoz and Losos 2018), but there has not been agreement on the scope of this role. Discussions of behavior's role in evolution have ranged from a general intuition of its widespread importance to an emphasis on behavioral capacities that are largely taxa-specific. Researchers from Baldwin (1896) to Mayr (1963) have proposed behavior as

a causal mechanism in evolution. In general, their views reflect the idea that behavior is a ‘pacemaker’ of evolution because it is at the forefront of an organism’s interaction with its environment and so, in large part, will determine the selective pressures an organism experiences (e.g., Duckworth 2006).

Waddington (1959), in particular, proposed that evolutionary processes were causally affected by four coequal and mutually influencing systems: the genetic system, the natural selective system, the epigenetic system, and the exploitative system (Figure 12.2). The exploitative system refers to the ability of an organism to choose and modify its habitat. Waddington (1959) stated that:

... [evolution] has often been envisaged as consisting of no more than a set of genotypes which are influenced, on the one hand, by a completely independent and random process of mutation and, on the other hand, by processes of natural selection which are again in no way determined by the nature of the genotypes submitted to them. Perhaps such a simplification was justified when it was a question of establishing the relevance of Mendelian genetics to evolutionary theory, but it can only lead to an impoverishment of our ideas if we are not willing to go further...

By going further, he advocated including both the epigenetic (developmental) and exploitative (behavioral) systems on equal footing with genetic and natural selective systems. In particular, he emphasized that, because behaviors like habitat selection were simultaneously affected by natural selection (could evolve) and also affected natural selection and development (by determining the environment), evolutionary dynamics could only be understood by incorporating feedbacks between behavioral processes, development, and evolution. Thus, Waddington was one of the earliest proponents of a systems approach to evolution—an approach which emphasizes feedbacks, nonlinear dynamics, and networks of interactions across scales (see Box 12.1; Oyama 1985; Nijhout et al. 2017; Badyaev 2019; Frank 2019).

These feedbacks largely come from the ability of organisms to choose and modify their environments because the traits involved are both determining (within-generation) and determined by (across generations) the selective environment. Such reciprocal feedbacks are not limited to animals with brains and there are many examples of ‘niche constructing behavior’ (behavior that alters the local environment, Box 12.1) among non-neural organisms (Odling-Smee et al. 2003) such as fungal auxin production which can change host plant growth patterns (Chanclud and Morel 2016), dopamine/L-dopa release which causes growth inhibition in rival plants, thus reducing competition (Soares et al. 2014), and bacteria that become social during stressful or low nutrient conditions (Swiecicki et al. 2014; Muñoz-Dorado et al. 2016). Plants also exhibit habitat choice through maternally influenced seed dispersal (Donohue 2003) where plants produce alternative dispersal morphs of seeds depending on the quality of the maternal environment (e.g., Larios and Venable 2015). Moreover, many plants can delay germination with consequences similar to dispersal in animals because, even though it doesn’t involve movement, the seeds are essentially seeking out a better environment. Their habitat choice in this case is simply expressed across time instead of across space (Buoro and Carlson 2014). Therefore, feedbacks between habitat modifications and natural

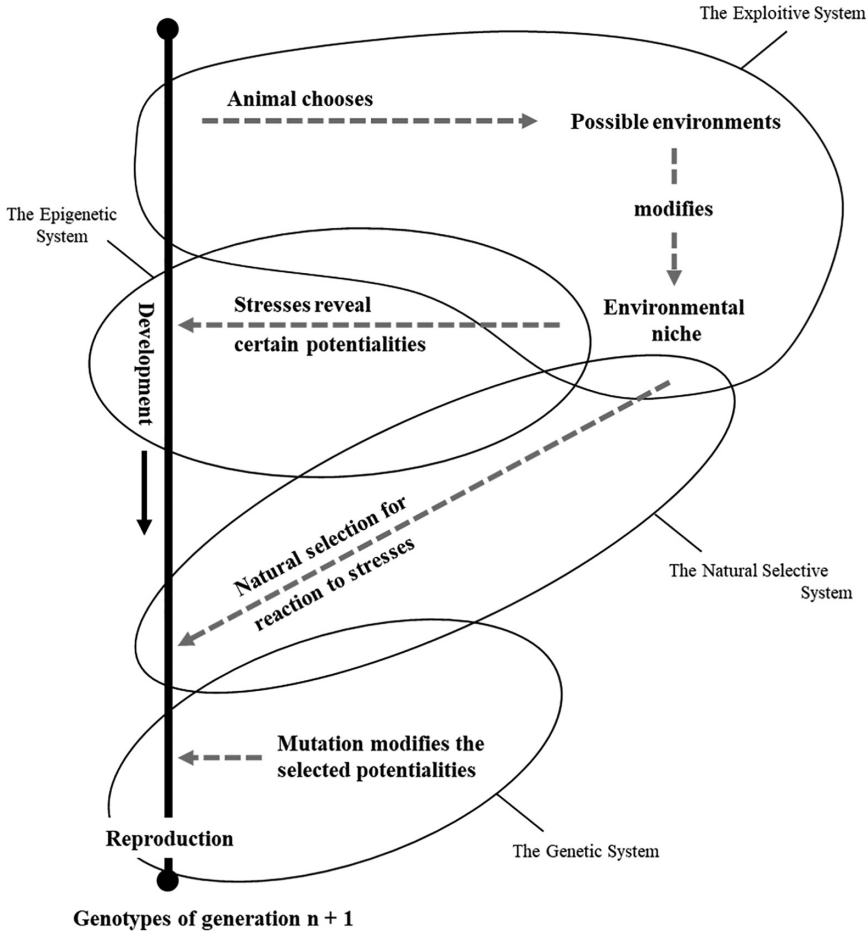


FIGURE 12.2 Waddington advocated a ‘systems’ approach to studying evolution. In his scheme, the exploitive system emphasizes habitat choice and modifications as a coequal force in evolutionary dynamics. See text for details. (Redrawn with permission from Waddington, C. H. 1959. Evolutionary adaptation. *Perspect. Biol. Med.* 2:379–401.)

selection are relevant to all organisms, irrespective of their mobility and expression of behavioral complexity.

However, concurrently with arguments for the role of habitat selection and niche construction, there has been a separate argument for the role of learning and behavioral innovation in evolution (Dukas 2013). Some of these studies have linked behavioral flexibility (often using relative brain size as a proxy) to either higher rates of diversification (Sol et al. 2005; Sayol et al. 2019) or higher rates of anatomical evolution (Wyles et al. 1983). Higher diversification rates could result either from the ability of species with relatively larger brains to survive in novel conditions and therefore avoid extinction, or could result from higher speciation rates (Sayol et al. 2019).

Because relatively larger brains enable both higher levels of behavioral innovation and are often associated with social behavior (e.g., Reader and Laland 2002), they simultaneously facilitate the development and transmission of novel behaviors that expose populations to new selective pressures, thus promoting evolutionary diversification. However, much of this work has focused on avian taxa and it possible that the association between brain size and diversification may be due to other factors, such as the link between diversification and song learning (Mason et al. 2017). If song evolution turns out to be more important than behavioral innovation in explaining the diversification in birds, then this may weaken the evidence for a unique role of learning in evolution. This is because song plays an important role in species recognition and sexual selection (Irwin 2000) similar to the role of floral evolution in flowering plants, another highly diverse clade (Givnish 2010). There is some evidence for this because, while songbirds are highly intelligent, their sister clade, the parrots are arguably even more intelligent; however, parrots are much less diverse and also do not have song-based species recognition and sexual selection. Thus, it may be that diversification in birds is more directly related to traits that are important in species recognition and sexual selection with brain size as an indirect correlate of these traits. Overall, this points to the need for more work on linking behavioral flexibility and diversification across a much broader variety of taxa, ideally, even including non-neural taxa.

Any associations between behavioral flexibility and diversification dynamics may also depend on the scale at which these processes are studied. One of the most convincing studies showing a link between relative brain size and diversification focused on the subspecies level. Sol et al. (2005) showed that Holarctic passerines with relatively larger brains had a greater number of subspecies compared to taxa with relatively smaller brains. They controlled for other geographic factors typically associated with higher diversification rates, such as range size and latitudinal variation as well as plumage dimorphism (a proxy for sexual selection; Barraclough et al. 1995). Yet, while this study provides convincing evidence of a link at the subspecies scale, there is a well-known bias against the survival of taxa that are longer-lived and have larger body sizes during mass extinction events (Hull 2015). During modern times, some of the most threatened taxonomic groups (e.g. non-human primates, elephants, several species of whales and parrots) are also the largest in their respective taxonomic groups, as well as some of the most cognitively sophisticated. These patterns likely reflect a trade-off between the cognitive benefits of having a large brain and the life history and dietary needs of supporting such an energetically expensive organ (Dunbar and Shultz 2007). Thus, increased cognitive abilities, while potentially contributing to diversification on short time scales, might pre-dispose taxa to heightened risk of extinction on longer evolutionary scales.

One area where greater behavioral complexity clearly has an important and distinct evolutionary role is cultural evolution. Cultural evolution requires some form of social learning such that individuals learn skills and behaviors from members of their group or community leading to changes in behavioral expression at the population level over time (Whiten et al. 1999). Such learning does not have to involve active communication as it can include the use of social information that is publicly

available and can even occur through heterospecific observations (Danchin et al. 2004). Because new patterns of behavioral expression are transmitted horizontally, cultural evolution can occur extremely rapidly. Thus, it can have important effects on genetic evolution, particularly because, by its very nature, it can influence an entire population of individuals at once (Wcislo 1989; West-Eberhard 2003).

While such rapid population-wide changes in behavior due to social learning can certainly influence evolutionary dynamics, they are not necessarily always a force in driving or accelerating evolutionary change. In fact, many have argued that learning and cultural evolution may just as likely *inhibit* genetic evolution by allowing animals to adapt plastically to environmental change without the need for evolutionary change in other traits (Price et al. 2003; Dukas 2013). Examples in humans abound. One particularly well-studied cultural change—the incorporation of cow’s milk in the diets of certain human populations—has clearly led to genetic evolutionary change (Beja-Pereira et al. 2003). However, there are numerous examples of cultural changes that are either neutral in terms of genetic evolution or may actually inhibit evolutionary change. An example of the former is changes in the popularity of baby names, a cultural trait that changes through drift (Hahn and Bentley 2003) and is unlikely to have any effect on genetic evolution in a population. An example of the latter are any changes in tools, dwellings, or clothing that enable humans to maintain thermal homeostasis (Flouris 2011), functionally inhibiting genetic evolution of physiology and morphology in populations that inhabit relatively extreme climates (e.g., deserts and tundra). Thus, while cultural changes clearly have great potential to influence genetic evolution, their influences are likely to be diverse with equal occurrences of inhibiting or driving genetic change.

Interestingly, debates about whether learning (specifically) and behavior (in general) primarily drives or inhibits evolutionary change also evoke elements of a systems approach to evolution. A fundamental tenet of this approach is to understand how complex systems respond to environmental change with the idea that robust systems can maintain a steady state in the face of a wide variety of environmental challenges. Proponents of behavior as an inhibitor of evolutionary change are essentially making the argument that behavioral flexibility maintains a population at a robust or steady phenotypic state. These arguments have ranged from a focus on how behavioral changes enable organisms to maintain homeostasis (Bradshaw 1972; Huey et al. 2003; Badyaev 2005) to an emphasis on the role of learning and problem solving in enabling organisms to avoid novel selection pressures (Plotkin 1988b; Wcislo 1989; Dukas 2013).

‘Robustness’, while typically studied at lower biological scales, is a ubiquitous property of biological systems (Kitano 2004; Wagner 2005; Duckworth 2019). In general, to achieve stability at a higher level of organization, the lower scale entities must be in constant action—modifying their behavior and interactions in response to environmental changes. Hence, robust systems maintain a dynamic stability with built-in flexibility that tracks and responds to internal and external changes to maintain a steady output (Nijhout and Reed 2014; Badyaev and Morrison 2018). Behavioral responses and interactions at all biological scales, from molecular interactions and physiological controls to organismal and ecosystem homeostasis, are at the forefront

of how systems maintain robustness in the face of environmental change. Thus, it is not a foregone conclusion that greater behavioral complexity will necessarily drive evolutionary changes in other traits.

The systems approach also provides a framework for understanding how robust systems might change when encountering environments outside the normal range. When a complex system experiences a disturbance that is outside its normal environmental range, it can either adapt and improve or the system may fail completely. In evolutionary terms, populations, which can be thought of as complex systems, will either evolve or go extinct. Behavior is thought to be a driving force in evolution during times of major disturbance because behavioral changes are at the forefront of enabling organisms to respond rapidly and survive (West-Eberhard 2003; Losos et al. 2004). Moreover, once a novel behavioral pattern is established, it can create a consistent organism/environment interaction that stabilizes any changes in natural selection. Thus, while behavioral flexibility can enable organisms to avoid novel selection pressures under normal conditions, it also can take the lead in driving evolutionary changes during periods of disturbance by enabling organisms to persist through responses that themselves create novel selection pressures.

Consequently, from a systems perspective, the debate about behavior's role as a driver versus inhibitor of evolutionary change is a false dichotomy. Behavioral interactions and responses create a stable system of feedbacks and interactions when populations experience environmental variation within their historical norm, but unexpected perturbations can disrupt an otherwise steady dynamic equilibrium so that a population must either evolve or go extinct. It is the behavior and interaction of organisms that either maintains the stable state or directs subsequent changes in the event of a major disruption. The most important insight here is that incorporating behavior into evolution requires a shift from a static perspective, where organisms are passive recipients of mutations and natural selection, to a focus on evolutionary dynamics, where the interaction and behavior of organisms is an important co-determiner of the selective environment. This perspective requires a greater emphasis on the feedbacks and interactions across biological scales that provide the mechanistic underpinnings of evolutionary dynamics (Duckworth 2019).

Returning to our question at the beginning of this chapter, is behavior special? The answer is both 'yes' and 'no.' Behavior *is* special in the sense that it is an essential part of understanding evolutionary mechanisms because the underlying causes of patterns cannot be understood without reference to the behavior of the entities involved. But behavior is *not* special in the sense that this truism is such a basic tenet of most scientific disciplines—from molecular biology to chemistry to physics—that it does not even need to be stated. To understand how complex systems work, molecular biologists study enzyme kinetics and flux of molecular pathways; chemists study diffusion gradients, and the behavior and dynamics of how molecules interact and transform; and physicists study the movement and interaction of all matter, from the smallest subatomic particles to the largest bodies in the universe. Investigating how the behavior and interaction of entities at one scale produces patterns at another is the main object of scientific inquiry (Levin 1992).

Behavior is special in evolution simply from its absence as a core focus in evolutionary research. A static view of evolution treats the dynamics of biological systems as only relevant for studying within-generation phenotypic change and thus separates developmental dynamics, physiology, behavior, and ecological interactions from the study of genetic variation and selection. Yet, the former are processes that unfold each generation as the building blocks of longer-term evolutionary change and are key to not only understanding but also predicting evolutionary dynamics.

The implication of shifting from a static to dynamic perspective in evolution is that studying how organisms respond to their environment and how they interact is key to gaining a full picture of the causes of both evolutionary stasis and change. But, while studying dynamics is important across scientific disciplines, the behavior of living organisms is clearly different than the behavior of inanimate matter. Furthermore, the complexity of behavioral responses is also highly variable across taxa. This brings us back to Plotkin's distinction between behavior of "a choosing intelligence" and all other behavior and whether this distinction is important for understanding behavior's role in evolution. It is likely that different levels of behavioral complexity (e.g., social behavior, types of learning, levels of problem-solving) influence evolutionary dynamics in different ways. However, rather than implying that behavior's causal role in evolution is limited to a small subset of taxa, characterizing the fundamental differences in the complexity of behavior among taxa and determining their consequences are the core problem to be investigated in the field of evolutionary dynamics.

12.5 CONCLUDING REMARKS

In this chapter, we have emphasized that behavior is what biological organisms do and applies to all life, from the movement of bacteria to the growth of plants toward a source of light, from the aggressive defense of a territorial boundary to the construction of a home to live in. These interactions of organisms and their responses to the environment are what underlie the dynamics of both evolutionary stasis and change, and we suggest that the main challenge of the future is to determine how different types of behaviors may produce both similar and distinct evolutionary dynamics.

Evolutionary biology has long endured calls for a more expansive conceptual framework, from the emergence of evo-devo in the 1980s (Arthur 2002; Gilbert 2003; Love 2003) to recent arguments for an extended evolutionary synthesis (Laland et al. 2015). Integrating static and dynamic views (Box 12.1) of evolutionary theory may resolve many of these debates. A static view focuses on detecting patterns of variation in traits and genomes using more and more sophisticated statistical tools to deconstruct sources of variance and determine correlative links between the two. A dynamic view asks what are the processes that have led to these patterns. Neither of these views is better than the other; instead they complement one another. The search for pattern is essential to highlighting the important evolutionary phenomena to be explained, and the study of the developmental, behavioral, and ecological dynamics underlying these patterns is essential to determining their mechanisms. In Box 12.2, we offer some suggestions for future research.

BOX 12.2 SUGGESTIONS FOR FUTURE RESEARCH

- Investigation of the mechanisms and repertoire of behaviors in non-neural taxa. It is clear that plants, fungi, and unicellular organisms have sophisticated systems of detecting and responding to environmental variation; however, the extent that they can store and analyze information to influence future behavioral responses is less clear. We encourage additional rigorous and replicated experiments on learning and memory in a diversity of non-neural taxa.
- Determine how differences across taxa in problem-solving ability, social behavior, memory, and learning may influence evolutionary dynamics in different ways. Recent work putting together supertrees across vertebrates and other taxa means that we have more tools available to ask these questions than ever before. For example, are there really differences across taxa in their diversification rates that can be attributed to differences in cognitive behavior? Do these associations change depending on the timescale of the investigation? Comparative studies, combined with renewed research efforts on the behavioral capabilities of non-neural organisms, means that we are poised to make exciting new advances in this field.
- Integrating static and dynamic views of evolutionary theory. This requires viewing quantitative and population genetic studies as a starting point of evolutionary inquiry. These studies are essential for pointing out interesting patterns of selection and changes in genetic variation over time, but they provide an incomplete picture of causality in evolution without an understanding of how exploitative systems determine selective environments in the first place, and how epigenetic systems link genotype to phenotype.

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