The Contingent Animal: Does artificial innateness misrepresent behavioral development?

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42
43   ABSTRACT
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45   While organisms are continually experiencing and interacting with their environments, the
46   role and extent of experiences in behavioral development has been controversial. Some
47   argue that adaptive behaviors are acquired through experiences, while others claim they are
48   the result of innate programs that don't require environmental input. Such controversies have
49   historically occurred within animal behavior and psychology, but similar debates are
50   emerging in the field of artificial intelligence. Here the debate is centered on those who
51   design experience-dependent systems that are trained to learn the statistical properties of
52   'environmental' inputs, and those advocating the use of pre-packaged artificially 'innate'
53   responses tailored to prespecified inputs. Those favoring artificial innateness draw analogies
54   with animal behavior to argue that innateness is necessary for the emergence of complex
55   adaptive behavior. But does behavioral development in animals reflect the unfolding of innate
56   programs? Here we highlight the widespread role of specifically causal experiences in the
57   ontogeny of species-typical behaviors. All behaviors are an outcome of a chain of organism-
58   environment transactions – called ontogenetic niches— that begin in the earliest periods of
59   life. This challenges the notion that organisms come prepared with innate programs for
60   behavior. We suggest that an artificial intelligence that matches the complexity of animal
61   behavior should be based on principles of behavioral development, where experiences are
62   necessary and specifically causal factors in the emergence of behavioral abilities.

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INTRODUCTION

Across their lifespan organisms are continually experiencing their environments. Nonetheless, the exact role that experiences play in the development of species-typical behaviors has been controversial (Gottlieb, 1997; Oyama, 1985; Schneirla, Lorenz, 1965). Some argue that behaviors can be partitioned into acquired behaviors that require experiences or innate behaviors, that are preprogramed and don't require experiences (Mayr, 1974; Pinker, 2003). This belief has ancient roots in human history, as folk wisdom has long proposed that many behaviors are caused by a fixed, unobserved, and inborn nature (Bluck, 2011). Such folk wisdom was first used to explain the highly organized behavior exhibited in animals during early life, but quickly moved to shape the conceptual foundations and debates surrounding the development of complex behavior (Z.-Y. Kuo, 1976; Morgan, 1896; Riskin, 2016).

Innateness remains popular in psychology, biology, and cognitive science. Despite such popularity there is little agreement on how to measure innateness, and how to demarcate the innate from acquired behaviors. Mameli & Bateson (2007) surveyed the literature and recorded at least 26 distinct definitions of innateness. These definitions span from adaptive, to present at birth, to shared by all members of a species, and beyond. Because of the difficulties in identifying innateness many researchers have critiqued its utility for understanding behavioral development (Barnett, 1975; Kruijt, 1966; Z.-Y. Kuo, 1976; Lehrman, 1953; Schneirla, 1956; West & King, 1987). However, other researchers have argued that concept of innateness is necessary to oppose the assumption that the mind is a *tabula rasa,* where any potential behavior can occur if an organism is given the right experiences (G. Marcus, 2018a, 2018b; Pinker, 2003; Vallortigara, 2021; Versace et al., 2018; Zador, 2019). It is argued that organisms must come "built in" with innate programs that allow them to process information from the environment and behave appropriately regardless of their individual experiences. Without such programs it is claimed it will be difficult to understand the evolution and expression of the behavioral abilities across species (Cofnas, 2017; Lehrman, 1953).

The concept of innateness is finding new ground in the field of artificial intelligence (Koulakov et al., 2021; G. Marcus, 2018a, 2018b; Versace et al., 2018; Zador, 2019). Within artifical intelligence there exist a debate between those who design experience-dependent programs that are trained to learn the statistical properties of 'environmental' inputs, and those advocating the use of pre-packaged artificially "innate" programs that incorporate algorithms with innate machinery, or "computational primitives" (G. Marcus, 2018b). Those favoring "artificial innateness" often take inspiration from animal behavior to argue that innateness is necessary for the emergence of complex behavior. The way such innateness should be implemented in AI is not discussed in detail, but among possible implementations are inductive biases (Battaglia et al., 2018), transfer learning (Grbic & Risi, 2021), the use of genetic algorithms in an outer loop that would mimic the process of evolution to evolve separate, "instinctive" modules with fixed weight to allow much faster and more reliable learning (Grbic & Risi, 2020; Le, 2019) (Grbic, 2020; Le, 2019) or evolving networks with fixed weights (Gaier & Ha, 2019), thus generating "hardwired" neural network that would be able to solve specific tasks without any learning at all. We call this concept artificial innateness,

125 defined as an attempt to implement innate mechanisms in AI algorithms to mimic the
126 behavior of organisms.

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128   The solutions proposed by advocates of artificial innateness are supposed to
129 eliminate the biggest shortcomings of artificial neural networks - the need of huge amount of
130 data needed to train the network, and the time and resource cost related to the process of
131 training (Zador, 2019). Artificial neural networks are loosely inspired by the organization of
132 biological neural networks. They consist of a series of interconnected artificial neurons, and
133 the strength of the connection between artificial neurons is modified in a training process.
134 This training process consists of exposing a network to a series of inputs, calculating the
135 difference between the resulting and the expected output and then using this error to change
136 weights in a way that would minimize it. Artificial neural networks do not contain any latent
137 task-specific instructions but extract rules from the environment by learning the relationship
138 within and across a series of inputs. The domain general architecture of most artificial neural
139 networks allows them to extract statistical regularities in a wide range of different stimuli and
140 use those regularities to create category boundaries between different stimuli. As the
141 outputs from artificial neural networks are shaped by the statistical properties of the inputs
142 themselves, this requires a large amount of input data to extract the statistical rules uniting
143 them. For example, to construct a concept of a "horse" a neural network will need to be
144 input with thousands of pictures of horses and other animals to build a representation of a
145 horse in contrast to other animals. Here the artificial neural network will learn how the
146 distribution of pixels in an image corresponds to the label of a horse. Once these acquired
147 mappings are validated, they can then be extrapolated to novel datasets to see if they
148 generalize.

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150   Proponents of artificial innateness contrast the performance of artificial neural
151 networks with behavior of animals that are supposed to be able to perform many behaviors
152 efficiently without any previous learning (Versace et al., 2018; Zador, 2019). Among examples
153 of supposedly innate behaviors cited are ability to detect and escape predators, the ability to
154 walk or swim soon after birth, and the ability to recognize and interact with members of your
155 own species (Gaier & Ha, 2019; Vallortigara, 2021; Versace et al., 2018; Zador, 2019). Authors
156 argue that as those behaviors are crucial for survival, and thus their development cannot be
157 dependent on experience. Relying on experience is supposed to be unreliable, as cues
158 necessary for the animal to learn proper response might be rare; or, in case of predator
159 recognition, first-time exposure to them might expose an animal to significant risk. Learning
160 is also expected to be costly in terms of time and resources (e.g. requiring more computing
161 power and more complex neural networks, (Johnston, 1982)). It is assumed that evolution
162 would have selected for experience-independent innate algorithms to overcome those
163 shortcomings.

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165   By leveling the sophistication of animal behavior against the performance of artificial
166 systems, many researchers are making the explicit assumption that animal behaviors can be
167 treated as exemplars for innateness. The shortcomings of artificial neural networks are being
168 used to reintroduce innateness back into the study of animal behavior. Zador (2019) states if
169 artificial neural networks "alone cannot explain how animal's function so effectively at (or
170 soon after) birth, what is the alternative? The answer is that much of our sensory
171 representations and behavior are largely innate". He further states that, "innate mechanisms,

172 rather than heretofore undiscovered unsupervised learning algorithms, provide the base for
173 Nature's secret sauce." Advocates of artificial innateness claim that by failing to incorporate
174 these hypothesized innate algorithms and instead relying on extensive experiences, artificial
175 neural networks will never approximate the cognitive or behavioral sophistication seen in the
176 simplest of animals and will remain inefficient in terms of time and resources.
177
178   Proposed implementations of artificial innateness (e.g. inductive biases, genetic
179 algorithms used to fine-tune initial weights of a network) are supposed to alleviate this
180 shortcoming by reducing the need of a lengthy training process. The role of experience is
181 minimized (or eliminated in case of weight-agnostic neural networks). What is more, the
182 program is equipped with a predefined structure that is supposed to well match the
183 properties of expected input and produce optimal output. Such programs are *prefunctional*,
184 they behave as if they have latent knowledge about the world as their algorithmic structure is
185 unambiguously designed (or evolved) for specific inputs before those inputs are experienced.
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187   In this paper, we highlight how the emergence of artificial innateness centers on the
188 role of experience in development. Individual experiences are assumed to be unreliable,
189 costly, and potentially risky source of information for constructing species-typical behaviors.
190 Organisms are assumed to come "preprogrammed" with latent biological instructions in
191 advance of experience for future functions. In the following sections, we will introduce the
192 classical conception of innateness first outlined by the early ethologists. We highlight how
193 both the ethological and artificial conceptualizations of innateness depend on two critical
194 factors: (1) The innate program is latent and emerges independent of specific individual
195 experiences, and (2) that innate behaviors are prefunctional, as they are prepared to function
196 in response to specific environmental factors not yet experienced. We discuss how both
197 assumptions contrast with the realities of individual experience and behavioral development.
198
The classical definition of innateness
200
201   The purpose of the next section is to examine the connections between historical and
202 artifical innateness concepts. We aim to outline how the modern concept of innateness
203 emerged and how the persistent problems it accumulated during its history are still reflected
204 in how innateness is used in artificial intelligence. While vernacular use of the term 'innate'
205 stretches back into antiquity, the first systematic program to develop a science based on
206 innateness started within animal behavior (Morgan, 1896). In particular, the ethologists aimed
207 to construct a comparative approach to classifying and comparing species-specific
208 behavioral traits to gain insights into the evolutionary forces shaping behavioral organization.
209 According to Lorenz and Tinbergen (Lehrman, 1953), behaviors were innate if the behavior
210 was: "(1) stereotyped and constant in form; (2) characteristic of the species; (3) appears in
211 animals which have been raised in isolation from others; and (4) it develops fully-formed in
212 animals which have been prevented from practicing it".
213
214   The ethologists broadly partitioned behavior into innate fixed action patterns that met
215 the above criteria and general behavioral traits that did not. The fixed action pattern is the
216 historical precursor to artifical innateness. A canonical fixed action pattern is the egg rolling
217 behavior in the greylag goose (*Anser anser*). In this example, the incubating greylag geese
218 retrieves an egg that has rolled out of the nest with a stereotyped motor pattern

219 (*Erbkoordination*). This motor pattern involves placing the egg at the tip of the bill and rolling
220 it backwards with a sagittal movement of the head. Once activated by the visual stimulation
221 of an egg outside the nest, the motor pattern was expressed to completion: even if the egg
222 was removed mid-behavior, the bird would complete the action pattern and roll the now-
223 missing "egg" back into the nest (Lorenz & Tinbergen, 1970; Schleidt, 1974).
224
225   According to the ethologists, the structure of the fixed action pattern is the result of an
226 encoded program in the animal's neural circuity that itself is instantiated in the animal's
227 genome (Lorenz, 1965; Ronacher, 2019). The exact structure of this program was proposed
228 by Lorenz in his "psychohydraulic model". Lorenz proposed that a latent program for a
229 specific behavior was primed to activate if supplied with enough stimulus energy from a
230 releasing stimulus. If the level of stimulus energy reached a critical threshold, an innate
231 releasing mechanism activated a stored motor pattern, and the full behavior was expressed
232 (Ronacher, 2019). These innate releasing mechanisms were hypothetical neural and genetic
233 behavioral instructions that both stored the form of a complex motor pattern and determined
234 the amount of stimulus energy necessary to "release" it. Lorenz's ideas can be viewed as a
235 predecessor of today's artificial innateness (Versace et al., 2018), in which prespecified
236 inputs, algorithmic structure, and outputs map on to Lorentz's releasing stimuli, innate
237 releasing mechanisms, and fixed action patterns (Versace et al., 2018; Zador, 2019).

239   Showing that specific stimuli could drive stereotyped motor patterns, however, is not
240 enough for behaviors to be considered innate. This is because behaviors learned via
241 reinforcement show similar patterns, where reinforced stimuli eventually elicit complex but
242 stereotyped motor patterns (Hogan, 2017; Skinner, 1975). Innateness requires that organisms
243 come pre-programmed with ability to respond appropriately. To show evidence of innate pre-
244 programming versus learned responses, researchers needed to show that individual
245 experiences play no causal role in the development of the behavior. Previous experiences
246 must be controlled for, and isolation studies are needed to show that a behavior emerges
247 when individuals are isolated from prior relevant experiences. The centering of innateness
248 around the role of experience in development is a uniting feature behind both artificial and
249 ethological innateness concepts. However, as will be discussed later, it is the nature of
250 development to be experience-dependent, even if those experiences share no obvious
251 connections with the behavior under investigation.
252
253 ### Independence from individual experience
254
255   In this section we investigate the assumption that innate behaviors emerge outside of
256 an individual's experience with the world. This assumption, central to both classical and
257 artificial innateness concepts, has historically been investigated using isolation tests. The
258 isolation test aims to show the resilience of behavioral development to extreme deprivation
259 and interprets that resilience as evidence for innateness. We first outline a history of isolation
260 tests to show how historical controversies surrounding the tests shaped modern
261 conceptions of innateness. Next, we highlight how studies of behavioral development in
262 animals challenge the assumption that we can identify *a priori* which experiences are
263 important for the development of behavior.
264

265   In an isolation experiment, a young organism is isolated from most outside stimulation
266   during critical periods of their development. Douglas Spalding (Spalding, 1875) was the first
267   to use this approach in his studies of birds. He raised barn swallows (*Hirundo rustica*) in
268   small cages during early life without the opportunity to stretch their wings. Upon release,
269   barn swallows could fly normally after a short amount of time. He also raised young chickens
270   (*Gallus gallus*) in isolation and documented the development of fully formed foraging
271   behavior such as scrapping, pecking, and ingesting food. These experiments were the first
272   to treat the expression of stereotyped behavioral responses after isolation as evidence that
273   experience did not play a causal role in their development.
274
275   The primary aim of the isolation approach is to control for all experiences that could
276   play a causal role in the development of behavior. It's supposed that by removing all
277   confounding sources of experience, one's confidence in a behavior's innateness grows. As
278   such, the isolation approach doesn't aim to provide any positive evidence for innateness. In
279   other words, no program-like mechanism for development is identified via isolation, but its
280   existence is inferred via the resilience of the behavior to extreme deprivation. We call this
281   argument the "innateness in the gaps" approach, as innateness of a trait is assumed based
282   on gaps in our knowledge of development, and not positive evidence for a program-like
283   unfolding of behavioral over development.
284
285   All isolation studies rely on two assumptions: (1) That experiences before the period of
286   isolation did not causally contribute to the development of the targeted behavior, and (2) the
287   method of isolation succeeded in removing all experiences that could causally shape the
288   development of the behavior. However, these two assumptions are rarely warranted, which is
289   a serious problem with this approach. In practice the "innateness in the gaps" approach
290   assumes that the researcher knows *a priori* the range, timing, and quality of experiences that
291   could causally contribute to the emergence of a specific behavior. For instance, in many
292   cases individuals can only be isolated after birth, which assumes that prenatal experiences
293   do not contribute the development of specific behavioral abilities.
294
295   Such isolation studies were the main focus of Lehrman's (1953) classic critique of
296   innateness. Lehrman convincingly argued that isolating individuals from a prespecified range
297   of experiences does not necessarily control for the "processes and events which contribute
298   to the development of any particular behavior pattern" and that "the important question is
299   not "is the animal isolated?" but "from what is the animal isolated?". Partially in response to
300   Lehrman's critique, the primary means of identifying innateness shifted from isolating
301   individuals, to documenting the resilience and specificity of behavioral expression across
302   environments and contexts (Reber et al., 2021; Sandoval & Wilson, 2022)In his investigation
303   of the vernacular use of innateness, Griffiths et al (Griffiths et al., 2009) found that fixivity, or
304   the resilience of a trait to different environmental influences, is still the most important factor
305   in categorizing a trait as innate.
306
307   It is assumed that by raising individuals across a wider range of environmental
308   contexts individuals will have less opportunities to share similar experiences (Ariew, 2007). If
309   a behavior is expressed across those different contexts, it is presumed that an innate
310   program is the most parsimonious causal factor in its development, with experiences playing
311   a negligible causal role. Zador (2019) and others (Lukhele et al., 2022) primarily use the

312 predictability and resilience of behavioral expression as the means for identifying innate
313 traits. However, much like the isolation study, no effort is made to investigating 'which'
314 experiences might have a causal role, and if these experiences are shared across contexts.
315 Instead —much like the isolation test — there's faith that the experimenter's choice of
316 different contexts successfully controlled for all potential causal experiences.
317
318   Showing that a behavior develops across contexts does not necessarily mean that
319 experiences are unimportant. Defenders of innateness routinely acknowledge the essential
320 role of environments for development in general, as organisms isolated from all
321 environmental interactions would quickly die. However, it is assumed that environments only
322 play a *supportive or permissive* role in keeping the animal alive wherein behaviors emerge
323 due to unfolding of latent programs. As such, behaviors develop in different environments
324 because these environments are similarly supportive, and not because any shared factor in
325 those environments causes the behavior.
326
327   In his recent book "Born Knowing", Vallortigara (2021, pp 25, 31-33) begins by making
328 a distinction between supportive (or permissive) versus constructive (or instructive)
329 experiences. Constructive experiences represent specific experiences that are necessary for
330 a behavior to develop, and its absence results in a targeted deficiency in the behavior of
331 interest. Proponents of artificial innateness assume that some behaviors are so essential to
332 survival and reproduction that relying on constructive experiences would place the individual
333 organism at significant risk. For example, Marcus (2018b) states that "If you are baby ibex
334 scaling the side of cliff, you may be better off with a small but focused set of innate priors
335 than with a more plastic system that would require a large number of life-threatening
336 experiences." This likely stems from the assumption that information from individual
337 experiences needs to be extensive and recurring to have a substantial causal influence on
338 development. While some examples of reinforcement learning do require significant training,
339 this is not necessarily the case across all constructive experiences. There are many avenues
340 wherein experiences shape, reorganize, stabilize, facilitate, maintain, canalize or diversify
341 developmental pathways. For instance, experience pecking at food almost immediately
342 integrates pecking behavior with hunger perception, and individuals not able to peck at solid
343 items during early life fail to develop proper ingestion behavior (Hogan, 1971). In many cases
344 of "insight" in animals a single experience integrates previously acquired responses into a
345 novel behavior (Wasserman & Blumberg, 2010). The challenge of developmental science is
346 describing the types of experiences organisms typically have, and testing to see if and how
347 these typical experiences shape ontogeny.
348
349   Numerous studies have shown that normally occurring experiences are constructive
350 for basic species typical abilities. Among the most essential features necessary to survive
351 and reproduce is the ability to recognize your own species, and if any species possesses an
352 innate species recognition program it would be the Brown-headed cowbird (*Molothrus ater*)
353 (Mayr, 1974). Brown-headed cowbirds (hereafter cowbirds) are obligate brood parasites,
354 meaning they lay their eggs in other species nests and rely on those foster species to raise
355 their offspring. They are unique in being a very *generalist* brood parasite and have been
356 recorded to parasitize over 200 other bird species. This presents a significant problem for
357 young cowbirds — not just because if they imprint on foster parents they won't recognize
358 their own species, but because the large range of potential host species make it unlikely that

359   hosts share some common feature that young cowbirds use to eventually recognize fellow
360   cowbirds. So how do cowbirds recognize other cowbirds? Due to the lack of predicable
361   contact with members of their own species, many have suggested that they should have
362   evolved an "innate species-recognition program"(Mayr, 1974).
363
364   Nonetheless, subsequent research has shown that brown-headed cowbirds require
365   substantial social experiences with other cowbirds to master recognizing members of their
366   own species and acquiring the skills to interact with them. Research done by Freeberg,et al.
367   (1995) showed that males raised with canaries but without female cowbirds preferred to
368   direct singing behavior at canaries. This persisted even after individuals were placed in
369   aviaries containing both canaries and receptive female cowbirds. Thus, male cowbirds
370   depend on interactions with female cowbirds for proper species identification. Males also
371   depend on interactions with females to guide the development of their singing behavior
372   (West & King, 1988, 2008) Young male cowbirds produce a babble-like series of songs that
373   often lack the structure and coherency of adult songs. When young males produce a
374   coherent song variant non-singing females often respond with a wingstroke (a slight
375   outwards movement of a wing). These visual cues serve as an effective reinforcer, with males
376   who received more wingstrokes developing higher quality song variants (also see in zebra
377   finches, (Carouso-Peck & Goldstein, 2019). Thus, even in a species where innate species
378   recognition and social programs would be particularly advantageous, we find that regularly
379   occurring experiences play constructive role in the formation of species-typical abilities.
380
381   Constructive experiences are also essential in the development of mammalian
382   behavior. For example, in rodents, the ability to construct nests and retrieve neonates is
383   essential for offspring survival. This behavior involves continually retrieving offspring who
384   stray from the nest by picking them up, placing them in the mouth, and quickly heading back
385   to the nest. In naturalistic settings, pregnant female rats will begin to build nests and retrieve
386   offspring during their first pregnancy, leading many to assume that the behavior does not
387   depend on previous experience. However, studies have shown that experiences picking up
388   and handling objects are specifically causal to the development of retrieval abilities. Young
389   rats raised without the ability to pick up objects in their environment fail to develop proper
390   pup retrieval behavior (Lehrman, 1953); nest building behavior is also experience -
391   dependent (Van Loo, 2004). In summary, a previous regular occurring experience, the ability
392   to pick up and manipulate objects, is essential to constructing pup retrieval behavior.
393
394   While such examples highlight the causal role of experiences, one could make the
395   claim that isolation tests would show the above behaviors to be experience dependent, and
396   thus not innate. However, other examples show that subtle experiences may not be easy to
397   remove, even when individuals are isolated directly after birth. The role of constructive
398   experiences begins in pre-natal environments and includes self-stimulative experiences with
399   your own body (Blaich & Miller, 1988; Cheng, 2003; Gottlieb, 1997). For example, domestic
400   fowl chicks must see their own toes after hatching to consume mealworms, as chicks raised
401   without the experience of seeing their toes often fail to pick up and ingest mealworms
402   (Wallman, 1979). Female Ring-necked doves require the ability to hear their own 'coo'
403   vocalizations to prime their reproductive physiologies, and the ability to listen to your own
404   vocalizations is a core feature of vocal learning in many species (Cheng, 2008). During sleep
405   experiencing your own body twitching is essential to the development of the primary motor

cortex, and serves to change this brain region from a somatosensory area to one that actively controls motor functions (Dooley & Blumberg, 2018).

One of the biggest research programs dedicated to investigating the role of pre-natal experiences came from the lab of Gilbert Gottlieb. Research done by Gottlieb and his students showed how behaviors that were classified as innate depended on constructive pre-natal experiences (Gottlieb, 1997). Much of his research focused on the response of ducklings to maternal assembly calls. Upon leaving the nest for the first-time, young ducks immediately orient towards and follow the sound of their mother's assembly call. This seemingly automatic response to the maternal call the first time it is heard suggests a prefigured genetic program instructs fledglings to respond in appropriate ways. Nonetheless, Gottlieb's research showed that pre-natal experiences are essential for these responses. In wood ducks (Gottlieb, 1997), embryos require exposure to the sounds of their siblings calling in neighboring eggs, and mallard embryos require hearing their own embryonic vocalizations to orient towards and follow the maternal contact call. Without these experiences, fledglings failed to develop the orienting and following response to maternal contact calls. As such, these experiences are constructive.

Another species-typical behavior shown across many vertebrate species is the freezing response. The freezing response occurs when an individual adopts a motionless low posture in response to a threatening stimulus. Because the response is essential to survival during early life, many have considered it to be innate. In response to these claims, David Miller and colleagues investigated the development of this behavior in Mallard ducks (Blaich & Miller, 1988; Miller, 1997). They have shown that –much like the ducklings' response to maternal contact calls—exposure to hearing your own embryonic vocalizations is essential for the development of the freezing response. Individuals who were devocalized as embryos failed to show the freezing response during early life, and required extensive social experiences after hatching to regain it. If groups of de-vocalized nestlings were raised with typical individuals, they acquired the freezing response, while de-vocalized individuals raised without typical individuals did not (Blaich & Miller, 1988; Miller & Blaich, 1988). In summary, these examples highlight that basic species-typical abilities are dependent on causal experiences from the earliest periods in life.

For Lorenz, experiences were akin to 'individually acquired information", and although "practically every functional unit of behavior contains individually acquired information", the influence of outside experiences on innate behaviors was relegated to introducing noise around a fixed innate core (Lorenz, 1965). Nonetheless, the examples highlighted above show that we cannot discount the influence of constructive experiences in the emergence of any behavior. There is no aspect of an organisms that is free from experiences, and unlike the extensive period of training required for artificial neural networks, even seemingly trivial experiences have significant influences on species-typical development.

Prefunctionality

While the assumption of experience-independence is still critical to modern conceptions of innateness (Ronacher, 2019; Sandoval & Wilson, 2022; Zador, 2019), the concept underwent significant changes in response to critiques. Many researchers, including

Lorenz (1965), revised their original assumptions to emphasize that innate programs—regardless of their developmental histories—are prefunctional. Here prefunctional means in that the underlying biological mechanisms (neural, genetic, or physiological) are preprogrammed for future environments. This assumption is now a core feature of modern innateness. For example, Haidt (Haidt & Joseph, 2007) claims that innateness is highlighted by "structure in advance of experiences", and Marcus (G. F. Marcus, 2004) claims that that "nature bestows upon the newborn a considerably complex brain, but one that is best seen as prewired…rather than hardwired". In this section we will look at how these historical changes expanded the concept of innateness, while not addressing many of its critical flaws.

According to the prefunctional view, the biological structure underlying species-typical behaviors is prepared for environmental *givens* (Cofnas, 2017). Environmental givens are predictable aspects of the environment that individuals have yet to experience but must ultimately navigate to successfully survive and reproduce. In response to such givens, it is assumed that selection will instantiate a program for innate behavior. Once established, releasing environmental stimuli (or input) simply activates this program resulting in the full expression of the behavior. Exposure to releasing stimuli, such as a maternal contact call, activates a genetic or neural program for its recognition, while the feeling of substrate on one's foot after hatching activates a program for walking. Examples of such preparedness are the ability of broody hens to sit on eggs during their first breeding attempt, the ability of hatchling sea turtles to navigate from the beach to the ocean, the ability of precocial birds to walk directly after hatching, and the ability of newborn humans and primates to recognize faces (Blumberg, 2017; Hogan, 2017).

The difficulty with delineating innate programs based on prefunctionality is that one must show that biological, cognitive, or psychological organization for behavior is latent, in that it exists in a functionless state until it's exposed to the right environmental stimuli. Ultimately, this would require identifying genetic programs that directly encode specific responses to a stimuli with no functional precursors. This is also complicated by the fact that the concept of function itself has diverse range of meanings, and it is not clear how one could demonstrate evidence of functionlessnes (Wouters, 2005). For example, knowing that some neural circuitry involved in birdsong develops prior to singing does not mean that its prior organization is functionless. This would require that the development of such circuitry is functionally isolated and has no effects on the organism outside its targeted future influence on singing. In practice, this would require showing that such circuitry does not contribute to any other behaviors that occur before singing.

Studies investigating prefunctionality rarely aim to demonstrate prior functionlessness, but instead aim to show that behavioral responses to a specific stimulus are not influenced via prior learning or experience with that stimulus. This is done by showing that a releasing stimuli does not occur in the environment before an animal responds to it. If this is true, it is then assumed that there are no functional precursors to the response, and thus the animals were prepared with the biological machinery for those stimuli the first time they encountered it. For instance, hens often show broody responses to eggs during their first breeding attempt, and one could investigate if previous experiences with eggs are necessary for this behavior. If an individual lacks any experiences with eggs, it's assumed there's no

499   information from eggs that could shape these responses and thus these responses are
500   preprogrammed into the hen before they are expressed.
501
502   One difficulty with this view is that—just like isolation studies—it relies on the
503   researcher's perception of the releasing stimulus to determine if an animal encountered it
504   during an earlier period of development. Our own assessments may not map onto the
505   animal's perceptions, as animals will often not be responding to the whole stimulus, but to
506   properties of the novel stimulus that are shared with previously encountered—but
507   fundamentally distinct—stimuli. For instance, an egg is a multisensory stimulus, containing
508   both texture, shape, color, and tactile cues that may be shared with previously encountered
509   stimuli. To truly control for previously confounding experiences, we would first need to
510   explore how the animal perceives the releasing stimuli, and what aspects of the animal
511   perception elicits the response (Von Uexküll, 2013). The challenge is attempting to show that
512   those aspects of an animal's perception don't occur during early period of development and
513   not necessarily the exact stimuli itself.
514
515   The sudden appearance of an organized behavior can also reflect the reorganization
516   of previously functional responses (Raevskii, 2002). As Greenberg and Partridge (Greenberg
517   & Partridge, 2000) state, "all complex behavior can be understood….as consisting of new
518   organizations and integrations of old behavior units – organization upon organization upon
519   organization". It's been shown that a single experience with a novel stimulus can be enough
520   to *cause* the biological organization underlying a behavior to emerge, rather than activate it.
521   One example can be seen in the development of pecking in young chicks. During early
522   development, hunger perception is independent of pecking. Hungry chicks do not engage in
523   more pecking behavior than satiated chicks, and pecking is used primarily to explore objects
524   in the environment (Hogan, 2017). Predictable but incidental experience with pecking at food
525   items during early development integrates hunger perception with pecking and transforms it
526   almost immediately into an ingestive behavior. If individuals are not allowed to peck at food
527   items during early development, they may exhibit the pecking response, but not utilize it
528   gather food and often die as a result (Hogan, 2017). The sudden emergence of species-
529   typical behaviors may better reflect a functional reorganization in response to current
530   experiences than a latent preparation for future ones.
531
532   Many behaviors are classified as prefunctional because they occur right after birth, yet
533   research in behavioral embryology has shown that young individuals often acquire highly
534   organized behavioral responses through pre-natal experiences that are repurposed after birth
535   (Z.-Y. Kuo, 1976; Lickliter, 2007). Chicks immediately begin to peck at the ground right after
536   hatching (Morgan, 1896). Kuo (Z.-Y. Kuo, 1932a, 1932b) discovered that all the components
537   of pecking (opening and closing of the bill, bill thrusting, bill up-lifting, bill clapping and
538   swallowing) are already present in the embryo after seven days of incubation as responses to
539   the embryonic heart beats and ingest of the amnion fluid. These movements are repurposed
540   soon after hatching to develop pecking behavior. Walking also occurs immediately after
541   hatching in precocial birds (Morgan, 1896; Zador, 2019). As observed by Kuo (Z.-Y. Kuo,
542   1932b), proper placement of the legs under the yolk is essential for walking, and chicken
543   embryos often use an alternating movement of the legs in the egg to gain proper placement
544   around the yolk and the wall of the egg. After hatching, chicks respond to similar tactile cues
545   from the ground with the same alternating leg movement that are now repurposed for

546 walking. Such examples highlight how non-obvious experiences and behaviors can be
547 immediately repurposed in novel contexts in what seems like preparation for these new
548 environments (Turvey & Sheya, 2017).
549
550   Classifying behaviors as prefunctional often reflects a particular approach to
551 developmental questions. Instead of viewing organisms as complex adaptive agents, the
552 prefunctional view hold that organisms are evolved "toolkits" that come with a set of
553 prespecified programs allowing fast and rapid responses to the environment. Nonetheless,
554 as shown in the paragraphs above, the organism's ability to produce such rapid responses is
555 itself a built on a long period of interaction between an organism and its environment
556 stretching into pre-natal periods.
557

Prospective and Retroactive Perspectives

559
560   Imagine the life cycle of an organism stretched out onto a straight line beginning with
561 conception and ending with death. On this lifeline are markings designating the extract time
562 that specific behaviors first occurred. Now imagine a researcher is choosing a behavior of
563 interest on that timeline. To investigate that behavior developmentally, the researcher has a
564 choice: they can look backwards towards conception, a view known as the retroactive view,
565 or they can look forward towards death, a view known as the prospective view. Both views
566 represent a legitimate approach to understanding behavioral development, but both come
567 with a very different means to investigate the causal factors shaping the ontogeny of
568 behavior.
569
570   By grasping development at its outcomes rather than at its beginnings, a retroactive
571 perspective forces the researcher to reconstruct an organism's past without directly
572 observing it. Reconstructing past events can be done through the careful collection and
573 analysis of physical traces of past events. For example, archeologists and paleontologists
574 cannot travel to the past and observe the unfolding of history directly, but infer historical
575 processes by comparing artifacts or fossils made at different times. The difference between
576 the archeologist and the developmentalist, is we rarely have traces of physical traces of an
577 individuals developmental history, and thus it is solely up to the researcher to hypothesize
578 both which past events occurred, and which events had a causal influence on the behavior
579 being studied.
580
581   This highlights the primary limitation of the retroactive perspective; it relies on
582 judgment of the researcher to determine which past experiences are important to the
583 development of a behavior. By looking back in time to earlier periods, the researcher will
584 select those experiences that bear some perceptual similarity to the outcome they are
585 interested in. In practice, this often assumes that "like-causes-like" across ontogeny. For
586 example, exposure to song causes you to learn that song, and exposure to social
587 interactions causes one to become better at interacting socially. A classic example of this is
588 songbird learning. Upon finding that two canaries sing two different songs, a researcher
589 often investigates periods of early development to identify the timing and context wherein
590 the different individuals were exposed to those different songs. If a canary is raised in
591 isolation from hearing a specific song and is still able to sing that fully organized song, then
592 it's assumed that a hidden variable such as a genetic program must have "built" the song

593 into the canary's biology. This linear and additive view states that exposure to some factor X
594 during development will cause an individual to possess X or acquire some other variant of X.
595 While such an approach is often essential in the beginnings of an investigation, what if the
596 experiences necessary for the development of behavior don't share such obvious
597 precursors?
598
599 As stated in the section above, our own perceptions may not match those of the
600 animals, and thus experiences lacking an obvious connection in our eyes may be overlooked
601 but necessary aspects in behavioral development. In contrast to the linear view of the
602 retroactive perspective interactions between developmental factors often have multiplicative
603 effects on the phenotype. But what do we mean by multiplicative? As stated by Gottlieb
604 (1997), "the coaction of X or Y often produces W rather than more of X or Y or some variant
605 of X or Y." In such cases, if either X or Y do not have an obvious connection with W, it may
606 be easy to mischaracterize its development as lacking any obvious precursors.
607
608 Due to the multiplicative nature of behavioral development, taking a retroactive
609 perspective may be grabbing development at the wrong end. It may be difficult to know
610 which previous events might have an influence on the outcome of interest if such events do
611 not have any obvious connections with that outcome. A prospective position may be
612 necessary to construct a more complete a picture of the origins of behavior. Specifically, this
613 prospective perspective needs to capture the range of factors – both within and outside the
614 organism – that could influence how they change over time. To do this, we propose that
615 researchers start with a description of an *ontogenetic niche* without recourse to an outcome
616 of interest.
617
618 An ontogenetic niche is a description of the interactions between an organism and its
619 environment at a particular timepoint. The niche an organism occupies will constrain,
620 facilitate, and scaffold the transition to future niches that it will occupy (Fig 2). Any
621 transaction between an organism and its environment at time t is going to change the way
622 that organisms interacts with the environment at time $t + 1$. For example, at time t an
623 organism's niche may be characterized by strong relationships between siblings within a
624 small family group. These sibling relationships allow the organism to acquire skills such as
625 the ability to approach others without initiating a withdrawal. These skills feedback to allow
626 individuals to approach more unrelated conspecifics at time $t + 1$, when individuals enter a
627 group of unrelated individuals. Exposure to more unrelated individuals may induce changes
628 in internal physiology and gene expression, such as during periods of sexual maturity,
629 resulting in changes in which mates they prefer or avoid at time $t + 2$. In this hypothetical
630 scenario, consistent experiences with siblings are a non-obvious precursor to mate choices,
631 but the siblings themselves do not contain the program or blueprint outlining an individual
632 mate choice. No single factor, be it a stimulus, a hormone, or a gene has the informational
633 capacity to program a behavior, but what's important is the *contingent processes* that bind
634 them together.
635
636 When investigating development prospectively the role of contingent experiences
637 between an organism and its environment takes center stage. No longer can any aspect of
638 an organism be abstracted away from its environment, as each time an organism interacts
639 with its environment it changes, however slightly, its internal biology. Changes in internal

640   biology will influence how individuals interact with the environment in the future. What occurs
641   across development is a predictable series of antecedent-consequent processes that occur
642   as an organism engages its surroundings, but no specific aspect of these processes can
643   "see" into the future. It's thus better to think about ontogenetic niches as emerging from past
644   niches, rather than showing a directional impulse towards future ones.
645
646   As ontogeny builds upon previous niches, it is difficult to maintain that any set of
647   factors (gene, hormone, stimuli, ect) contains a "program" for future states. The function of
648   any factor is dependent on the niche that it occurs in. Just as yelling "fire" in a crowded
649   theater versus in front of a bonfire would cause drastically different outcomes, the functions
650   of specific hormones, genes, and stimuli defined by contexts within a specific niche. For
651   example, the typical function of oxytocin in promoting pro-social behavior in animals can be
652   shifted to other functions such aggression and social avoidance in other contexts (Ne'eman
653   et al., 2016). Another example is GABA, the main an inhibitory neurotransmitter in the adult
654   brain, that has an excitatory role during the early development (Murata & Colonnese, 2020)
655   Moreover, the knockout of the same gene can have the opposite effect on behaviour in
656   different mouse strains (Sittig et al., 2016). The function of each factor is thus radically
657   relational and situated; the same genes can have drastically difference functions in different
658   tissues and across different timescales, and the same stimuli can elicit drastically different
659   behaviors based on when, how, and where it is presented. As stated by Oyama (1988) "the
660   informational function of any developmental interactant is dependent on the rest of the
661   system. This means that what counts as information is itself contingent and relational."
662
663   Investigating development prospectively allows us to garner a better picture of the
664   way which complex behavior emerges, without postulating hidden variables such as a plan,
665   blueprint, or goal. For example, most rats are born into an environment containing their
666   mothers presence. During birth, the mother's grooming behavior predictably moves amniotic
667   fluid onto her stomach region. The newborn rat neonate follows the scent of the amniotic
668   fluid to the mother's stomach region where they're likely to encounter her nipple and begin
669   suckling (Alberts, 2008). This highlights how a seemingly automatic and programmed nursing
670   behavior within the rat neonate, when observed closely, reveals itself as a series of
671   contingent transitions between different ontogenetic niches. However, a naïve investigator
672   only observing a rat fetus in the womb would never be able to reconstruct the properties of
673   future niches. This is because these future niches depend on how the interactions in the
674   womb reorganize based on factors that are not currently present in that niche at that specific
675   time. While antecedent pre-natal niches constrain and facilitate future nursing niches they do
676   not determine, plan, or prefigure them.
677
678   So how does the retroactive versus prospective viewpoints inform debates within
679   artificial intelligence? The debate surrounding artificial innateness revolves around the role of
680   experience and prefunctionality in complex behavior. The existence of organized behavior
681   during early life is not surefire evidence for a program as some have claimed (Zador, 2019).
682   Artificial innateness assumes that acquisition of information from experiences is costly and
683   inefficient, and that animals and their artificial analogs should avoid this though the use of
684   tailored programs. In assuming that previous experiences are too poor, missing, or
685   unpredictable to structure complex behaviors, this position draws strongly from the
686   retroactive view of development. But, as we have seen, this hypothesis belays the

687 contingent, snaking, non-obvious processes wherein experiences shape development, as
688 shown through prospective developmental research. Highly organized complex species-
689 typical behaviors are the outcome of a dynamic series of ontogenetic niches. The challenge
690 is how—or if—this process should inform artificial systems.
691
692 ***Moving from Programs to Processes***
693
694   Animal behavior is often used as barometer for advancements in artificial intelligence
695 (Crosby, 2020; Crosby et al., 2019; Shanahan et al., 2020). Humans have long attempted to
696 mimic the behavior of animals using engineered objects to gain insight into the workings of
697 behavior, cognition and intelligence. Before the age of computation and information,
698 clockwork facsimiles of behaving animals, called automata, could be found across Europe
699 (Anger, 2009; Riskin, 2016; Taylor & Dorin, 2020). These automata were able to mimic the
700 foraging behavior of swans, the digestive abilities of ducks, and even the writing abilities of
701 humans with clockwork, springs, levers, ropes and pulleys. It was these objects that inspired
702 the conceptual foundations upon which the behavior of animals was studied for generations
703 (Anctil, 2022). Thinkers, philosophers and scientists from Descartes, Aquinas, and others
704 made references to automata to support the idea that behavior was largely the result of static
705 mechanisms immune from the more sophisticated rational thought present in humans
706 (Ablondi, 1998).
707
708   Today's algorithms, neural networks, and computational models are fast becoming the
709 conceptual platform from which to interpret, explain, and understand animal behavior.
710 Questions such as "What is better at distinguishing this Monet from Cézanne, a neural
711 network or a pigeon?" seek to uncover an as-of-yet-unseen unity across complex behaviors
712 regardless of their biological or artificial origin. In 2019 there was even an Animal-AI
713 Olympics that directly compared the performance of animals to artificial intelligence
714 (Shanahan et al., 2020). Research comparing computer vision algorithms with imprinting
715 chicks seeks to provide direct insights into the inner workings of animal behavior (Lee et al.,
716 2021; Wood et al., 2020). Some even proposed that standard ethological methods—once
717 solely used to research organisms—can be extended to understanding the behavior of
718 artificial systems (Rahwan et al., 2019). When the sophistication of modern machine learning
719 or algorithmic approaches is directly contrasted with the performance of animals on similar
720 tasks, one is often making the implicit assumption that the underlying architecture of
721 behavior is comparable, such that understanding the performance of artificial systems will
722 ultimately provide a unified conceptual foundation for understanding the emergence of
723 complex behavior broadly, be it in animals or machines (Rahwan et al., 2019).
724
725   It is within this paradigm that we must situate the revival of innateness. Artificial
726 innateness assumes complex intelligent systems must have a fixed underlying architecture
727 that is prepared for specific inputs, and this is directly drawn from assumptions about the
728 development and evolution of behavior in organisms. As stated by Marcus "Evolution
729 (whether through natural selection or simulated artificial techniques) is a means towards
730 building machinery with embedded prior knowledge". Such statements highlight the
731 tendency to treat innateness as an unassailable bedrock of adaptive behavior. The
732 consideration that adaptive behaviors may not necessarily be caused by fixed embedded

733 programs but the recurrence of contingent niche transitions does not yet have a place within
734 discussion of artificial intelligence.
735
736   A focal difference between artificial intelligence and organisms is how these systems
737 engage with and utilize their environments. Whereas artificial innateness acts as a standard
738 input-output device that merely depends on a supportive environment for input, neural
739 networks are primarily extractive, using the environment to passively gather and classify
740 information. Neither of these are *constructive*, they do not show the ability to integrate
741 experiences within specific ontogenetic niches as necessary components in the
742 development of an underlying algorithmic structure. In this paper we have highlighted the
743 necessity of experiences as an essential factor in the emergence of adaptive behaviors by
744 modifying an organisms internal organization and the niches they inhabit. This core
745 developmental principle, the bottom-up scalable chain of experiences, action, and niches
746 has yet to be truly instantiated in an artificial system.
747
748   A common retort to developmental considerations is to emphasize that selection acts
749 in opposition to the complexity of ontogeny to assure the instantiation of fixed genetic
750 programs necessary to survival and reproduction (Dawkins, 2004). By turning to natural
751 selection, defenders of the artificial innateness seek to bypass the messy complexity of
752 development. This can be seen especially in studies where evolutionary algorithms are used
753 to evolve innate network modules with fixed weights in reinforcement learning simulations
754 (Grbic & Risi, 2021; Le, 2019) or to evolve whole fixed networks (Gaier & Ha, 2019) to ensure
755 fast and reliable learning. In those programs, "evolved" networks are fixed and their weights
756 do not change during learning, and there is usually 1:1 relationship between the genotype
757 and the phenotype.
758
759   However, as we have shown above, the fact that species-typical behaviors that
760 facilitate survival and reproduction persist and increase in the population tell us little about
761 the roles that genes play in development and evolution. As stated by Oyama (1985), "nature
762 does not inhere in genes, but emerges in processes; it is on these processes and their
763 phenotypic outcomes that natural selection operates". Selection is a consequence of
764 phenotypic form, not a cause of it, and that phenotypic form (including behavior) is itself an
765 outcome of developmental processes, not programs. The complexity and intelligence shown
766 by organisms is not as much a reflection of selection secondarily instantiating them in a
767 population, but in development for producing them in individuals in the first place.
768
769   So how can animal behavior inform artificial intelligence? Behavioral development has
770 no clear computational analog, as the structure of computational systems does not yet
771 capture the self-sustaining, self-creating, far-from equilibrium organization present in all living
772 organisms (Koutroufinis, 2017). Organisms are not passive receptacles of environmental
773 information nor are they the result of inbuilt programs — they are active niche creators who
774 at must discover complimentary aspects of the environment to either develop or perish.
775 Adaptive biological systems are thus able to create and scale their own ontogenetic niches
776 with the aim of persisting in the current context. A focal point centering the underlying the
777 prospective construction of ontogenetic niches is not the program but the organism, a self-
778 creating system. Until we agree on what type of biological processes give rise to the
779 organism's self-maintaining abilities, our ability to instantiate them in artificial systems will be

780 limited, and the inferences from organisms to machines (and vice versa) should be
781 approached with caution.
782
783   A promising start at integrating the developmental processed discussed above within
784 artificial intelligence is coming from the field of developmental (epigenetic) robotics
785 (Lungarella et al., 2003; Prince et al., 2005). This new research field is centered on creating
786 artificial agent possessing the ability to form, maintain, and change its agent-environment
787 relationships over time in ways result in the emergence of complex behaviors analogous to
788 those seen in biological systems.
789
790   Such approaches could underscore the constructive role of experience in scaffolding
791 intelligent artificial systems, and explore how interactions between embodied agents and
792 their environment allows development of behavior in a way that may resemble progress
793 through developmental niches. A good example is study by Nagai (2011) on the
794 development of a Mirror Neurons System (MNS). Mirror neurons are active both during the
795 execution of an action by an animal or human and during the observation of a similar
796 movement executed by another individual (di Pellegrino et al., 1992). MNS is often supposed
797 to be an innate module (Heyes, 2010), and is supposed to be important for processes such
798 as understanding actions of others or empathy (Keysers, 2011).
799
800   More recent studies are suggesting that the development of MSN is dependent on
801 experience, though (Heyes, 2010). Nagai (2011) hypothesized that its development is
802 enabled by a low resolution of vision at early developmental stages. In a proposed
803 computational robotic model, this low resolution of vision makes a robot agent interpret all
804 actions - either self-executed or observed - as equivalent, what leads to the formation of an
805 association between those observations and motor commands. Only later, when the visual
806 acuity increases, the robot is capable of differentiating between its own actions and the
807 actions of others. The association formed at the early stage is preserved, though, resulting in
808 an activation of a motor system in response to observed action (Nagai et al., 2011). This
809 study simulates progress through developmental niches, when the state of an organism at
810 one niche (early stage of development with a low visual acuity) facilitates the progress to the
811 next niche, with a developed mirror system. This niche, in turn, may lead to the development
812 of the ability to imitate actions of other individuals that will emerge after interactions between
813 the agent and others. In a similar manner, individuals' own motor development may facilitate
814 the ability to predict actions of others (Copete et al., 2016).
815
816   The proponents of artificial innateness are right in their claim that learning systems
817 that are supposed to learn quickly and efficiently require constraints on learning. Using the
818 biological concept of innateness as an inspiration, though, they focus only on one possible
819 source of constraints - specific, predefined neural wiring. Aforementioned studies, taking
820 advantage of creating embodied agents that can interact with their environment, show that
821 such constraints can can emerge in those interactions thanks to limitations of body
822 morphology, topology of an environment and other factors. In this context, constraints don't
823 need to be predefined, just like in an animal progressing through developmental niches.
824
825   Our technologies have long shaped the way we conceptualize adaptive behavior. In
826 this paper we proposed that to understand, and ultimately replicate, the adaptive behavior of

organisms we must first understand the developmental processes that create such behaviors. Using animals as exemplars of innateness reflects the tendency to simplify developmental processes to meet it the constrains of our current technological limitations. In our efforts to simplify biology to inspire new technologies we may miss one of the most critical feature of organisms: that the organisms and its behavior is both the cause of, and consequence of, their experiences in the world.

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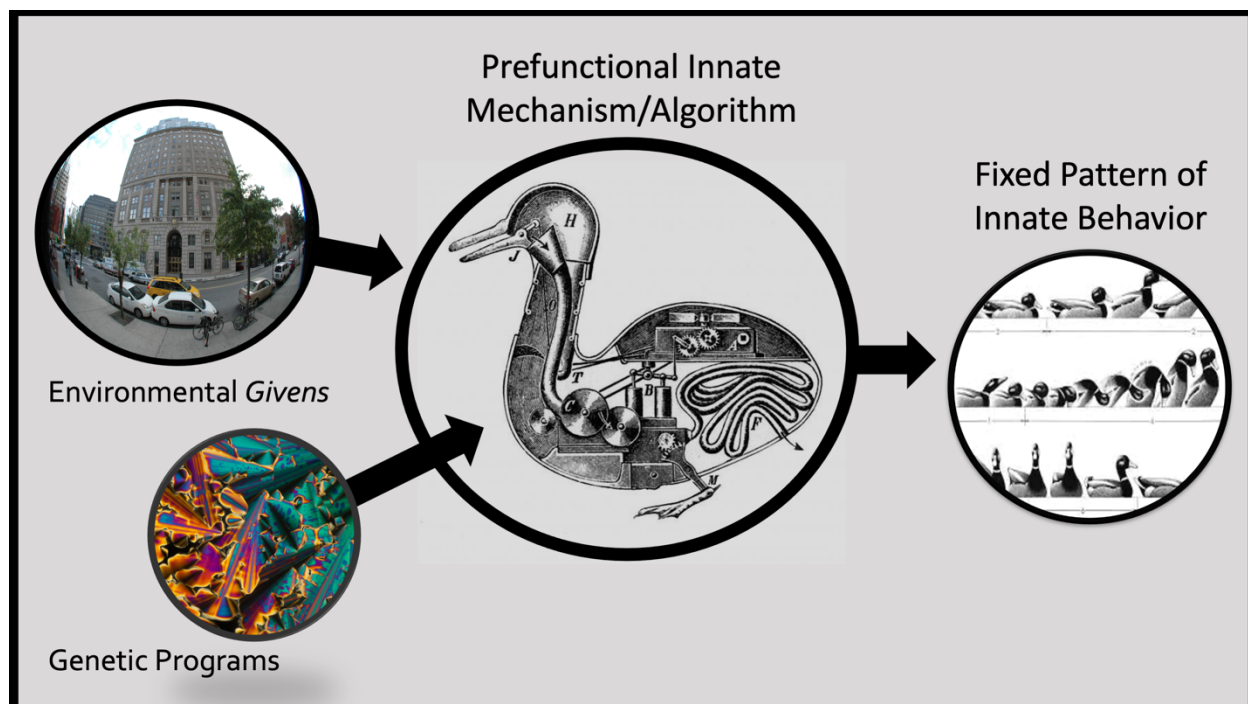
Figure 1: The Architecture of Innateness
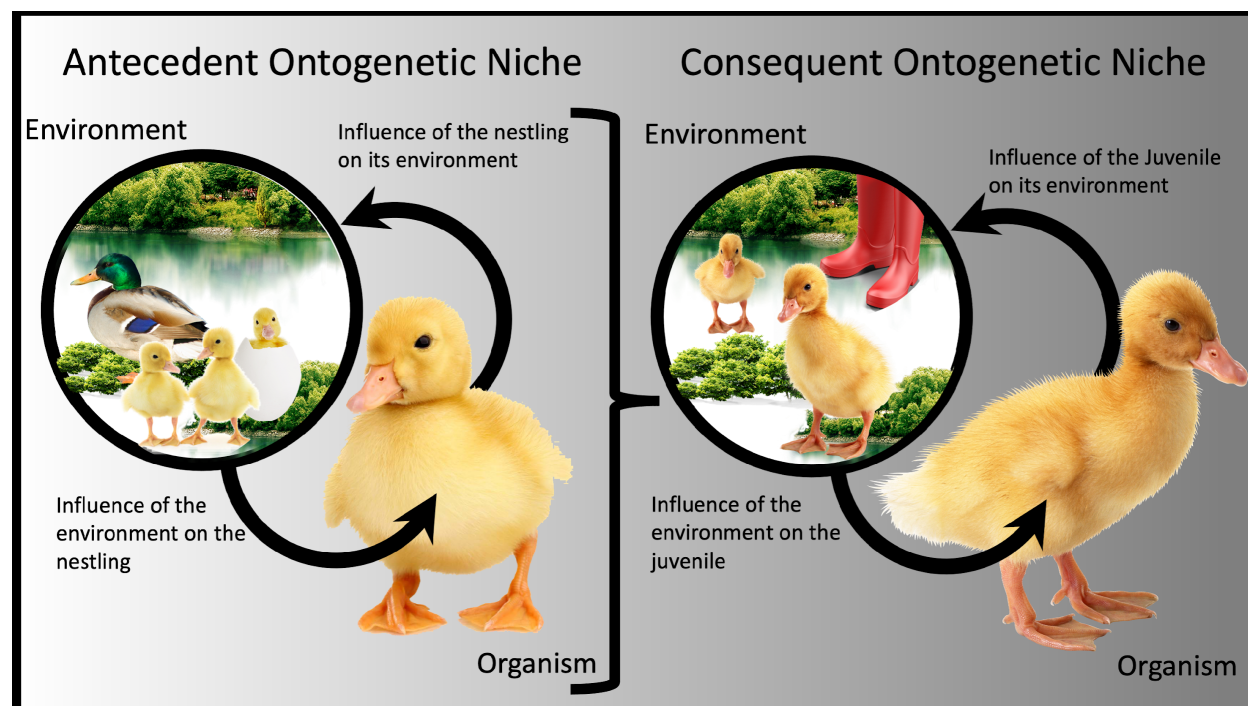
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1176 Figure 2: Development of behavior via ontogenetic niche transitions.
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1180 Caption: Diagram showing development as a process of ontogenetic niche construction