

## Selection as a domain-general evolutionary process

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### ABSTRACT

The behavioral phenotype of an organism results from selective processes acting on variation in behavioral traits during ontogeny (during life span) and phylogeny (across generations). Different adaptive processes can be categorized as environment-phenotype feedback loops. In this cross-disciplinary approach, we discuss the interaction of ontogenetic selective processes, traditionally studied by behavior analysts, and phylogenetic selection processes, traditionally studied by biologists. We elaborate upon the *Extended Evolutionary Synthesis* by addressing the connection between selection as a domain-general process and phenomena such as classical and operant conditioning, imprinting, adjunctive behavior, and gene-culture coevolution. Selection is in this context understood as a dynamic iterative feedback loop producing a phenotype beyond the strict morphotype. The extended phenotype is related to the concept of *niche construction* in which the behavior of organisms shapes their environment, which again selects the behavior of the organisms in an iterative process. A discussion of interacting environmental factors selecting human food choice both during phylogeny and ontogeny exemplifies the generality of selection processes acting on behavior.

### 1. Introduction

Darwin's (1874) elucidation of selection of traits across generations, together with Mendelian genetics, rediscovered in 1900, laid the groundwork for the so-called *Modern Synthesis* (MS), a framework of evolutionary biology that subsequently fertilized disciplines such as ethology, behavioral ecology, behavioral biology, behavioral genetics, and evolutionary psychology since the early twentieth century. During the last two decades, scholars have repeatedly questioned whether the traditional framework satisfactorily accommodates recent findings in genomics and developmental biology (e.g. Gilbert et al., 1996; Gould, 2002; Laland et al., 2014), resulting in a variety of enhanced approaches, which Laland et al. (2015) labeled the *Extended Evolutionary Synthesis* (EES). One of the advantages of the EES over the traditional MS is its focus on a “variety of distinct routes to phenotype-environment fit [which] furnish the EES with explanatory resources that traditional perspectives lack” (Laland et al., 2015, p. 9).

Contrary to the traditional MS' assumption of mono-directional gene-to-trait causality, Laland et al. (2015) argue that accommodating a plurality of underlying causes of evolution will deepen our understanding of the mechanisms of evolution. The EES goes beyond gene-environment interaction by integrating mechanisms of within-generation changes and by attending to how the expression of genes and environmental influences interdepend. Thus, instead of one component

(e.g. the genome) exerting exclusive control over another (e.g. the phenotype), causation also flows back from more complex levels of organismal organization to gene structure and gene expression.

In this article we discuss interaction processes which specify phenotypic plasticity, non-genetic transmission of traits and niche construction as evolutionary causes of behavioral and morphological diversity and adaptation. We discuss plasticity as a set of processes which were phylogenetically selected and which have evolved such as to generate evolutionary dynamics on their own.

We review a variety of phenomena that support Laland et al.'s (2015) assertion that the “EES recognizes that the evolutionary process has a capacity for ‘bootstrapping’ such that prior evolution can generate supplementary [...] adaptation-generating evolutionary processes, expressed in plasticity, learning, non-genetic inheritance, niche construction and culture.” (p.9). Phenotypic diversity within a population is not only a consequence of natural selection—it also depends on individuals' ontogenetic adaptations. *Ontogeny* here denotes an individual's entire life span. In particular, we elaborate on “learning” in terms of behavioral change during the lifetime of the individual, as one of the adaptation-generating evolutionary processes. After all, much organism – environment contact, which may result in selective transmission of traits, consists of behavior.

Influential works such as Dawkins' *Selfish Gene* (1976) acknowledge, the possibility of a range of evolutionary processes and it has long been

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recognized that “learning is the pacemaker of evolution” (Wilson, 1975, p. 156). Nevertheless, explanations of behavior have largely focused on phylogenetic causes of behavior, “covering” adjustments of behavior during life span by terming them *learning*. *Learning* is a vague concept, which explains too little of how behavior comes about. As Glenn and Field (1994, pp. 241–242) pinpoint:

Processes that account for behavior acquired during a human lifetime have been lumped together under the general term *learning*. To attribute ontogenic behavior change to learning is somewhat like attributing changes in the organic world to *evolution*, an attribution that was common even before Darwin. Darwin’s great achievement was to identify processes accounting for the origin and evolution of the organic content of the biosphere (Mayr, 1982, chap. 11). (Glenn and Field’s reference and italics).

Thus, this article defends a more specific conception of learning, which regards it as a result of both natural selection and another evolutionary process in its own right by identifying the processes that allow organisms to generate and refine novel adaptive behavioral variants.

The leading figures of sociobiology, E.O. Wilson, and of radical behaviorism, B.F. Skinner, have explicitly argued for pushing the boundaries of discipline-based dogmatism in favor of understanding the evolutionary basis of human behavior (Naour, 2009). Likewise, many current researchers of behavior from different disciplines explicitly acknowledge that behavior results from an interaction of genes and the environment (e.g. reflected in commentaries on Skinner’s (1981) “Selection by Consequences” in *Behavioral and Brain Sciences*, 1981, and in the 2016 special issue of *Norsk Tidsskrift for Atferdsanalyse*). Nevertheless, ethologists and evolutionary psychologists focus almost exclusively on the role of a species’ evolutionary history when explaining current behavior and often incorrectly depict behavioristic approaches as misconceiving organisms as born as “blank slates” (e.g. De Waal, 2016; Kappeler, 2011; Kuczynski, 2012; Pinker, 2003; Tooby and Cosmides, 1995).

*Phenotypic accommodation*, referring to mutual functional adjustment between the organism and its environment during ontogeny, typically not involving genetic mutation (West-Eberhard, 2003), is a key concept in Laland et al.’s (2015) EES. We discuss one of the EES’ central features, the “general ability of developmental processes to accommodate novel inputs adaptively” (Laland et al., 2015, p. 9) with a different emphasis from Laland et al. The EES focuses on “*organismal causes of development, inheritance, differential fitness, [and] the role of constructive process in development and evolution*” (Laland et al., 2015, pp. 2–3, our emphasis) and is “characterized by the *central role of the organism in the evolutionary process*” (Laland et al., 2015, pp. 2–3, our emphasis). Our approach ascribes the central role in evolutionary processes to organism–environment interactions, instead of to organisms. “Organismal causes” include causes within the organism, which we regard as intermediate (Newtonian) causes of behavior, whereas the ultimate (historical) causes of adaptive behavior we argue for here are ecological; that is, they lie in the contact between the organism and its current and past environment. Jablonka’s (2016) review of the implications of recent epigenetic findings for social systems argues against assigning primary significance to either Newtonian or historical causes. We follow her line of reasoning that epigenetic correlates of learning blur traditional distinctions between phylogenetic and ontogenetic influences.

We argue for a unified approach to behavior in which we treat ontogenetic and phylogenetic sources of behavioral change as an integrated process. Selective forces are a domain-general phenomenon that reduces variance of traits and optimizes phenotypes by selecting for adaptive behavior regardless of timescales and mechanisms. We discuss this domain-general process by: (a) describing its workings in natural selection; (b) applying it to behavior change during the lifetime of individuals; and (c) clarifying the interaction between different selective processes.

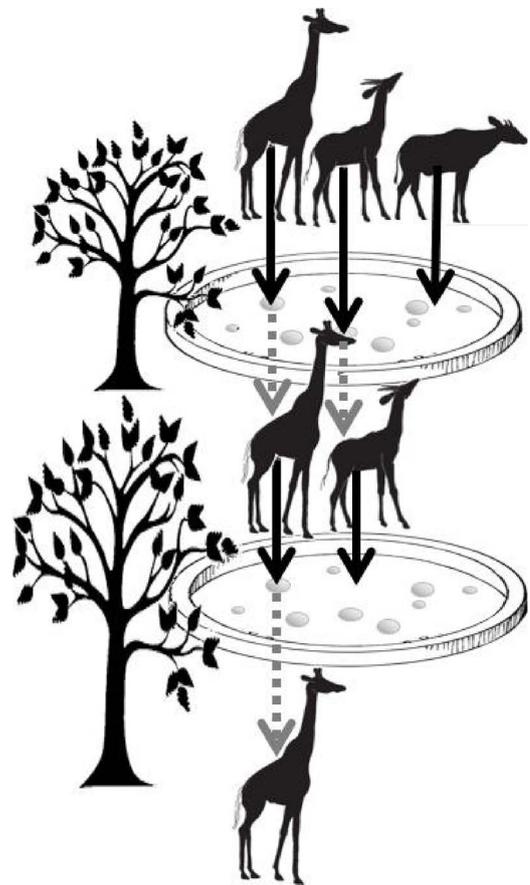


Fig. 1. Basic properties of selection seen as a sieve selecting for a gradual change in giraffes’ neck lengths.

The two oval shapes in the center of the figure represent selection pressure consisting of the interaction of the giraffes’ neck lengths and the height of vegetation. Those giraffes with neck lengths, which are most effective in reaching the vegetation pass through the holes of the sieve representing reproductive success. The sieve changes across iterations. Across generations of giraffes, selection pressures changes in an iterative process with vegetation height represented by the trees. Note that this simplified illustration ignores many characteristics of selection as a causal mode for the sake of clarity. During ontogeny, there may also be behavioral modifications not shown in the Figure. These modifications operate at a life-duration time scale (i.e. search for the “right” vegetation, migrations to taller vegetation, and conspecific encounters) and adjust an individual’s position relative to the holes.

## 2. The phylogenetic “sieve”

Evolution requires three main ingredients: Variation, recurrence, and selection of traits. Selection in the context of evolution refers to traits being favored by the environment, including a wide range of abiotic and biotic properties, as well as interactions with conspecifics and other species. Phenotypes favored under the current circumstances are passed on to future generations with a higher probability if they promote relative fitness. Naturally selected traits are genetically coded and some gene variants (alleles) are selected over others. An organism’s phenotype consists of an individual’s observable characteristics, including both morphology and behavior.

Natural selection may be compared to the workings of a sieve (Dawkins, 1995; de Vries and MacDougal, 1905; Sober and Lewontin, 1984) that selects the best available alleles coding for physiological characteristics and behavioral traits across generations. Well-adapted traits have the highest probability of fitting through the “holes of the sieve,” thus, of passing on to future generations. The example of giraffes’ morphology, which evolved as a result of “sieving longer necks”, demonstrates how gradually selected modifications rooted in genetic changes led to this particular – and peculiar – shape of holes (Fig. 1).

Within generations (i.e. during ontogeny), a suite of processes affects individuals' fitness and modify the likelihood of transmitting a genotype through the sieve. Some of these modifications are heritable, others not, but they work along with the evolutionary changes that occur across generations, as will become clear when we discuss the interplay between these two processes operating at different timescales. In accordance with the EES (Laland et al., 2015) and with what Jablonka (2016) called a *Waddingtonian system approach*, we accentuate that evolution involves more than shifts in gene or allele frequencies over time.

After dismissal of Lamarckian theories for the evolution of giraffes' necks, several competing selectionist theories attempt to explain why giraffes have long necks. A long-necked giraffe has access to leaves in higher vegetation, reaches to the ground even if it has longer legs (which are advantageous for escape from predators), can more effectively dissipate heat, and has a better leverage when swinging its head to drive off sexual competitors (Holdrege, 2003). Within a population of giraffes, individuals vary in neck length and part of this variance likely is coded genetically. For pedagogical reasons, we will here concentrate on the "tall vegetation theory" alone. As taller vegetation became more frequent, or others had overgrazed lower vegetation, the longer necked giraffe variants had an advantage, and those with genes coding for long necks passed through the holes with higher frequency. Fig. 1 illustrates this sieve-like selection process. The first row of giraffes symbolizes a population of giraffes with high variation in neck lengths. The longer-necked variants in the population better reach high vegetation, symbolized by the tree. On average, these variants (genotypes and phenotypes) survive longer and produce more offspring than shorter-necked variants. This relation is symbolized by solid and dashed arrows from the longer necked giraffes going through the holes of the sieve to the next generation of giraffes. The sieves between the rows of giraffes stand for natural selection. The next generation, illustrated by the giraffes in the middle, consists of fewer short-necked giraffes and more longer-necked giraffes than the first generation. Selection narrows down variability towards longer-necked variants. From top to bottom, Fig. 1, shows several giraffe populations, trees, and sieves, which illustrates that the selection process iterates, continuing to sieve traits (here neck length) from generation to generation.

Generally, the genotype guides the somatic and behavioral phenotype. However, not only genes in a strict sense, that is, the protein-coding parts of DNA, shape the phenotype, but also the non-coding parts that dominate the genomes of most organisms. For example, transposons, repetitive elements, and pseudogenes might shape the phenotype. The role of these non-coding parts for the organism is currently hotly debated (Graur et al., 2013; Hessen, 2015). As we will argue below, epigenetic modification is here a kind of "in-between mechanism", since it affects genomic structure and gene expression during ontogeny driven by ambient conditions. However, an epigenetic change rarely affects a genome sequence per se, and although it may be transmitted for one or two generations, it is generally not fixed in the germ-line, and should thus not be seen as a Lamarckian way of evolution.

The majority of evolutionary research has focused on different kinds of genetic transmission, to the extent that *evolutionary* is almost synonymous with *genetic* (Wilson et al., 2014). However, an evolutionary process does not necessarily require a genetic transmission mechanism. Cultural evolution may be genetically rooted in the ability to learn or adapt, but is not based on, for example, the selection of one allele over another (Richerson and Boyd, 2005). Selection occurs because individuals interact with their environment. Complex behavioral patterns, which make for the contact between organism and environment, may result from variation, selection, and retention of simpler acts, just as the complex structure of morphological features like macromolecules or complex eyes evolved as a result of variation, selection, and retention of simpler light-sensitive organs (Dawkins, 1997; Zettel, 1955).

If individuals that could react flexibly to their current environment

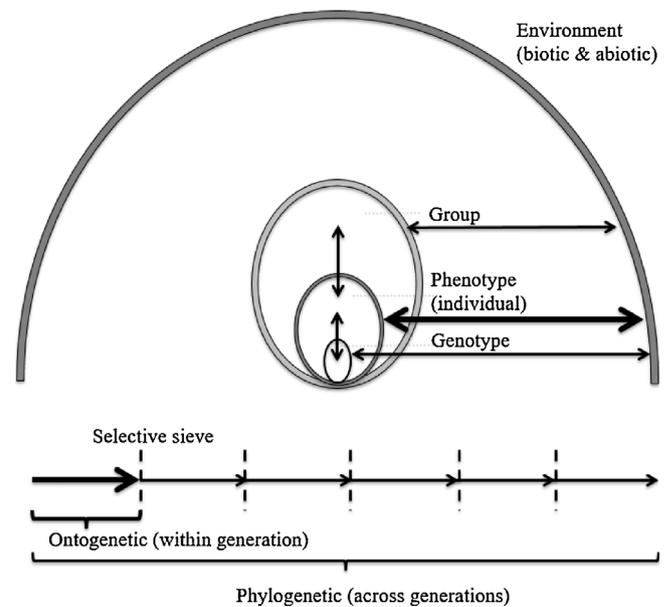


Fig. 2. Conceptual illustration of the interplay between different organizational levels of ontogenetic and phylogenetic evolution.

At all levels, there are mutual feedbacks related to the ambient environment. In most cases, the effects are strongest from the environment, but especially at the individual or group level, there are also feedbacks to the environment (e.g. the extended phenotype effect). The text provides examples of genotype, phenotype and group interactions with the environment. Phenotypic responses on the environment, focusing on behavioral iterations during ontogeny, feed back on phylogenetic responses over time, determining evolutionary trajectories, that is, which geno- and phenotypes pass through the holes of the selective sieve. The illustration distinguishes between types of selection (acting during ontogeny and during phylogeny on the bottom) and units of selection (on the top) but does not relate units and types to each other.

produced more offspring, and if this flexibility is genetically coded, this genotype will be selected, creating an additional sieve. Koppe et al. (2017) found that a knockout of the *CACNA1C* gene in mice led to different learning strategies compared to controls. As opposed to controls, knockout mice based their responses more on the previous food location than on food-indicating stimuli. This genetic influence on ontogenetic behavioral flexibility supports the idea that the sieve of natural selection, selected the workings of another sieve. In many species, this other sieve "sifts" traits over the course of an organism's ontogeny by selecting for environment-behavior feedback loops (Baum, 1973, 1981, 1989, 2015, 2016). These interactions, which we discuss in detail in the next sections, are schematized in Fig. 2.

Fig. 2 illustrates the interplay between phylogenetic and ontogenetic selection. The area of the smallest circle in the middle represents an organism's genotype, the area of the mid circle represents an organism's phenotype and the largest circle represents a group's or population's phenotype. All interact with the environment, symbolized by the double-sided arrows between the circles and the outer bow standing for the environment. Even if there are mutual feedbacks to and from the ambient environment selection of traits by the environment is strongest. We describe the effects of individual and group phenotypes on the environment in more detail in Section 5.3. *The Extended Phenotype*. The two horizontal lines beneath the bow and the circles stand for the timeframes in which selection processes tailor traits to the environment. In the context of behavioral adaptations, the upper line represents within-generation (ontogenetic) selection composed of many iterations whose beginning and end are marked by vertical dashed lines. All of these alterations together make for an organism's ontogeny, which is part of - and, thus, effects - the species phylogeny, together with preceding and following generations' ontogenies. The lower line represents selection across generations (phylogenetic selection). The relation between the upper and the lower vertical lines shows the

relation between ontogeny and phylogeny.

Evolution requires variation and selective transmission of some traits over others. Differences in environmental effects yield differences in recurrence, which then feed back to affect the pool of variants (Baum, 2017a). The supposed phenomenon of gamblers beginner's luck illustrates how variation in behavioral patterns is reduced by selective transmission. Beginners' luck is the *impression* that gambling novices experience a disproportionate frequency of success.

Gambling novices achieve varying success, and only those who are successful when they start gambling continue with that activity. Moreover, we tend to remember the successful ones. If we do not ask long-term gamblers how successful they were in the beginning, but instead sample the winning rate of novices, we see that non-successful gamblers do not continue (Taleb, 2007). The next section explains how a similar process of selective transmission limits variation of behavior during ontogeny.

### 3. The ontogenetic sieve

According to Laland et al. (2015), a distinctive feature of the EES is its recognition that adaptation can arise through both natural selection and internal and external constructive processes. For instance, organisms can respond plastically to novel conditions to generate functional variation. While plasticity is well recognized within the field, what is less well appreciated is that the specific *adaptive phenotypes generated need not be the direct targets of past* [here phylogenetic] *selection*, but may be the expression of the *more general ability of developmental processes to accommodate novel inputs adaptively*, thereby enabling functionally integrated responses to a broad range of conditions (Gerhart and Kirschner, 2007; West-Eberhard, 2003). (p. 9 our emphasis).

In the following, we specify this “*general ability of developmental processes to accommodate novel inputs adaptively*”. Thus, we discuss the relations between the following phenomena of behavioral change during ontogeny and selective processes illustrated by the sieve metaphor: Operant and classical conditioning (the latter including the special case of food aversion learning), imprinting, imitation learning and adjunctive behavior.

#### 3.1. Operant conditioning

##### 3.1.1. Phylogenetically Important Events

Fitness-promoting behavior may be selected for and is, thus, evolvable. Individuals' behavior adapts during their lifetime to their environment as a result of its relation to what Baum (2012, 2016, 2017b) labeled *Phylogenetically Important Events* (PIEs). PIEs are fitness-affecting events such as predation, finding food when foraging, and mating. If PIEs induce behavior, some stimulus control is due to ontogeny and some to phylogeny. In the jargon of operant conditioning procedures, stimulus control is said to exist when the organism behaves differently in the presence of a given stimulus than in its absence. The contingency between behavior and PIEs can select behavior during ontogeny because the affectability of behavior by such events has been advantageous for fitness during phylogeny.

##### 3.1.2. Contingencies

A contingency between two events, such as behavior and a PIE, exists when the probability of event A differs, given event B (Baum, 2012; Rescorla, 1968, 1988). These events may either coincide or occur at different points in time but for behavior to become susceptible to a probability of events, there need to be several occurrences of the events. This makes accidental contingencies rare, as the accidental conjunction would have to occur at least twice. If the probability of, say, being praised, is the same regardless of performance, then no contingency exists between praise and performance. Thus, praise would not select performance. Greater temporal closeness between the two events often enhances the susceptibility of behavior to the contingency. Hence, a

contingency relates or connects behavioral and environmental events. It links a PIE to an activity and results in an increase or decrease in the activity.

Traditionally, operant conditioning is assumed to occur primarily due to temporal proximity between discrete responses and reinforcers or punishers (e.g. Skinner, 1948). Yet, Rescorla (1988) presented data supporting an alternative view, which he summarizes as follows: “a modern view of conditioning as the learning of relations sees contiguity as neither necessary nor sufficient. Rather, that view emphasizes the information that one stimulus gives about another. We now know that arranging for two well processed events to be contiguous need not produce an association between them; nor does the failure to arrange contiguity preclude associative learning.” (p. 152).

Rescorla (1988) exposed rats to a tone (CS) that occurred for two-minute periods and applied brief electric shocks (US) with no particular temporal relation to the tones. For one group of rats, Rescorla only applied scheduled shocks during the tones. This means that both groups of rats were exposed to the same contiguity between tone and shock but the contingency between tone and shock differed between groups. One group's likelihood of shock was independent of tone. In the other group, shock occurred during tone only. Only the behavior of rats in the “contingency” group associated tone and shock, no such learning occurred in the “contiguity but no contingency” group. This means that the contingency between tone and shock selected the tone's influence on the rat's behavior. The procedure of the contingency group arranged for a covariance between presence and absence of shock and tone but not for a covariance of shock and other ambient variables as, for example, comparably stable smell, light or texture of the experimental chamber. To sum up, also in classical conditioning procedures the contingency between two events, the CS and the US, selects the CS from all other stimuli in the organism's environment. We discuss more parallels between results of classical and operant conditioning procedures in Section 3.2.

Due to the detrimental focus on the role of contiguity (temporal proximity) between events in traditional approaches to operant conditioning, we, here, adopt the vocabulary of ontogenetic selection to emphasize that a contingency, which makes for behavioral change, is not merely defined by which events co-occur but also includes which events do not co-occur. To be sure, contiguity between activities and PIEs (in a contingency) catalyzes behavior change. Thus, one may define contingency as both a temporal and a probabilistic relation. However, in order to distinguish our position from the traditional exhaustive definition of contingency as contiguity (e.g. Skinner, 1948), contiguity of a response and a PIE are here not part of our working definition of *contingency*. Instead, we refer to a contingency between an activity and a PIE as the relative probability of occurrence of a PIE given an activity as contrasted with the PIE's probability in the absence of the activity. We regard the temporal relation between these events as a gradual relation whose relevance for behavioral change is an empirical question and not part of our definition of *contingency*.

Dispensing with Skinner's (1948) position that “conditioning takes place presumably because of the temporal relation only, expressed in terms of the order and proximity of response and reinforcement” (p. 168), is congruent with Baum's (2013, 2016) multi-scale view. The multi-scale view (Baum, 2015) is based on acknowledging that all behavior takes time. During the lifetime of an organism, its activities recur – but recurrence is selective. Ontogenetic selection of activities occurs, on the one hand, because the total time an organism can spend behaving is limited and, on the other hand, because some activities lead to events more advantageous to fitness than others. Different behavior produces different PIEs. If a food-deprived rat gets a food pellet when pressing a lever, the pressing rate increases while other activities decrease. The food modifies the lever's effect on the rat's behavior. The food's effect on the rat's behavior is such that, once the lever press appears, it may be molded or “shaped”. If this moldability promotes relative fitness, it will increase across generations of rats. The

contingency between the activities and PIEs makes for recurrence or extinction of activities within a generation and eventually affects behavior across generations.

The growing field of artificial intelligence and robotics also illustrates behavior change during ontogeny by means of iterative feedback (see Luo and Hauser, 2017; Peters et al., 2003 for examples of application in robotics). With few initial instructions and iterative feedback for performance, bipedal robots can learn to walk. In the world of robotics, this evolution is still limited to ontogeny, but there are realistic hopes – and fears – that there will be a phylogenetic perspective here as well.

A difference between selection for activities such as lever pressing and phylogenetic selection is that activities are not transmitted to other organisms unless they are socially learned or epigenetically guided. Generations of activities of the same organism are sifted throughout the organism's lifetime. In ontogeny, the (recurring) unit of selection going through iterations of the sieve is the behavioral pattern, which may be exhibited by a single or a group of organisms (Rachlin, 2014; Simon, 2016a,b, 2017). The activity-PIE contingency is doing the selecting across “behavioral generations” within an organism's lifetime, which do not correspond to generations of organisms. The EES and Jablonka's (2016) Waddingtonian approach do not presuppose that selected phenotypes have a one-to-one causal relationship to genotypes, that is, to inherited transmitters. Neither does selection of behavior within the lifetime of the organism require (inherited) transmitters other than activity-PIE contingencies.

### 3.1.3. Events in a contingency with Phylogenetically Important Events: PIE-proxies

The change in rats' lever pressing, as a function of their contingency with PIEs, is an example of operant behavior. Operant behavior is, by definition, behavior that affects its environment. The contingency between behavior and certain events in the environment selects which behavior recurs during ontogeny. Some of these events, PIEs, acquire during phylogeny their power to induce behavior during ontogeny. Other events that induce behavior during ontogeny have gained their power to influence behavior during ontogeny. These are, in Pavlov's (1928, 1927) terms, *conditional stimuli*, or *proxies of PIEs* in Baum's (2012) terms. Not only does behavior change due to its contingency with PIEs, but also as a function of its contingency with proxies of PIEs. The proxies of PIEs do not directly affect fitness, but tend to co-occur with PIEs. If money correlates with resources, our behavior changes as a function of its correlation with money.

Traditionally, operant conditioning, having its origin in Thorndike's (e.g. 1911/2000) work, and respondent conditioning, having its origin in Pavlov's work (e.g. 1928, 1927), are regarded as two distinct learning mechanisms. From an evolutionary perspective, however, it is more likely that a single learning process with diversity in implementation was selected (Donahoe and Vegas, 2004). As we will see in the following section, data support this view.

### 3.2. Classical conditioning and the unified view of ontogenetic selection of behavior by its contingency with PIEs

*Classical conditioning* traditionally denotes behavior change resulting from pairing of two stimuli. Before the procedure starts, one stimulus, the conditional stimulus (CS), does not elicit any response. Another stimulus, the unconditional stimulus (US), consistently elicits a response, called unconditional response (UR). After pairing, or contiguous presentation, of the originally neutral CS and the US, the CS comes to elicit the response (CR). Donahoe and Vegas' (2004) work suggests regarding both classical and operant conditioning effects as stemming from the same learning principle. This view of a single process adjusting behavior to the environment assumes that the relation between environmental *stimuli* and *behavior*, not primarily between two stimuli, the CS and US, makes for the behavior change.

Donahoe and Vegas (2004) designed an assembly of experiments in which, unlike in traditional procedures, the CS and the US were not confounded. They injected water (the US) into the oral cavity of restrained pigeons and measured the latency and rate of the pigeons' following bout of throat movements (the UR). A light served as the CS. Throat movements have an appreciable latency and duration, which makes it possible to differentiate the ordinal temporal relation of the CS to the UR from that of the CS to the US. When Donahoe and Vegas introduced the CS after US onset but before UR onset (US-CS-UR procedure), throat moving (the CR) in response to the light (CS) occurred. Having tested different orders of introducing CS and US before and during UR onset, Donahoe and Vegas concluded that the relation between the CS and the UR, not between CS and US, is fundamental to learning. This finding suggests an alignment of classical and operant conditioning not only in the sense that they both tailor an organism's behavior to the environment but also in the sense that both view behavioral change as a result of the relation of a conditional stimulus (or discriminative stimulus) to subsequent behavior.

Donahoe and Vegas' (2004) experiments suggest a unified account of learning processes not based on learning (unconditional) *stimulus*-(conditional) *stimulus*-pairings but on *behavior* – *stimulus* contingencies. Rescorla's (1988) findings support the importance of contingencies, as opposed to mere contiguous pairing of conditional and unconditional stimuli. Applied to Baum's (2012) concept of PIE-proxies, which we discussed in the previous section, Donahoe and Vegas' and Rescorla's findings imply that events become proxies of PIEs when they enter into a contingency with behavior. Behavior would need to occur to become under control of PIE-proxies and the presence of PIEs during the conditioning process induces it. Thus, there needs to be a contingency between PIEs and PIE-proxies, and between both of them and behavior.

Ontogenetic behavior change through exposure to contingencies may at times be subsequently phylogenetically transmitted. Dias and Ressler (2014) used a classical conditioning procedure exposing mice before pregnancy to a contingency between a particular smell and electric shock. Two subsequently conceived generations also partly showed startle-responses when exposed to this particular odor without conditioning during their ontogeny.

Even if conditioning procedures show that the environment alters behavior and these alterations may sometimes be transmitted to future generations, heredity and tradition make for stability. Heredity and tradition make sure that behavior also resists change. As Jablonka (2016) points out, experience changes behavior but not randomly or without limit. What is the nature of the constraints to behavioral change? Why is not all behavior equally likely acquired during ontogeny? Natural selection made for differential susceptibility to ontogenetic learning processes. Reactions of disgust to a rotten carcass are more easily acquired than disgust or fear of electrical outlets (Mineka and Öhman, 2002). This reflects how tightly interwoven different selection processes, shown in Fig. 2, are. In the following, we discuss a special case of classical conditioning, food aversion learning.

### 3.3. Food aversion learning

Food aversion learning (presumably first described by Garcia et al., 1955) is one of the best documented cases of phylogenetically acquired high susceptibility of behavior to environmental events during the organism's ontogeny. When nausea follows an animal's food consumption, the animal avoids that food in the future. Usually, illness following food indicates that the food is poisonous but this effect may occur without an actual causal relation between the food and the sickness. Yet, given the food was noxious, avoidance of similar substances in the future improves relative fitness. In most learning situations, conditioning of a stimulus (food) and a response (regurgitation) requires several exposures – allowing for more certainty about the causal relation between the two. However, avoidance of some non-poisonous food is on average less disadvantageous to fitness than consuming poisonous

food once more. Thus, phylogeny brought about an especially sensitive ontogenetic selection mechanism, which results in avoidance of eating bad food at the cost of risking some “false positive responses”, that is, not eating good food.

We are born with a tendency to acquire easily reactions of disgust, for example, to rotten food. This special preparedness results from phylogenetic selection. When our educators provide consequences such as praise or disapproval contingent on our interaction with certain events, this feedback further ensures avoidance of certain smells or flavors. Consuming or avoiding certain meats such as cattle, pork, dogs, insects, and so on are examples of behavioral patterns selected by consequences during our ontogeny. This means that an ontogenetic selection process acts on top of phylogenetic preparedness.

### 3.4. Imprinting

We have discussed how classical and operant conditioning relate to the sieve metaphor. How does a learning process called “imprinting” relate to selection? Ethologists have described the behavior of ducklings following moving objects, which they were exposed to when hatching, as a result of what Lorenz (1937) called *imprinting*. Imprinting is a “process by which certain stimuli become capable of eliciting certain ‘innate’ behavior patterns” (Jaynes, 1956, p. 201). As early as 1960, Peterson conducted an experiment indicating that the duckling’s following does not merely result from phylogenetically selected patterns, but also from selection of the ducklings’ activities after hatching. The experiment shows that ducklings are not “hard-wired” to follow their mother or whatever object they see after hatching, but that they rather have a tendency to remain as close as possible to that object. Thus, if one makes the object’s approaching of the duckling contingent on the duckling’s moving away from the object, the contingency between moving away and the increased proximity to the object selects the duckling’s moving away.

We can “teach” children to run away from us if we follow and hug them when we catch them. Children are not “preprogrammed” to approach us, but increasing closeness to a trustworthy adult is presumably an event that, during our species history, gained the power to select behavior (e.g. running away) during the lifetime of the individual. This suggests that which events can have the effect of selecting behavior (e.g. physical closeness to organisms we depend upon) is naturally selected (phylogenetic sieve).

The sensitivity of behavior to contingencies between PIEs and proxies of PIEs is also naturally selected. The contingency between following after or running away with the PIE-proxy physical closeness, selects following after or running away. The phylogenetic sieve selects the function of the ontogenetic sieve by limiting which events can select which behavior during the lifetime of the individual. Natural selection sets the frame for selection of behavior during ontogeny as we have seen in food aversion learning. The question of where a behavioral pattern lies on the continuum from “hardwired” to “not hardwired,” corresponds to the empirical question of what each sieve contributes.

We are born with some behavioral tendencies (originating in the phylogenetic sieve) upon which the environment acts and shapes behavior (the contribution of the ontogenetic sieve). Imitation learning is yet another phenomenon illustrating that natural selection limits the parameter space of behavioral options that are “filtered” by the ontogenetic sieve, and which then may provide feedback on the phylogenetic sieve.

### 3.5. Imitation

We are genetically equipped with mirror neurons that enable (basic forms of) imitation. Among others, Bråten (2006, 2007) documented that infants smile back when we smile at them. The ontogenetic sieve acts on those imitations. Successful imitations (those followed by fitness promoting consequences) become part of the behavioral repertoire. The

ontogenetic sieve selects these; other imitations are one-time occurrences. Less responsive and unsmiling children may run the risk of less care and less mutual child-mother oxytocin boost. Hence, this kind of imitation is clearly fitness promoting and is, thus, a target for selection. As humans have a long history of living in groups (Diamond, 2012), human behavior is especially susceptible to social consequences (Richerson and Boyd, 2005) such as signs of affection or threat of exclusion from the community. For example, we provide social stimuli inducing more imitation, as when we say “do like this” and praise the imitation (Baum, 2017b). Food choice provides examples of imitation-initiated behavior change without social consequences and behavior change, which the ontogenetic sieve selects, making the imitating behavior even more effective.

Consumption of delicious food initially imitated from a conspecific will recur, not requiring a positive social consequence, but many other changes in diet initially started by imitation are eventually a function of social PIE-proxies. Imitation is also embedded in reciprocity, tit-for-tat behavior (see Axelrod, 1997, for more detail) and social norms. Nyborg et al. (2016) pointed out that social norms guide group behavior, which can change in response to positive or negative feedback loops. For example, variation in grocery prices, incomes, and nutrition content across countries cannot fully explain variation in diets. Likely, social norms (contingencies between diet and PIE-proxies) can partially account for such differences. Differences in diets make cooking shared meals cumbersome. If people tend to prefer the foods they are used to, this will be a stabilizing factor until new norms or access change this. Hence, if a less meat-intensive diet became the norm, individuals might conform partly owing to the social consequences of being environmentally friendly and respectful of animal ethics. Nyborg et al.’s argument suggests that access to pleasant and convenient joint meals could be another social PIE-proxy selecting a less meat-based diet.

### 3.6. Adjunctive behavior

*Adjunctive behavior* (see Pierce and Cheney, 2013 for an overview) is yet another phenomenon constituting a piece in the larger puzzle of interconnected sieve-like evolutionary processes outlined by Jablonka (2016), Jablonka and Lamb (2007) and Laland et al. (2015). *Adjunctive behavior* denotes behavior occurring during the interim period between accesses to both response-dependent and response-independent PIEs, which either occur at fixed or variable time intervals (see Azrin et al., 1966; Burks, 1970; Flory, 1969; Staddon and Simmelhag, 1971, for further discussion). In contrast to adjunctive behavior, an activity such as a lever press that produces a scheduled PIE, is denoted as a terminal response. Staddon and Simmelhag (1971) clarify the relation between adjunctive and operant behavior as follows:

The linkage between terminal and interim states is assumed to be direct and reciprocal, so that the strength (defined below in terms of rate) of activities during the interim period is directly related to the strength of the terminal response [...] the strength of behaviors associated with the interim period will be determined both by the value of the terminal reinforcement schedule, as well as by the value of the reinforcers proper to them (p. 35).

The distinction between adjunctive and terminal activities stems from traditional artificial procedures of behavioral selection (which Baum, 2002 calls Skinner’s molecular account). An experimenter who wants to bring about a certain type of (terminal) activity, such as lever-pressing, likely experiences behavior that does not have the specified target properties (i.e. not pressing the lever) as intervening in his or her endeavor. Falk (1969) called this behavior *adjunctive behavior*. However, as both terminal and adjunctive activities appear to change together in response to PIE presentation, Baum suggested alternatively to view terminal and adjunctive behavior as a “behavior package” in the sense of being a cohesive temporally extended unit of behavior that takes up some time in an organism’s allocation of time to different

activities. How much time activities take up changes if the contingency between PIEs and parts of the allocation changes, such as when food is presented contingent on lever pressing.

Taking into account that experimentally scheduled PIEs are not the only PIEs present or putatively producible in a natural environment, we see why adjunctive behavior may have evolved. Optimally, both currently strong and growing organismic needs control behavior in the wild. Thus, it seems reasonable that allocating behavior so as to balance these needs was naturally selected. Some adjunctive behavior induced by a PIE affects the effects of the PIE (W.M. Baum, personal communication, October 3, 2017). Water consumption enhances the effects of food. In addition, adjunctive behavior ensures that animals do not linger near the source of a scheduled PIE (e.g. the lever or the food tray producing pellets) at times when food is unavailable. In the wild, adjunctive behavior would entail that the animal leaves the situation, allowing satisfaction of organismic needs that could not be satisfied while the scheduled PIE was produced or consumed. In the experimental chamber, the schedule, which governs PIE delivery, in addition to physical restraints, keeps the animal in vicinity of the withheld PIE. Staddon and Simmelhag (1971) hypothesize that, as a consequence of these restraints, behavior potentially leading to other PIEs than the scheduled ones may occur in extreme forms. Falk (1961) observed excessive drinking (polydipsia) in rats on a variety of intermittent schedules of food presentation. Early during the interim period between food pellet presentations, rats drank large amounts of water. In the wild, rats normally eat substantial meals instead of food-pellet-like portions. Perhaps each consumption of a pellet triggers drinking as if a meal had ended. This means that these extreme forms are non-adaptive by-products of an adaptive predisposition to terminate activities for periods in which they do not produce PIEs (cf. McFarland, 1966 on displacement activities, see Staddon and Simmelhag, 1971, for further discussion).

In summary, adjunctive behavior changes with terminal activities, which are selected and adaptive in non-restrained conditions. At the same time, the contingency with PIEs does not directly sift adjunctive behavior, and in certain restrained conditions, it constitutes a maladaptive byproduct. In the following, we discuss the sieve metaphor's scope of applicability by means of another example of behavioral change, which occurs under certain conditions as a maladaptive byproduct of a selected behavioral pattern.

#### 4. The sieve metaphor's scope of applicability and suitability

We have reviewed how phenomena as diverse as classical and operant conditioning, food aversion learning, imprinting, adjunctive behavior and imitation relate to selection as a causal mode. In this article, we elaborate on the EES' (Laland et al., 2015) claim that "learning" is a central factor in evolution by suggesting that selection is a common causal mode in behavioral change during ontogeny and phylogeny. The sieve metaphor attempts to explain *how* much behavior is learned, but does not make claims about *what* behavior is learned during ontogeny and *what* behavior is phylogenetically acquired. The environment's influence on behavior is not limited to an organism's current environment. Behavior is "under control of" or "shaped by" stimuli in the organism's historic and current environment. The historic environment consists of the organism's phylogeny and its ontogeny up to the present, where the latter also influences the former over time. Environmental and behavioral events may have a variety of probabilistic relations to each other. In the case of reflexes, the phylogenetic sieve selected (almost) a one-to-one relationship between environmental stimuli and responses occurring during ontogeny. This is not the case for operant behavior.

Selection processes do not explain all behavior but they explain why behavior adjusts within the lifetime of the individual as so to bring about certain consequences. Behavior that does not adjust in a way as to increase or decrease the probability of occurrence of a certain event, is

not directly selected. Some parts of "released behavior" such as the Greylag goose's egg retrieval movement (Lorenz and Tinbergen, 1938) are an example of behavior that does not directly result from selective processes, neither during ontogeny, nor during phylogeny. If an egg becomes displaced from the nest, Greylag geese roll it back to the nest with their beak. If the egg is removed from the goose during the performance of egg rolling, the bird commonly continues with the behavior as if the beak still maneuvered an imaginary egg. The phylogenetic sieve presumably directly selected the general occurrence of egg-retrieval; however, consequences did not select the continued egg-retrieval movement after an egg is removed. If they had, the behavior would adjust after the egg was removed. Continued egg-retrieval neither confirms nor disconfirms the role of selection in behavioral change, it simply falls outside of the scope of direct effects of selection. All behavior is due to evolution in the end but not necessarily directly selected. The general occurrence of egg rolling is likely an adaptation directly selected for. Continuation of the egg-rolling behavior probably is an indirectly produced byproduct of adaptive egg rolling.

The sieve metaphor only directly applies to adaptive traits. Behavioral tendencies can either be sieved during phylogeny, during ontogeny, or they can be non-adaptive. As Smith (1983) puts it;

Just as it is common to identify Darwinian biology with the proposition that all organic features are due to natural selection, so it is common to identify Skinnerian psychology with the proposition that all behavior (except reflexes) is the result of operant conditioning. Such identifications make for false drama, for each new discovery of a non-adaptive organic feature or of an innate behavior pattern refutes Darwinism or Skinnerianism respectively (p. 141).

The suggestion that much behavior results from a sieving-like process does not argue against the view that certain abilities are native. On the contrary, it argues that some behavior *is* innate since it accounts for adaptations of behavior to the environment during phylogeny and during ontogeny.

One of the benefits of illustrating selection as a causal mode by means of sequential sieves, shown in Fig. 1, is that the metaphor emphasizes that adaptation is a gradual process. Since PIEs or their proxies correlate differently with activities, they shape behavior. If an inexperienced seagull chick is too far from the parent's bill, its pecking thrust misses the target and the chick falls forward. If its pecking thrust is too strong, the chick is thrown back. Older chicks hardly make such mistakes. The experience of overshoots and undershoots allowed them to adjust their distance (Hailman, 1969). If, in an experimental chamber, the rat's environment changes, that is, if for example the number of lever presses required to obtain a pellet is gradually increased, the pressing pattern changes. Just as giraffes would likely have become extinct if the height of the edible leaves had suddenly jumped from ten to twenty feet, so a rat's lever pressing would likely disappear if the ratio of lever presses required to attain the food pellet was increased beyond the limit of the rat's capability (Rachlin, 2014). The natural variation in lever pressing at each stage must include patterns that will produce food at the next stage. However, since ontogenetic mechanisms may allow novel structures to be effectively integrated, this does not mean that adaptive mutations must have small effects (Laland et al., 2015).

Like natural selection, selection of responses during ontogeny works only on behavior that is already present as a consequence of variation at a previous stage. Thus, adaptations during ontogeny work on top of natural selection, which produced this additional selection mechanism (Baum, 2004; Rachlin, 2014; Skinner, 1981; Staddon and Simmelhag, 1971). These two evolutionary processes often work together. However, the illustration in the form of sieves does not cover one relation between selection during ontogeny and phylogeny: During ontogeny, selection acts on innate movements as well as on earlier ontogenetically selected behavior.

By talking about the sieves shaping ontogeny and phylogeny, we do

not mean to imply that there are two and only two types of selection. For example, if one wanted to explain cooperation between several individuals, one may want to include the spread of cultural practices, that is, behavioral patterns spreading across generations of individuals (see Simon and Baum, 2012, for a more detailed discussion), transmitted by contingencies with the environment, and at times involving correlations with genetic changes. An example of cultural selection is the selection of behavioral patterns consisting of the cumulative actions of several individuals, leading to a common PIE, such as prey resulting from cooperation in hunting (Glenn, 2003). We discuss these aspects, not reflected in the sieve metaphor, in the next section. McLaughlin (2007, 2011) describes further limitations of using the sieve as a metaphor for natural selection.

## 5. Interactions between selection processes

In the next sections, we discuss phenomena such as gene-culture coevolution, epigenetics, and niche construction where mechanisms on evolutionary and ontogenetic timescales interact.

### 5.1. PIE-behavior feedback loops

The driving force doing the selecting, may it be selection of behavior or morphological traits during ontogeny or phylogeny, is the organism's contact with PIEs. For example, during phylogeny, selection of food-intake specific morphology, and behavioral tendencies interacted. Darwin's "finches" (*Geospizinae*) beak shapes coevolved with the availability of insects, cactus seeds, and other foods (Darwin, 2003 (1859); Grant, 1999). Next to morphology's selection during the history of the species, also behavior optimizes nutrition. De Waal (2016) lists examples of non-human animals that have been observed to wash rice and to crack nuts. Woodpecker finches (*Camarhynchus pallidus*) break off cactus spikes that they use as tools to reach insects in trees (Teblich and Bshary, 2004). This is a behavioral pattern only shown when access to insects is limited.

Just as different alleles create variation in morphology and behavior upon which natural selection acts, variation in behavioral patterns resulting from learning during the lifetime will influence an individual's contribution to the next generation's genepool. Just as the degree of variation in organisms' morphology is sensitive to environmental conditions over generations, behavioral variability is highly sensitive to environmental contingencies (Grunow and Neuringer, 2002; Rachlin, 2014). Organisms' activities select their environment, while their environment, in turn, selects organisms' activities (Baum, 1973; Ferster and Skinner, 1957; Skinner, 1953). PIEs induce behavior and are consequential on behavior. A seed on the ground induces a Ground finch to peck, and more pecking in related areas results in finding more seeds, but more pecking in a constant limited area results in finding fewer seeds as this area now contains fewer and fewer seeds. Experiments show that the non-conditional presentation of water drops induces drinking in rats (e.g. Hughes et al., 1994). At the same time, occasionally finding water in certain areas maintains looking there. These examples of activities that recur because of the feedback show that ontogenetic and phylogenetic selection can work hand in hand. Selection processes, however, may also work at cross-purposes.

### 5.2. Ontogenetic and phylogenetic selection mechanisms working in opposite directions

A variety of behavioral problems results from ontogenetic and phylogenetic selection mechanisms working in opposite directions. Some of these problems have been described as problems of self-control (e.g. by Locey et al., 2013; Rachlin, 1995, 2004, 2016) or behavior-environment mismatches (e.g. by Buss, 1995, 2005; Buss, 2015; Buss and Kenrick, 1998; Cosmides and Tooby, 1997; Van Vugt, 2006).

Partly as a result of natural selection, we have different metabolic

responses to diets both in terms of quantity and quality. Previously sparse and valuable resources, that now have become available in surplus, become disadvantageous. This mismatch is a kind of "ecological trap" (for more extended discussion, see Battin, 2004; Kristan, 2003; Weldon and Haddad, 2005), occurring when the attractiveness of a once-scarce resource remains and promotes intake at rates and quantities that no longer promote fitness. With food continuously obtainable, overeating constitutes one of the factors contributing to individuals becoming overweight (Johnson et al., 1956; Ludwig et al., 1999; Ruhm, 2012; Shah and Jeffery, 1991). More than one third (78.6 million) of American adults are obese (Ogden et al., 2014). Obesity-related diseases such as heart disease, stroke, type-2 diabetes, and certain types of cancer are some of the leading causes of preventable death (Pi-Sunyer et al., 1998). Baschetti's (1998) observations show that different populations responded differently to the dietary changes of a more "western" diet. Individuals in some populations are more likely to develop diabetes and cardiac diseases than others, which suggests that the effects of diets have a strong gene-cultural component.

Sugar preferences are a function of age, and contingencies between sugar consumption and PIE-proxies can select limiting sugar intake during ontogeny. Mennella's (2014) review shows, on the one hand, that children initially prefer higher levels of sweet tastes and reject lower levels of bitter tastes than adults do but, on the other hand, these preferences can be shaped by sensory experiences. She shows further that infants who either consumed milk from mothers with low sugar diets or were repeatedly exposed to low sugar foods when starting to eat, tended to moderate sugar intake later in life. Proxies of PIEs such as social affection and consequences of good health that correlate with moderating sugar consumption may shape eating habits further throughout ontogeny.

The calorie choice example illustrates that ontogenetic and phylogenetic selection processes here work in opposite directions. One process (phylogenetic selection) results in making high-calorie choices whereas the other (ontogenetic selection) results in avoiding high-calorie choices. Evidently, this example is greatly simplified. It depicts the fictional extremes of a graded phenomenon such as calorie intake, which only in some organisms actually correlates with weight, social, or health consequences. Nonetheless, the sieve metaphor may function as a pedagogical aid illuminating queries into issues such as culturally differing food choices and change of children's food choices as they are exposed to a wider variety of food when growing older.

This possibility of goal-oriented behavior change during ontogeny resembles the possibility of morphological (and behavioral) change due to selective breeding across generations. To the extent that moderate eating is an extended behavioral pattern selectable during ontogeny, we may change an aspect of the organism's current environment (e.g. social feedback) so as to bring forward an adaptation to other aspects of the current (high-calorie) environment counteracting phylogenetically selected adaptations to former (low-calorie) environments. Ontogenetic selection can counteract phylogenetically selected traits. Sometimes phylogenetic and ontogenetic selection work hand in hand, an example of which is an organism's "extended phenotype".

### 5.3. The extended phenotype

As Winston Churchill phrased it "We shape our buildings; thereafter, our buildings shape us." (as cited in Kerst et al., 2007, p. 25). Behavior affects the ambient milieu in conspicuous ways that may act as a particularly strong selective force back on organisms. The behavior of organisms may literally shape their environment in ways that have obvious feedback on evolutionary traits (Laland et al., 2015).

The role of genes often reaches outside the individual's body. For example, birds' nests; beaver dams; beehives; termite mounds, and human constructions of all sorts of devices to farmlands and cities, have all been labeled instances of niche construction (Laland et al., 2016; Lindholm, 2012), or of the extended phenotype (Dawkins, 1983). The

ability to construct such extended phenotypes is likely in part genetically coded and selected for. The resulting products provide feedback on the organisms' morphology and behavior. They shape evolution (Laland et al., 2015) by selecting for traits that further promote niche construction, that is, the ability to produce better hives, dams, houses and the like. According to Creanza et al. (2012), some types of niche construction may be conceived as Lamarckian in the sense that traits acquired during ontogeny can be passed on.

Dawkins' (1983) concept of the extended phenotype focuses on the effects of genes on behavior that modifies the environment. The notion of the second sieve described here takes Dawkins' idea one step further by specifying how the organism-environment relation is modified during the lifetime of the individual based on modification of "non-hardwired behavior." In addition, some heritable phenotypes cannot be explained by changes in the DNA sequence but by changes in its expression. These play a central role in the EES. In the following section, we discuss these phenomena, referred to as *epigenetic*.

#### 5.4. Epigenetics and culture-gene feedback loops

Some behavioral patterns, such as being a risk seeker or not, being bold or shy, flexibility or rigidity, and the willingness to change and test new habits, are likely to involve a genetic component (Spector, 2012) and, no doubt, this will be instrumental for the individuals' responses to different situations during their lifetime. In addition, a suite of epigenetic modifications may potentially permit feedback from the environment. Presumably, these modifications affect behavior by alterations of an individual's gene-expression during ontogeny, from zygote to senescence. There are various mechanisms that cause methylation or "silencing" of genes, and briefly these epigenetic signals, which are often small RNA units, act as "on or off switches" on the genome. It is thus not the DNA sequence per se, but the expression (activity) of the affected genes that is modified.

Factors ranging from diet (documented e.g. by Gordon et al., 2012; Hardy and Tollefsbol, 2011) to stress (documented e.g. by Rutter et al., 2012; Spector, 2012) may make epigenetic modifications likely. In her thorough review of cultural epigenetics, Jablonka (2016) emphasizes that learning and memory have epigenetic correlates. She further points to a wide range of cases of cultural feedback where changes in nutrition and exposure to environmental hazards, leading to psychological stress, cause changes in the epigenetic profile of individuals. McNew et al. (2017) recently demonstrated that epigenetic variation might govern differences of "Darwin finches" adaptations in urban and rural populations. Jablonka predicts that the search for epigenetic modifications in ancient DNA, usable to trace cultural changes over time where they have left epigenetic footprints, will become an intensively researched field in the near future.

Examples of epigenetic impacts of diets abound (Hardy and Tollefsbol, 2011). Striking examples of both physiological and behavioral effects of dietary deficiency during the Dutch "hunger winter" not only demonstrate epigenetic impacts at the population level, but also suggest that such effects may be transmitted across generations (Heijmans et al., 2008). Numerous examples show how eating habits affect also subsequent generations in both men and mice (Jablonka, 2016; Pembrey et al., 2014; Spector, 2012; Zhang et al., 2013), but the eventual phylogenetic effects of epigenetic modifications are still debated. In the conventional view, epigenetic changes rapidly fade across generations. Yet, some changes may be more persistent. Gapp et al. (2014) found that small non-coding RNAs that induce epigenetic modifications in response to traumatic stress in mice, were inherited across three generations. If epigenetic modifications become fixed in the germline, traits acquired during ontogeny are linked to phylogeny, in the same manner as fixed mutations.

The interaction between ontogenetic and phylogenetic selection is also evident in the interplay between dietary culture and the functions of the symbiotic gut-flora. Diversity and community composition in this

highly variable microflora, assessed by metagenomic screening, have revealed a range of feedbacks on the organisms as a whole, ranging from metabolism, to obesity, diseases, and mood (Fond et al., 2015; Kassam et al., 2013). The symbiotic gut-flora, moreover, may be linked to epigenetic impacts on the microbiome itself (Kau et al., 2011). The microbiome, found in all multicellular organisms, consists of an ecological community of microorganisms such as viruses, fungi and bacteria, which are crucial to maintain an immunologic and hormonal balance in their host. A further discussion of epigenetics is beyond the scope of this paper. What we have said backs up Jablonka's (2016) reflection that "a change in the social landscape is likely to involve a change in the epigenetic landscape" (p.52).

While most of the direct impact that the ambient environment and behavior - including culture - have on the genome acts via epigenetic modifications during ontogeny, a growing number of examples demonstrate that the human genome itself is more responsive to rapid-acting cultural drivers than was previously assumed. Throughout human history, culture and evolution have interacted (see Boyd and Richerson, 1985; Richerson and Boyd, 2005 for book-length discussions), and in principle, cultural traits could also have direct consequences on the genome.

Rapid, cultural shifts in quality and quantity of food go along with changes in population health by a number of feedback mechanisms. Some of these are epigenetic, some related to our internal microbiome, plenty of them have an ontogenetic time frame, and many feedback mechanisms consist of combinations of these effects. There are, however, also examples of long-term evolutionary changes due to gene-culture interactions, inducing genetic changes. One well-known example of such genetic response to dietary selection is prolonged lactase expression into adulthood in humans (Tishkoff et al., 2007) resulting from keeping cattle. Thus, cattle could be seen as part of humans' extended phenotype. In fact, one could claim the opposite as well. Keeping cattle created a new, strong selective force, namely the ability to benefit from protein, fat, calcium and other nutrients in bovine milk. More cattle farming increases use of milk, which selects lactase production in future generations. Evidently, artificial cattle breeding also selects the cattle's morphology across generations. This in turn may influence where farmers settle and what else they consume, which also interacts with social consequences – one of the drivers of selection of behavior during ontogeny.

A suite of traits relates both to metabolism and other physiological systems resulting from gene-culture co-evolution (Laland et al., 2010; Sabeti et al., 2006). Frequently in these cases, single gene traits were persistently and repeatedly selected for in consecutive generations until fixation at the population level occurred, which was more likely to happen within small populations. Once the new trait, in this case lactose tolerance, was established, it was in itself a nutritional advantage, and may have intensified the interaction between humans and their domesticated animals. Similarly, the ability to digest starch might have tightened the link between humans and crops or even humans and dogs (Axelsson et al., 2013; Hardy et al., 2015).

In sum, we have put forward that the behavior of humans (artificial breeding) constitutes an evolutionary force acting on domesticated animals and plants. The cultural co-evolution examples above are cases where the feedback involved genetic changes in both humans and the domesticated plants and animals. Epigenetic responses involve subtler genomic feedback. The interconnectedness of selection processes, which we here discuss as one of the central achievements of the EES (Laland et al., 2015), shows itself, moreover, in the *relative* nature of selection processes.

#### 5.5. Relativity of selection

Let us remember that natural selection is a theory of relativity. Traits that are *better* adapted to the environment than other traits are those selected for. Giraffes' long necks were not selected because those

giraffes featuring them reached up to leaves on high trees (or ran, sweated, or fought effectively) *per se*, but rather the length common today was selected because it gave *better* access to leaves (flight, cooling, or victories) than those of the shorter (or much longer) necked giraffes. When playing the game Monopoly, we do not win if we merely gain capital; we only win if everyone else has less. Organisms have the highest *relative fitness* (Gillespie, 1977) if they carry the most suitable – not the strongest, heaviest, or largest – characteristics for their niche. When elk bulls fight with other male elk for access to females, those with larger antlers tend to win. There is, however, a tradeoff here because building antlers is costly. At a certain inflection point larger antlers become disadvantageous due to their mineral claims (Moen et al., 1999), their weight, and eventually because the animal cannot successfully move through the dense woods of its habitat. Thus, elk with the best size antlers have an advantage over others, leading to higher relative reproductive rate and better survival (Frank, 2011).

#### 5.5.1. Relative PIEs and their effect on behavior in general

Over the course of evolution, the behavior and morphology of organisms became susceptible to the consequences on the organisms' relative fitness. Those individuals whose behavior and morphology did not function to promote their fitness in excess of the extent to which characteristics of competitors promoted their fitness, reproduced less successfully. As explicated above, during ontogeny, contingencies with events that correlate with the organism's relative fitness select behavior. Due to time and resource constraints and the existence of variation in behavior, different activities have a stronger or weaker correlation with an organism's fitness (Baum, 2012, 2013, 2016; Baum and Davison, 2014), but they are not neutral to it.

If, during ontogeny, behavior is selected due to its effect on relative fitness, *relative* PIEs select it. They are *relative* in several senses. First, they are defined by their function, which depends on the context. If I have just eaten, food is not an effective event for a certain timespan. Second, they are relative because their function depends on the availability of other PIEs. If I have not eaten for many hours and can choose between a slice of bread and a full meal, the effect of the slice of bread will differ from when I am offered a choice between a slice of bread and a grape. Third, PIEs are relative because their effect upon one person's behavior depends upon their availability to others. In monogamous societies one can imagine that a potential mate's flirt will most likely induce different behavior when that person shortly after seduces someone else than when such allocation of behavior to competitors is absent. Consequently, their potential function defines PIEs, a function that they attain over the course of phylogenetic history. During ontogeny, they might be effective or ineffective for selecting a certain activity in a context, depending, among other things, on how tight the contingency with the activity and the availability of other PIEs.

#### 5.5.2. Relative PIEs and their effect on behavior in specific: the matching relation

In line with the concept of relative fitness central to biological evolution, one of the most tested and empirically supported "laws" of behavioral evolution, the matching relation (Baum, 1974; Herrnstein, 1961; McDowell, 1989), holds that relative effects of PIEs select an individual's allocation of time to activities. The matching relation states that given two concurrently available response alternatives, behavior is distributed in the same proportion that PIEs are distributed across those alternatives. Thus, to the extent that the matching equation holds, the phylogenetic sieve selected a direct relationship between allocation of activities and *relative* access to PIEs. This relationship corresponds to the contingency that selects activities during ontogeny.

The relativity, or context dependence, of selection processes, also shows itself in the proposition that units of selection can be nested into each other. Even though most evolutionists agree that the individual organism is the principal object of selection, dissension exists about also accepting units more or less complex than individual organisms, as

objects of selection (Mayr, 1997).

### 5.6. Multi-level and multi-scale selection

Multi-level selection is essential to understand the full scope of the concept of relativity inherent in the idea of selection and allows understanding the relation of different selectionist phenomena to each other. These phenomena include the interaction of sexual and natural selection, conflicting selection pressure acting on a common behavioral pattern of several organisms versus on a single organism's behavioral pattern, and conflicting selection pressure acting on an organism's behavioral patterns more versus less extended in time.

#### 5.6.1. Group behavior

Evolution across generations in a Darwinian sense corresponds to changes in alleles and allele frequencies in interplay with the individuals' phenotypic responses. The entire genome operates in an interplay with the cell, and in multicellular organisms, the cells cooperate to constitute a body. Social insects like ants cooperate almost in a body-like fashion, hence the term *superorganism* (Wilson, 1990). Thus, even if evolution goes along with changes in alleles, gene frequencies or gene expression, we regard these changes as responding to selective forces at different hierarchical levels. If group selection is a causal mode, the relative fitness of a group must be higher or lower than the arithmetic mean of the fitness of the composing individuals and an increase in fitness should be owed to a division of labor or some other kind of social activity, not isolated actions of groups members (Mayr, 1997).

Controversy still exists regarding whether group selection is a prerequisite for the explanation of human ethics as O. Darwin put forward in 1874. According to Darwin (1874), in social animals like humans, strong groups outcompete or outperform weak groups. This has created social bonds and group-promoting social attributes like empathy. Today, we know that social emotions correlate with hormones like dopamine, serotonin, oxytocin and vasopressin either promoting number of copies or expression efficiency of a gene.

Donaldson and Young (2008) give an overview of examples showing that social behavior correlates with specific neurogenetic structures, indicating that social bonds are partly naturally selected. Among these examples is Lim et al.'s (2004) study which shows the connection between a hormone's (vasopressin) reception and social interactions in voles. Prairie voles are monogamous. They care for offspring, display selective partner preferences and show selective aggression against conspecifics. Meadow voles are polygamous and do not engage in these behavior patterns. Lim et al.'s study indicates that the difference in these activities goes along with differences in vasopressin reception. When Lim et al. artificially increased reception of vasopressin in meadow voles; meadow voles displayed social behavior that resembles that of monogamous prairie voles, preferring social contact with their partner over a stranger.

Darwin (1874) suggested that social emotions are naturally selected. Social emotions go along with moral behavior and traits that are good for the group (Jablonka et al., 2012). How cooperative groups avoid invasion from selfish actors is a crucial issue in this context. Individuals' learning of reciprocity, partly reflected in cultural or religious norms and legal rules, functions to promote group coherence. Debunking of cheaters supports social norms in human and non-human animals (De Waal, 2016). Therefore, at the group level (from tribes to nations and beyond), this kind of social feedback is important for the fitness of the groups' individual members (i.e. to transmission of their genes). Social feedback affects the transmission of traits to future generations, involving both "genes for cooperation" and cultural (i.e. behavioral) norms.

As one of the authors has suggested elsewhere, extended behavior patterns – by single organisms or by groups – may be exposed to selection pressure in the same or the opposite direction as less extended patterns (Simon, 2016a). D. Wilson (2015) gives the selection of

altruistic behavior patterns as an example of selection pressure acting<sup>1</sup> in opposite directions (cp. section 5.2. “Ontogenetic and phylogenetic selection mechanisms working in opposite directions”). An individual’s actions are “altruistic” if they confer a fitness benefit on a second individual while incurring a fitness cost for the first individual. Wilson notes that selfish individuals outcompete altruistic individuals, but groups of altruistic individuals outcompete groups of selfish individuals. At the same time, reciprocal altruism is typically only a winning strategy to a certain level (“tit-for tat” behavior), as various game-theory models indicate (for more detail, see Axelrod, 1997; Nowak, 2006). Different conditions will pose different selective pressures on behavior both at the individual and group level. For example, feast or famine, or peace relative to war, may call for widely different strategies and will, thus, select differently among selfish versus altruistic behavior.

The proposition that selection acts on behavioral patterns exhibited by several organisms together and on patterns by single organisms, invites the idea that also one organism’s behavioral patterns more or less extended in time may be subject to selection pressure.

### 5.6.2. Nested activities

Just as genes are parts of cells, cells are parts of organisms, organisms are parts of groups, and groups are parts of nations (Sober and Wilson, 1994; Wilson and Sober, 1998), so are activities both nested in larger scale activities and composed of smaller scale activities (Baum, 2013; Rachlin, 2004). Activities on smaller scales (e.g. swinging a hammer) are less extended in time and constitute parts of temporally more extended activities (e.g. hammering in a nail). These are themselves part of even more extended activities (such as building a wall) and might consist of even larger scale activities (such as building a house), which can be part of a more extended behavioral pattern (i.e. providing shelter for your family). No selection of sub-patterns occurs if behavioral patterns consist of exchangeable (functionally equivalent) sub-patterns that stand in comparable contingency with PIEs, such as hammering in the nail with a green or a blue hammer. Selection occurs if activities on the same scale correlate differently with PIEs, such as using a stone versus using a hammer to get the nail into the wall. Just as an individual (lower-level unit) might be subject to a different selection pressure than the group (higher-level unit) of which it constitutes a part, so might a lower-scale behavioral unit be subject to different selection pressures than the larger unit it constitutes a part of.

Analogously to the selfishness-altruism conflict between selection acting on a group’s and on an individual’s behavior who is part of that group, selection may act in opposite directions on one individual’s more extended behavior pattern than on her less extended behavior. For example, occasional drinking of alcohol at a party outcompetes sobriety. However, sobriety and thus maintaining social relationships, housing and work, outcompetes an alcoholic’s drinking pattern – of which sometimes drinking at a party is a part as the individual is of the group (Rachlin, 2004). Imagine someone attempting to lose weight. A successful dieter shows a complex behavioral pattern that has evolved from simpler patterns over her lifetime just as the complex human eye evolved from simpler light-sensitive organs (Rachlin, 2014). The dieter’s behavior is selected on multiple scales.

The general tendency to choose high-calorie options was phylogenetically selected. During ontogeny, the immediate consequence of not taking the free cake sample when entering the bakery is contrary to the long-term abstract consequences of social acceptance and good health (Rachlin, 2014) – much as your personal interests could be contrary to your family’s interests, which might be at conflict with your religious group’s interests, or your nation’s, let alone the planet’s

<sup>1</sup> When stating that selection “acts”, we do not mean to imply that selection is an agent such as (Christian folk psychology views) a sculptor whose hands mold clay. Rather, selection “acts” in the sense that erosion acts on a landscape (see Ghiselin, 1981 for a more extended discussion).

interest (Wilson and Sober, 1998). If a process akin to group selection selects extended patterns of behavior of individual organisms, as Rachlin (2002) suggests, units of selection may be regarded as nested and selection may act on morphological and behavioral units with different degrees of complexity.

An individual’s behavior is allocated among several activities, some of which have advantageous effects on the individual’s relative fitness. Others have disadvantageous effects. Selection may even favor behavioral patterns of an individual if the individual’s fitness is not improved. This happens, for example, when the behavioral pattern is only advantageous for the individual’s fitness when most people around behave the same way, as Wilson’s (2015) example of altruistic behavior illustrates, which is favored only if the individual is part of a mainly altruistically behaving group. Conversely, sexual selection provides examples of selection not beneficial at the group level, but favoring the individuals that possess the traits.

### 5.6.3. Sexual selection

Sexual selection is a mode of natural selection where members of the same sex compete for access to mates of the opposite sex. Variation in individuals’ attractiveness and in their preference of attractive partners leads to variation in reproductive success. Strong sexual selection for certain traits may even result in a runaway selection at fitness costs to the individual. Plumage, oversized antlers, and behavior like mating displays or competing in a lek are examples. Darwin (1874) used peacocks’ tails as a classical example of runaway sexual selection. Analogously, Lorenz (1963) describes a number of traits related both to somatic morphology and behavior resulting from sexual selection. They are part of a wide repertoire marking rank without direct fights. While apparently dysfunctional, such traits still have evolved because they promote fitness by increasing rank and mating success. As females commonly prefer certain attributes of male body size, coloration, antlers, and tail feathers, they also often prefer certain behavioral patterns like songs and activities connected to risks. Examples are courtship behavior where birds or fish expose themselves to predators and reduce foraging and other activities during courtship periods (Zahavi, 1975).

Turtle hunting in the Australian Meriam community illustrates sexual selection in humans. Bird et al. (2001) observed that men in the community hunt turtles, which produces less calorie gain per hour than foraging for shellfish. Turtles are often served at large feasts in which other members of the community learn who brought them the turtle meat. Successful Meriam hunters experience greater social benefits and reproductive success than less successful hunters (Smith et al., 2003), which suggests that calorie gains are not the primary reason men hunt turtles. Signals such as turtle hunting (as opposed to shellfish hunting) evolve if they lead to behavior of the “listener” that benefits the signaler’s fitness. Signals may be honest in the sense that they lead to increased fitness in both individuals or dishonest in the sense of only generating advantageous PIEs for the signaler, while undermining the signaling system of the whole population.

Both the discussion of different levels of organismic and behavioral complexity and the discussion of the relation between natural selection and its special mode sexual selection, suggest that selection operates at different levels and that it can potentially do so with different “interests”.

## 6. Conclusions

Both phylogenetic and ontogenetic evolution contain processes that tailor the individual to its local environment. Phenomena as different as operant conditioning, classical conditioning, adjunctive behavior, and imprinting may stem from evolutionary processes consisting of variation, recurrence, and selection of traits. In this paper, we argued that this variety of traditionally discretely treated adaptive behavioral phenomena results from an iterative process consisting of selection processes acting on different scales. This sieve-like selection occurs both

within ontogeny and within phylogeny, whereby the former influences the latter and vice versa. Although the link between individual performance and selection is inherent in evolutionary theory, in the sense that best fit individuals produce more offspring and thus promote proliferation of their genotype, this link has been addressed less in behavioral sciences.

Although behavior is partly shaped by genes, it may itself feed back on the gene level directly, either via evolution as when farming practices affect digestive enzymes, or directly during ontogeny by epigenetic regulation of gene activity (Laland et al., 2015). We have argued that this interplay and iterative feedback between ontogeny and phylogeny, genes and culture, as well as different levels of selection, is a fruitful tool for understanding evolution of behavior. Our examples of the evolution of lactose tolerance extended into adulthood and cattle keeping illustrate aspects of behavioral epigenetics including both the role of epigenetic factors in influencing behavior and the effects of behavior on epigenetic states (Champagne and Rissman, 2011; Jablonka, 2016; Petronis and Mill, 2011).

To sum up, we elaborated on the EES (Laland et al., 2015) by presenting our interdisciplinary “modular” view of behavior based on treating organisms as learning systems functioning much like the “innate” and “adaptive” components of the immune system. Behavior connects organisms and the environment. In our view, adaptive behavior results on one timescale or another from consequences in the environment. Behavior changes when its correlation with PIEs changes. This connection evolved over the course of a species’ evolutionary history due to competition of contingencies between behavior and fitness-relevant events. Different contingencies correlate to varying degrees with the organism’s relative fitness.

In this paper, we have added to earlier efforts (e.g. Wilson et al., 2014) to expand the role ascribed to inherited mechanisms from directly governing present behavior to bringing about the processes of behavioral selection during ontogeny. This step in the direction of utilizing our power over environmental constraints on behavior allows us to guide them, instead of becoming slave to them in the name of “freedom” (see Rachlin, 2016; Skinner, 1953, 1972, for more detail).

Naturally occurring selection of organisms’ morphological traits during phylogeny is to artificial breeding as naturally occurring selection of organisms’ behavioral traits during ontogeny is to goal-directed selection of behavior in controlled experimental settings. Accordingly, an outline of the circumstances under which selection of behavior during ontogeny specifies what is generally called “learning,” will increase our ability to predict, influence, and understand behavior. Frequently, the question of whether a particular activity is selected during the lifetime of the organism constitutes an empirical question that can be answered in a controlled experiment in a laboratory setting. Such an identification of the causes of behavior has proven useful in numerous applied settings (see e.g. Cooper et al., 2014 for a textbook overview).

The present interdisciplinary work is “strengthening the ties to adjacent disciplines” (p. 10), which Laland et al. (2015) formulate as one potential benefit of work in the EES framework. It invites further queries into the philosophy of selection as a causal mode of evolution by posing yet unanswered questions, such as on the relation between the types and the units of selection shown in Fig. 2. It remains to be seen what aspects of our integrated view pass through the selective sieves of the scientific community considering our suggestion.

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## References

- Axelrod, R.M., 1997. *The Complexity of Cooperation: Agent-Based Models of Competition and Collaboration*. Princeton University Press.
- Axelsson, E., Ratnakumar, A., Arendt, M.-L., Maqbool, K., Webster, M.T., Perloski, M., et al., 2013. The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature* 495 (7441), 360–364. <http://www.nature.com/nature/journal/v495/n7441/abs/nature11837.html#supplementary-information>.
- Azrin, N.H., Hutchinson, R.R., Hake, D.F., 1966. Extinction-induced aggression. *J. Exp. Anal. Behav.* 9 (3), 191–204. <http://dx.doi.org/10.1901/jeab.1966.9-191>.
- Baschetti, R., 1998. Diabetes epidemic in newly westernized populations: is it due to thrifty genes or to genetically unknown foods? *J. R. Soc. Med.* 91 (12), 622–625.
- Battin, J., 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conserv. Biol.* 18 (6), 1482–1491. <http://dx.doi.org/10.1111/j.1523-1739.2004.00417.x>.
- Baum, W.M., Davison, M., 2014. Background activities, induction, and behavioral allocation in operant performance. *J. Exp. Anal. Behav.* 102 (2), 213–230. <http://dx.doi.org/10.1002/jeab.100>.
- Baum, W.M., 1973. The correlation-based law of effect. *J. Exp. Anal. Behav.* 20 (1), 137–153.
- Baum, W.M., 1974. On two types of deviation from the matching law: bias and undermatching. *J. Exp. Anal. Behav.* 22 (1), 231–242. <http://dx.doi.org/10.1901/jeab.1974.22-231>.
- Baum, W.M., 1981. Optimization and the matching law as accounts of instrumental behavior. *J. Exp. Anal. Behav.* 36 (3), 387–403.
- Baum, W.M., 1989. Quantitative prediction and molar description of the environment. *Behav. Anal.* 12 (2), 167–176.
- Baum, W.M., 2002. From molecular to molar: a paradigm shift in behavior analysis. *J. Exp. Anal. Behav.* 78 (1), 95–116.
- Baum, W.M., 2004. The accidental behaviorist: a review of the new behaviorism by John Staddon. *J. Exp. Anal. Behav.* 82 (1), 73–78.
- Baum, W.M., 2012. Rethinking reinforcement: allocation, induction, and contingency. *J. Exp. Anal. Behav.* 97 (1), 101–124. <http://dx.doi.org/10.1901/jeab.2012.97-101>.
- Baum, W.M., 2013. What counts as behavior? The molar multiscale view. *Behav. Anal.* 36 (2), 283.
- Baum, W.M., 2015. The role of induction in operant schedule performance. *Behav. Process.* 114, 26–33.
- Baum, W.M., 2016. Driven by consequences: the multiscale molar view of choice. *Manag. Decis. Econ.* 37 (4–5), 239–248.
- Baum, W.M., 2017a. Selection by consequences, behavioral evolution, and the price equation. *J. Exp. Anal. Behav.* 107 (3), 321–342. <http://dx.doi.org/10.1002/jeab.256>.
- Baum, W.M., 2017b. *Understanding Behaviorism: Behavior, Culture, and Evolution*, 3rd ed. John Wiley & Sons.
- Bird, R.B., Smith, E., Bird, D.W., 2001. The hunting handicap: costly signaling in human foraging strategies. *Behav. Ecol. Sociobiol.* 50 (1), 9–19.
- Boyd, R., Richerson, P.J., 1985. *Culture and the Evolutionary Process*. University of Chicago press.
- Bråten, S., 2006. *Intersubjective Communication and Emotion in Early Ontogeny*. Cambridge University Press.
- Bråten, S., 2007. On Being Moved: From Mirror Neurons to Empathy, vol. 68 John Benjamins Publishing.
- Burks, C.D., 1970. Schedule-induced polydipsia: are response-dependent schedules a limiting condition? *J. Exp. Anal. Behav.* 13 (3), 351–358.
- Buss, D.M., Kenrick, D.T., 1998. *Evolutionary Social Psychology*.
- Buss, D.M., 1995. Evolutionary psychology: a new paradigm for psychological science. *Psychol. Inquiry* 6 (1), 1–30.
- Buss, D.M., 2005. *The Handbook of Evolutionary Psychology*. John Wiley & Sons.
- Buss, D.M., 2015. *Evolutionary Psychology: The New Science of the Mind*. Psychology Press.
- Champagne, F.A., Rissman, E.F., 2011. *Behavioral Epigenetics: A New Frontier in the Study of Hormones and Behavior*. Academic Press.
- Cooper, J.O., Heron, T.E., Heward, W.L., 2014. *Applied Behavior Analysis*: Pearson Educational International.
- Cosmides, L., Tooby, J., 1997. *Evolutionary Psychology: A Primer*.
- Creanza, N., Fogarty, L., Feldman, M.W., 2012. Models of cultural niche construction with selection and assortative mating. *PLoS One* 7 (8), e42744.
- Darwin, C., (1997 (1874)). *The descent of man, and selection in relation to sex*. NY Prometheus Books, Amherst.
- Darwin, C., (2003 (1859)). *On the Origins of Species by Means of Natural Selection*. Murray, London.
- Dawkins, R., 1976. *The Selfish Gene*, vol. 1. Oxford Univ. Press, New York, pp. 976.
- Dawkins, R., 1983. *The Extended Phenotype: The Gene as the Unit of Selection*. 1982 edition. Freeman.
- Dawkins, R., 1995. *River out of Eden: A Darwinian View of Life*, Science Masters Series. Weidenfeld & Nicholson, London.
- Dawkins, R., 1997. *Climbing Mount Improbable*. WW Norton & Company.
- de Vries, H., MacDougal, D., 1905. *Species and Varieties: Their Origin by Mutation*. JSTOR.
- De Waal, F., 2016. *Are We Smart Enough to Know How Smart Animals Are?* WW Norton & Company.
- Diamond, J., 2012. *The World Until Yesterday: What can We Learn from Traditional Societies?* Penguin.
- Dias, B.G., Ressler, K.J., 2014. Parental olfactory experience influences behavior and neural structure in subsequent generations. *Nat. Neurosci.* 17 (1), 89–96.

- Donahoe, J.W., Vegas, R., 2004. Pavlovian conditioning: the CS-UR relation. *J. Exp. Psychol. Anim. Behav. Process.* 30 (1), 17.
- Donaldson, Z.R., Young, L.J., 2008. Oxytocin, vasopressin, and the neurogenetics of sociality. *Science* 322 (5903), 900–904.
- Falk, J.L., 1969. Conditions producing psychogenic polydipsia in animals. *Ann. N. Y. Acad. Sci.* 157 (1), 569–593.
- Ferster, C.B., Skinner, B.F., 1957. Schedules of Reinforcement.
- Falk, J.L., 1961. Production of polydipsia in normal rats by an intermittent food schedule. *Science* 133 (3447), 195–196.
- Flory, R., 1969. Attack behavior as a function of minimum inter-food interval. *J. Exp. Anal. Behav.* 12 (5), 825–828.
- Fond, G., Boukouaci, W., Chevalier, G., Regnault, A., Eberl, G., Hamdani, N., et al., 2015. The psychomicrobiotic: targeting microbiota in major psychiatric disorders: a systematic review. *Pathol. Biol.* 63 (1), 35–42.
- Frank, R., 2011. *The Darwin Economy: Liberty, Competition and the Common Good*. Princeton University Press, Princeton.
- Gapp, K., Jawaid, A., Sarkies, P., Bohacek, J., Pelczar, P., Prados, J., et al., 2014. Implication of sperm RNAs in transgenerational inheritance of the effects of early trauma in mice. *Nat. Neurosci.* 17 (5), 667–669.
- Garcia, J., Kimeldorf, D.J., Koelling, R.A., 1955. Conditioned aversion to saccharin resulting from exposure to gamma radiation. *Science* 122 (3160), 157–158.
- Gerhart, J., Kirschner, M., 2007. The theory of facilitated variation. *Proc. Natl. Acad. Sci.* 104 (Suppl. 1), 8582–8589.
- Ghiselin, M.T., 1981. Categories, life, and thinking. *Behav. Brain Sci.* 4 (2), 269–283.
- Gilbert, S.F., Opitz, J.M., Raff, R.A., 1996. Resynthesizing evolutionary and developmental biology. *Dev. Biol.* 173 (2), 357–372. <http://dx.doi.org/10.1006/dbio.1996.0032>.
- Gillespie, J.H., 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. *Am. Nat.* 111 (981), 1010–1014.
- Glenn, S.S., Field, D.P., 1994. Functions of the environment in behavioral evolution. *Behav. Anal.* 17 (2), 241–259.
- Glenn, S.S., 2003. Operant contingencies and the origin of cultures. *Behavior Theory and Philosophy*. Springer US, New York, pp. 223–242.
- Gordon, L., Joo, J.E., Powell, J.E., Ollikainen, M., Novakovic, B., Li, X., et al., 2012. Neonatal DNA methylation profile in human twins is specified by a complex interplay between intrauterine environmental and genetic factors, subject to tissue-specific influence. *Genome Res.* 22 (8), 1395–1406.
- Gould, S.J., 2002. *The Structure of Evolutionary Theory*. Harvard University Press.
- Grant, P.R., 1999. *Ecology and Evolution of Darwin's Finches*. Princeton University Press.
- Graur, D., Zheng, Y., Price, N., Azevedo, R.B., Zufall, R.A., Elhaik, E., 2013. On the immortality of television sets: function in the human genome according to the evolution-free gospel of ENCODE. *Genome Biol. Evol.* 5 (3), 578–590.
- Grunow, A., Neuringer, A., 2002. Learning to vary and varying to learn. *Psychon. Bull. Rev.* 9 (2), 250–258.
- Hailman, J.P., 1969. How an instinct is learned. *Sci. Am.* 221 (6), 98–108.
- Hardy, T.M., Tollefsbol, T.O., 2011. Epigenetic Diet: Impact on the Epigenome and Cancer.
- Hardy, K., Brand-Miller, J., Brown, K.D., Thomas, M.G., Copeland, L., 2015. The importance of dietary carbohydrate in human evolution. *Q. Rev. Biol.* 90 (3), 251–268. <http://dx.doi.org/10.1086/682587>.
- Heijmans, B.T., Tobi, E.W., Stein, A.D., Putter, H., Blauw, G.J., Susser, E.S., et al., 2008. Persistent epigenetic differences associated with prenatal exposure to famine in humans. *Proc. Natl. Acad. Sci.* 105 (44), 17046–17049.
- Herrnstein, R.J., 1961. Relative and absolute strength of response as a function of frequency of reinforcement. *J. Exp. Anal. Behav.* 4 (3), 267–272. <http://dx.doi.org/10.1901/jeab.1961.4-267>.
- Hessen, D.O., 2015. Noncoding DNA as a phenotypic driver. *Evol. Biol.* 42 (4), 427–431.
- Holdrege, C., 2003. The giraffe's short neck. Paper Presented at the In Context.
- Hughes, J.E., Amyx, H., Howard, J.L., Nanry, K.P., Pollard, G.T., 1994. Health effects of water restriction to motivate lever-pressing in rats. *Lab. Anim. Sci.* 44 (2), 135–140.
- Jablonka, E., Lamb, M.J., 2007. Précis of evolution in four dimensions. *Behav. Brain Sci.* 30 (04), 353–365.
- Jablonka, E., Ginsburg, S., Dor, D., 2012. The co-evolution of language and emotions. *Phil. Trans. R. Soc. B* 367 (1599), 2152–2159.
- Jablonka, E., 2016. Cultural epigenetics. *Sociol. Rev. Monogr.* 64 (1), 42–60.
- Jaynes, J., 1956. The interaction of learned and innate behavior: I. Development and generalization. *J. Comp. Physiol. Psychol.* 49, 201–206.
- Johnson, M.L., Burke, B.S., Mayer, J., 1956. Relative importance of inactivity and overeating in the energy balance of obese high school girls. *Am. J. Clin. Nutr.* 4 (1), 37–44.
- Kappeler, P.M., 2011. *Verhaltensbiologie*. Springer, Berlin, Heidelberg.
- Kassam, Z., Lee, C.H., Yuan, Y., Hunt, R.H., 2013. Fecal microbiota transplantation for Clostridium difficile infection: systematic review and meta-analysis. *Am. J. Gastroenterol.* 108 (4), 500–508.
- Kau, A.L., Ahern, P.P., Griffin, N.W., Goodman, A.L., Gordon, J.I., 2011. Human nutrition, the gut microbiome, and immune system: envisioning the future. *Nature* 474 (7351), 327.
- Kerst, A.M., Oleson-Kessloff, J., Roseland, P., 2007. *Rapid City: Historic Downtown Architecture*. Arcadia Pub.
- Koppe, G., Mallien, A.S., Berger, S., Bartsch, D., Gass, P., Vollmayr, B., Durstewitz, D., 2017. CACNA1C gene regulates behavioral strategies in operant rule learning. *PLoS Biol.* 15 (6), e2000936. <http://dx.doi.org/10.1371/journal.pbio.2000936>.
- Kristan III, W.B., 2003. The role of habitat selection behavior in population dynamics: source-sink systems and ecological traps. *Oikos* 103 (3), 457–468. <http://dx.doi.org/10.1034/j.1600-0706.2003.12192.x>.
- Kuczynski, J.-M., 2012. *Empiricism and the Foundations of Psychology*, vol. 87 John Benjamins Publishing.
- Laland, K., Odling-Smee, J., Myles, S., 2010. How culture shaped the human genome: bringing genetics and the human sciences together. *Nat. Rev. Genet.* 11 (2), 137.
- Laland, K., Wray, G.A., Hoekstra, H.E., 2014. Does evolutionary theory need a rethink? *Nature* 514 (7521), 161.
- Laland, K., Uller, T., Feldman, M.W., Sterelny, K., Müller, G.B., Moczek, A., et al., 2015. The extended evolutionary synthesis: its structure, assumptions and predictions. Paper Presented at the Proc. R. Soc. B.
- Laland, K., Matthews, B., Feldman, M.W., 2016. An introduction to niche construction theory. *Evol. Ecol.* 30 (2), 191–202.
- Lim, M.M., Wang, Z., Olazábal, D.E., Ren, X., Terwilliger, E.F., Young, L.J., 2004. Enhanced partner preference in a promiscuous species by manipulating the expression of a single gene. *Nature* 429 (6993), 754–757.
- Lindholm, M., 2012. *Evolusjon: naturens kulturhistorie*. Spartacus Forlag.
- Locey, M.L., Jones, B.A., Rachlin, H., 2013. Self-control and altruism. In: Madden, G.J., Dube, W.V., Hackenberg, T.D., Hanley, G.P., Lattal, K.A. (Eds.), *APA Handbook of Behavior Analysis, Vol. 1: Methods and Principles*. American Psychological Association, Washington, DC, US, pp. 463–481.
- Lorenz, K., Tinbergen, N., 1938. Taxis und Instinktthandlung in der Eirollbewegung der Graugans. *Z. Tierpsychol.* 2, 1–29.
- Lorenz, K., 1937. Imprinting. *Auk* 54 (1), 245–273.
- Lorenz, K., 1963. Das Sogenannte Boese, Zur Naturgeschichte der Aggression (The So-Called Evil, Contribution to the Natural History of Aggression). Borotha-Schoeler, Vienna, pp. 327.
- Ludwig, D.S., Majzoub, J.A., Al-Zahrani, A., Dallal, G.E., Blanco, I., Roberts, S.B., 1999. High glycemic index foods, overeating, and obesity. *Pediatrics* 103 (3) e26–e26.
- Luo, J., Hauser, K., 2017. Robust trajectory optimization under frictional contact with iterative learning. *Auton. Robots* 41 (6), 1447–1461.
- Mayr, E., 1997. The objects of selection. *Proc. Natl. Acad. Sci.* 94 (6), 2091–2094.
- McDowell, J.J., 1989. Two modern developments in matching theory. *Behav. Anal.* 12 (2), 153–166.
- McFarland, D., 1966. On the causal and functional significance of displacement activities. *Ethology* 23 (2), 217–235.
- McLaughlin, P., 2007. On selection of, for, with, and against. *Thinking About Causes*. pp. 265–283.
- McLaughlin, P., 2011. The arrival of the fittest. *Explanation, Prediction, and Confirmation*. Springer, pp. 203–222.
- McNew, S.M., Beck, D., Sadler-Riggelman, I., Knutie, S.A., Koop, J.A., Clayton, D.H., Skinner, M.K., 2017. Epigenetic variation between urban and rural populations of Darwin's finches. *BMC Evol. Biol.* 17 (1), 183.
- Mennella, J.A., 2014. Ontogeny of taste preferences: basic biology and implications for health. *Am. J. Clin. Nutr.* 99 (3), 704S–711S.
- Mineka, S., Öhman, A., 2002. Phobias and preparedness: the selective, automatic, and encapsulated nature of fear. *Biol. Psychiatry* 52 (10), 927–937. [http://dx.doi.org/10.1016/S0006-3223\(02\)01669-4](http://dx.doi.org/10.1016/S0006-3223(02)01669-4).
- Moen, R.A., Pastor, J., Cohen, Y., 1999. Antler growth and extinction of Irish elk. *Evol. Ecol. Res.* 1 (2), 235–249.
- Naour, P., 2009. *EO Wilson and BF Skinner: A Dialogue Between Sociobiology and Radical Behaviorism*. Springer Science & Business Media.
- Nowak, M.A., 2006. Five rules for the evolution of cooperation. *Science (New York, N. Y.)* 314 (5805), 1560–1563. <http://dx.doi.org/10.1126/science.1133755>.
- Nyborg, K., Anderies, J.M., Dannenberg, A., Lindahl, T., Schill, C., Schlüter, M., et al., 2016. Social norms as solutions. *Science* 354 (6308), 42–43.
- Ogden, C.L., Carroll, M.D., Kit, B.K., Flegal, K.M., 2014. Prevalence of childhood and adult obesity in the united states, 2011–2012. *JAMA* 311 (8), 806–814. <http://dx.doi.org/10.1001/jama.2014.732>.
- Pavlov, I.P., 1927. *Conditional Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex*. H. Milford.
- Pavlov, I., 1928. *Lectures on Conditioned Reflexes*, vols. 1 and 2 International Publishers, New York.
- Pembrey, M., Saffery, R., Bygren, L.O., Carstensen, J., Edvinsson, S., Faresjö, T., et al., 2014. Human transgenerational responses to early-life experience: potential impact on development, health and biomedical research. *J. Med. Genet. jmedgenet-2014-102577*.
- Peters, J., Vijayakumar, S., Schaal, S., 2003. Reinforcement learning for humanoid robotics. Paper Presented at the Proceedings of the Third IEEE-RAS International Conference on Humanoid Robots.
- Peterson, N., 1960. Control of behavior by presentation of an imprinted stimulus. *Science* 132 (3437), 1395–1396.
- Petronis, A., Mill, J., 2011. *Brain, Behavior and Epigenetics*. Springer Science & Business Media.
- Pi-Sunyer, F.X., Becker, D., Bouchard, C., Carleton, R., Colditz, G., Dietz, W., et al., 1998. Clinical guidelines on the identification, evaluation, and treatment of overweight and obesity in adults: executive summary. *Am. J. Clin. Nutr.* 68 (4), 899–917.
- Pierce, W.D., Cheney, C.D., 2013. *Behavior Analysis and Learning*. Psychology Press.
- Pinker, S., 2003. *The Blank Slate: The Modern Denial of Human Nature*. Penguin.
- Rachlin, H., 1995. Self-control: beyond commitment. *Behav. Brain Sci.* 18 (1), 109–121. <http://dx.doi.org/10.1017/S0140525X00037602>.
- Rachlin, H., 2002. Altruism and selfishness. *Behav. Brain Sci.* 25, 239–250. <http://dx.doi.org/10.1017/S0140525X02000055>.
- Rachlin, H., 2004. *The Science of Self-Control*. Harvard University Press, Cambridge, MA, USA.
- Rachlin, H., 2014. *The Escape of the Mind*. OUP, USA.
- Rachlin, H., 2016. Self-control based on soft commitment. *Behav. Anal.* 39 (2), 259–268. <http://dx.doi.org/10.1007/s40614-016-0054-9>.
- Rescorla, R.A., 1968. Probability of shock in the presence and absence of CS in fear

- conditioning. *J. Comp. Physiol. Psychol.* 66 (1), 1–5.
- Rescorla, R.A., 1988. Pavlovian conditioning: it's not what you think it is. *Am. Psychol.* 43 (3), 151.
- Richerson, P., Boyd, R., 2005. *Not by Genes Alone*. University of Chicago Press, Chicago.
- Ruhm, C.J., 2012. Understanding overeating and obesity. *J. Health Econ.* 31 (6), 781–796.
- Rutter, M., Kumsta, R., Schlotz, W., Sonuga-Barke, E., 2012. Longitudinal studies using a natural experiment design: the case of adoptees from Romanian institutions. *J. Am. Acad. Child Adolesc. Psychiatry* 51 (8), 762–770.
- Sabeti, P.C., Schaffner, S.F., Fry, B., Lohmueller, J., Varylly, P., Shamovsky, O., et al., 2006. Positive natural selection in the human lineage. *Science* 312 (5780), 1614–1620. <http://dx.doi.org/10.1126/science.1124309>.
- Shah, M., Jeffery, R.W., 1991. Is obesity due to overeating and inactivity, or to a defective metabolic rate? A review. *Ann. Behav. Med.* 13 (2), 73–81.
- Simon, C., Baum, W.M., 2012. Expelling the meme-ghost from the machine: an evolutionary explanation for the spread of cultural practices. *Behav. Philosophy* 39/40, 127–144.
- Simon, C., 2016a. Cultural group selection in the light of the selection of extended behavioral patterns. *Behav. Brain Sci.* 39. <http://dx.doi.org/10.1017/S0140525X1400106X>.
- Simon, C., 2016b. Towards a fully rounded selectionist approach. *Norsk Tidsskrift for Atferdsanalyse* 43 (1), 71–76.
- Simon, C., 2017. Why norwegians don't have their pigs in the forest: illuminating Nordic 'co-operation'. *Behav. Soc. Issues* 26, 172–186.
- Skinner, B.F., 1948. 'Superstition' in the pigeon. *J. Exp. Psychol.* 38 (2), 168. <http://dx.doi.org/10.1037/h0055873>.
- Skinner, B.F., 1953. *Science and Human Behavior*. Simon and Schuster.
- Skinner, B.F., 1972. *Beyond Freedom and Dignity*. Springer.
- Skinner, B.F., 1981. Selection by consequences. *Science* 213 (4507), 501–504. <http://dx.doi.org/10.1126/science.7244649>.
- Smith, E.A., Bird, R.B., Bird, D.W., 2003. The benefits of costly signaling: Meriam turtle hunters. *Behav. Ecol.* 14 (1), 116–126.
- Smith, T.L., 1983. Skinner's environmentalism: the analogy with natural selection. *Behaviorism* 11 (2), 133–153.
- Sober, E., Lewontin, R., 1984. *The Nature of Selection: Evolutionary Theory in Philosophical Focus*. MIT, Cambridge, Bradford.
- Sober, E., Wilson, D.S., 1994. A critical review of philosophical work on the units of selection problem. *Philos. Sci.* 534–555.
- Spector, T., 2012. *Identically Different: Why You can Change Your Genes*. Hachette UK.
- Staddon, J.E.R., Simmelhag, V.L., 1971. The superstition experiment: a reexamination of its implications for the principles of adaptive behavior. *Psychol. Rev.* 78 (1), 3–43. <http://dx.doi.org/10.1037/h0030305>.
- Taleb, N.N., 2007. *The Black Swan: The Impact of the Highly Improbable*, vol. 2 Random house.
- Teblich, S., Bshary, R., 2004. Cognitive abilities related to tool use in the woodpecker finch, *Cactospiza pallida*. *Anim. Behav.* 67 (4), 689–697.
- Thorndike, E.L., 1911/2000. *Animal Intelligence: Experimental Studies*, The Macmillan company, New York.
- Tishkoff, S.A., Reed, F.A., Ranciaro, A., Voight, B.F., Babbitt, C.C., Silverman, J.S., et al., 2007. Convergent adaptation of human lactase persistence in Africa and Europe. *Nat. Genet.* 39 (1), 31–40. <http://dx.doi.org/10.1038/ng1946>.
- Tooby, J., Cosmides, L., 1995. The psychological foundations of culture. *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. pp. 19–136.
- Van Vugt, M., 2006. Evolutionary origins of leadership and followership. *Pers. Soc. Psychol. Rev.* 10 (4), 354–371.
- Weldon, A.J., Haddad, N.M., 2005. The effects of patch shape on Indigo Buntings: evidence for an ecological trap. *Ecology* 86 (6), 1422–1431.
- West-Eberhard, M.J., 2003. *Developmental Plasticity and Evolution*. Oxford University Press.
- Wilson, D.S., Sober, E., 1998. Multilevel selection and the return of group-level functionalism. *Behav. Brain Sci.* 21 (2), 305–306. <http://dx.doi.org/10.1017/S0140525X98221194>.
- Wilson, D.S., Hayes, S., Biglan, A., Embry, D., 2014. Evolving the future: toward a science of intentional change. *Behav. Brain Sci.* 37 (04), 395–416.
- Wilson, E.O., 1975. *Sociobiology*. Harvard University Press.
- Wilson, E.O., 1990. *Success and Dominance in Ecosystems: The Case of the Social Insects*.
- Wilson, D.S., 2015. Does Altruism Exist?: Culture, Genes, and the Welfare of Others. Yale University Press.
- Zahavi, A., 1975. Mate selection—a selection for a handicap. *J. Theor. Biol.* 53 (1), 205–214.
- Zettel, J.J., 1955. Evolution and the human eye. *Optom. Vis. Sci.* 32 (7), 343–353.
- Zhang, T.Y., Labonté, B., Wen, X.L., Turecki, G., Meaney, M.J., 2013. Epigenetic mechanisms for the early environmental regulation of hippocampal glucocorticoid receptor gene expression in rodents and humans. *Neuropsychopharmacology* 38 (1), 111.