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Biological Purposes Beyond Natural Selection: Self-Regulation as a Source of Teleology¹

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Abstract

Selected-effects theories provide the most popular account of biological teleology. According to these theories, the purpose of a trait is to do whatever it was selected for. The vast majority of selected-effects theories consider biological teleology to be introduced by natural selection. We want to argue, however, that natural selection is not the only relevant selective process in biology. In particular, our proposal is that biological regulation is a form of biological selection. So, those who accept selected-effects theories should recognize biological regulation as a distinctive source of biological teleology. The purposes derived from biological regulation are of special interest for explaining and predicting the behavior of organisms, given that regulatory mechanisms directly modulate the behavior of the systems they regulate. This explanatory power, added to the fact that regulation is widespread in the biological world, makes the idea that regulation gives rise to its own form of teleology a substantial contribution to the debate on biological teleology.

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Selected-effects theories provide the most popular account of biological teleology. According to these theories, the purpose of a trait is to do whatever it was selected for (Millikan 1984, 1989; Neander, 1991; Griffiths, 1993; Godfrey-Smith, 1994). The vast majority of selected-effects theories consider biological teleology to be introduced by natural selection (an exception is Garson (2012, (2017, 2019b)). We want to argue, however, that natural selection is not the only relevant selective process in biology. In particular, our proposal is that biological regulation is a form of biological selection. So, those who accept selected-effects theories should also recognize biological regulation as a distinctive source of biological teleology. The purposes derived from biological regulation are of special interest for explaining and predicting the behavior of organisms, given that regulatory mechanisms directly modulate the behavior of the systems they regulate. This explanatory power, added to the fact that regulation is ubiquitous in the biological world, makes the idea that regulation gives rise to its own form of teleology a substantial contribution to the debate on biological teleology.

We intend for our proposal to have a conciliatory, pluralistic spirit. An important upshot of the paper is that evolutionary accounts of teleology do not need to be in competition with approaches that, like ours, focus on the current organization of biological systems. As we will show, in both cases teleology can be seen as underlain by selective mechanisms. However, this does not mean that these approaches are equivalent. Given that they involve very different types of selective processes (natural selection and regulation, respectively), the resulting attributions of purposes and teleological explanations also tend to be significantly different. Nonetheless, these teleological explanations can be compatible and complementary. What we want to stress is that selected-effects theories do not commit one to considering natural selection to be the only source of genuine biological teleology. Regulation provides a clear example of a biological selective process that operates at the level of the dynamics of individual organisms, and that generates a distinctive form of biological teleology.

This is the plan for the paper. In the first section we examine standard etiological accounts of biological teleology, which rely on natural selection. These etiological accounts are typically underpinned by selected-effects theories of teleology. In the second section, we offer some general motivation for such selected-effects theories. After that, we characterize the phenomenon of biological regulation. Finally, we argue that biological regulation is a form of selection, and that, therefore, according to selected-effects theories, it should be regarded as a source of teleology. We also show how our proposal avoids counterexamples faced by other selected-effects theories.

1 Etiological-evolutionary Accounts of Biological Teleology

Teleological notions such as purpose, goal, or function are widespread in biological discourse. Such teleological notions are associated with standards of success. Purposive behavior is successful if it reaches its purpose or goal, and failed otherwise. In virtue of this link with success and failure, teleology has an evaluative dimension—understanding evaluative normativity as having to do with what is good or bad

(beneficial or detrimental) in some way (McLaughlin, 2009). Standards of success are evaluative, insofar as successful performances count as good qua instances of purposive behavior. Saying that some purposive behavior has been successful is a way of evaluating it (positively), with respect to the purpose of that behavior.

We will assume here that biological teleology is observer-independent, rather than being due to projections of purposes by external observers (or being a form of metaphorical or loose talk). According to this assumption, there are some entities in the biological world such that being those entities entails having certain purposes, and therefore being evaluable in terms of success, independently of projections from external observers. We will also assume that biological organisms are (sophisticated) complex physical systems. The question that arises is how certain physical systems (i.e. biological organisms) become subject to teleological standards.

A popular answer to this question appeals to the etiology of the relevant biological trait, more specifically to its evolutionary history (Millikan, 1984, 1989; Neander, 1991; Griffiths, 1993; Godfrey-Smith, 1994).¹ Broadly, the idea is that the purpose of a biological trait is doing what it was naturally selected for doing. So, a token of a biological trait has as its purpose producing some effect if producing that type of effect is what explains the proliferation of the ancestors of that token in the face of the pressures of natural selection. We will call this kind of approach an *etiological-evolutionary* account of teleology. To repeat a classic example, the purpose of hearts is to pump blood, because pumping blood explains why hearts managed to proliferate.

An initial virtue of this approach is that it seems to capture the circular dependence between effects and causes distinctive of teleology. According to Wright's analysis of teleology (1976: 39), the presence of a purposive trait is explained by its tendency to produce certain effects, which constitute its purpose. Similarly, Walsh (2008: 113) claims that "teleology is a mode of explanation in which the presence, occurrence, or nature of some phenomenon is explained by the end to which it contributes." In the case of purposive biological traits, the existence of a current token of the trait would be explained by the fact that past members of its lineage or reproductive chain produced certain effects, which are therefore the effects that the current token of the trait is supposed to have.

However, even if it is granted that the continued presence of a biological trait is explained by its tendency to produce certain effects, it is not immediately clear why this, on its own, would entail that the trait has a purpose and is subject to standards of success. One should not conflate necessary conditions for perpetuation with purposes. Existing because of the tendency to produce some effect is not the same as existing in order to produce that effect.

We think that the best way to vindicate etiological-evolutionary accounts is to focus on the role of selective processes in Darwinian evolution. Most advocates of etiological-evolutionary approaches appeal, explicitly or implicitly, to *selected-effects theories* of teleology, according to which selective processes give rise to purposes (Millikan, 1984, 1989; Neander, 1991; Griffiths, 1993; Kitcher, 1993;

¹ Alternative accounts of biological teleology, which we will not discuss here, are provided, among others, by systemic or dispositional theories (Cummins, 1975; Craven 2001; Boorse 2002) and by organizational approaches (Christensen & Bickhard, 2002; Mossio et al., 2009).

Godfrey-Smith, 1994). In Griffiths's words, "where there is selection there is teleology" (1993: 420). From the perspective of these theories of teleology, purposes are selected effects: the purpose of some entity is to produce certain effects if its tendency to produce those effects explains why the entity was preserved through a selective process.

Selected-effects theories of teleology offer direct support to the view that biological purposes are introduced by natural selection, provided that it is assumed that natural selection is a genuine selective process. So, biological teleology would result not merely from the circular dependence between effects and causes in biological traits, but from the fact that such dependence is mediated by natural selection.

We will not oppose here the view that natural selection is a source of biological teleology. Our goal is rather to show that natural selection is not the only relevant form of selection in biology. In particular, biological regulation should be counted as a selective process too, at least inasmuch as natural selection can be so counted. What we want to argue is that those who are happy to appeal to selected-effects theories in relation to natural selection should also be willing to do the same in relation to biological regulation, and therefore to recognize it as a distinctive source of biological teleology. So, for our purposes in this paper, we could just take selected-effects theories for granted. Nevertheless, in the next section we offer further clarification of such theories and provide some motivation for them. We will argue that the idea that selection introduces purposes is particularly plausible once we consider the type of (thin) evaluative normativity characteristic of teleology.

2 Selected-effects Theories of Teleology

Selection is closely related to evaluation. Indeed, selection can be seen as classification plus evaluative valence. Selective processes involve sorting items into groups with positive and negative valences—items selected *for* are positively evaluated, while items selected *against* receive negative evaluations, relative to the evaluative standard associated with the relevant selective process.

Of course, if the notion of selection is taken to be constitutively linked to evaluative standards, then the claim that there is evaluation wherever there is selection will be trivially true. However, we are interested in using selected-effects theories to offer a naturalistic account of the emergence of evaluative standards in biology. In order to do so, we need to characterize selective process without presupposing evaluative standards. Otherwise, we would have not explained how evaluative standards arise in biology. The aim, therefore, is to describe, in non-evaluative terms, biological processes that can be counted as forms of selection, and then argue that these processes give rise to evaluative standards.²

Campbell (1960) considers that any selection process involves blind variation and selective retention. An attractive option is to generalize this idea, thinking of selection in terms of differential reinforcement over a set of items featuring variability

² For abstract characterizations of selective processes, see Darden and Cain (1989) and Hull, Langman and Glenn (2001).

in their properties. In selective processes, items with certain features are retained, reproduced or promoted, which can be seen as a form of positive reinforcement, whereas other items are inhibited or rejected, which is a form of negative reinforcement. The features or effects selected for are those that explain why the relevant items are positively reinforced. Imagine, as an example, a gardener tending their garden by preserving flowers and cutting weeds. This gardener will be positively reinforcing the presence of flowers, while inhibiting the presence of weeds. It is natural to think of the gardener as selecting flowers, but not weeds, as a satisfactory contribution to their garden.

In general, processes driven by differential positive and negative reinforcement are intuitively seen as instances of selection. It makes sense to consider natural selection a selective process precisely because it involves differential reinforcement, in the form of differential reproductive rates. Learning by trial and error is another example of selection underlain by reinforcement (see, among others, Millikan 1984; Garson, 2017). In this case, the learner develops dispositions to repeat some behaviors and not others depending on whether they are observed to produce certain outcomes reliably.

It should be stressed that differential reproduction is only one of the possible forms of reinforcement that can underlie selection. Given the prominence of Darwinian evolution in biological research, it is understandable that biological selection tends to be identified with natural selection, and therefore with differential reproduction. However, biological selection can take place via other forms of reinforcement. For instance, Garson (2011, (2012, (2017, 2019b)) describes neural selection as a case of biological selection involving differential retention without differential reproduction. And, in principle, there could be further types of selective reinforcement, for example differential activation of certain processes or differential recruitment of some mechanisms (that is, situations in which several mechanisms are available for a given task and some of them are recruited more frequently than others, even if all those mechanisms are retained). It is wise to remain fairly liberal about the types of reinforcement potentially involved in biological selection, given the variety of shapes that reinforcement can take in ordinary cases of selection (for example, selecting one's clothes for an interview, selecting candidates for a job, selecting a film to watch, crop selection, or animal breeding).

Differential reinforcement does not presuppose evaluative standards, so we can use the characterization of selection given above to account for the emergence of biological teleology. Let us call the causal powers responsible for the relevant patterns of reinforcement "selective pressures." In the selected-effects theory we are exploring, selective pressures introduce teleological evaluative standards. The reason why these standards can be said to be teleological is that they satisfy the teleological loop postulated by Wright (1976): the reinforcement of the selected items is explained by their tendency to produce those effects that got them selected. Notice that this type of teleological explanation can be applied to instances of selection regardless of the form of reinforcement involved. So, when reinforcement takes place as differential reproduction, we would explain such differential reproduction by appeal to certain effects of the items that managed to reproduce (this is what happens in explanations of natural selection). In a similar way, when selection happens via differential retention, we would point to relevant effects of the items selected in order to explain why they have persisted. The teleological nature of selection does not depend, therefore, on the involvement of differential reproduction (see Garson 2017, 2019b).

We are not claiming, to be clear, that all instances of differential reinforcement will automatically count as cases of selection. Fuzzy, borderline cases are to be expected. However, we think that when the relevant differential reinforcement is sufficiently complex and flexible, the resulting processes can share enough features of paradigmatic forms of selection to deserve being classed as such. At least, we think, this is something that defenders of selected-effects theories should concede. In particular, as we will argue below, biological regulation can legitimately be seen as a type of selective process.

According to the view we are exploring, selective pressures do not presuppose evaluative standards, but rather institute them. Thus, selected-effects theories would be an instance of a more general metanormative approach in which evaluative standards are taken to be generated by responses or pressures that can be characterized in non-evaluative terms (in this case, in terms of reinforcement). This metanormative commitment may seem contentious, at least when applied to normative issues generally. However, selected-effects theories become far less controversial once we observe that they only address the type of thin evaluative normativity underlying teleology. The evaluations linked with ascriptions of success involve what is usually known as attributive goodness, rather than predicative goodness (for this distinction, see Geach 1956; Thomson, 2008). One makes attributive evaluations when one says that something is good as an instance of a certain kind (for instance, that some footballer is good as a goalkeeper). By contrast, in evaluations involving predicative goodness, one treats something as good simpliciter, and not just as an instance of a kind. An example is saying that peace is good and war is bad.

When we treat a performance as successful we are assessing it as good only with respect to the purpose of the relevant behavior (that is, good as purposive behavior). It does not follow from this attributive evaluation that that successful performance is good simpliciter (good in a predicative sense), or good when not assessed as an instance of the relevant purposive behavior but as an instance of a different kind. It may well be that things that are good as instances of a kind are not, all things considered, desirable, admirable, or worth promoting. So, we are not claiming that successful behaviors are always good in a way that makes them desirable or worth promoting. In many cases, rather the opposite is true; for example, successful murdering behaviors are to be stopped and prevented.

It is also important to distinguish *evaluative normativity*, which concerns what is good and bad, from *prescriptive normativity*, which concerns obligations, permissions and prohibitions. Attributive evaluations, like those associated with assessments of success, do not need to have immediate prescriptive implications. There may be no obligation whatsoever to engage successfully in a certain purposive behavior.

Thus, the type of normativity that we are associating with teleology is quite lightweight, in that it does not involve prescriptions or what is good simpliciter. We can remain neutral about whether more substantial normative standards (like those associated with morality, or with goodness simpliciter) are generated by reinforcing responses. As far as selected-effects theories are concerned, we only need to endorse the plausible view that reinforcing responses can determine what counts as good with respect to the standards governing activities shaped by those responses (regardless of whether it is good simpliciter to engage in such activities). More specifically, the pressures giving form to a certain selective process would determine what counts as good according to the standards governing that selective process. Let us insist that this is only attributive goodness, internal to the standards of a process of selection. In fact, it may be that there is nothing good simpliciter in the existence of a certain selective process, and it can even be the case that there are strong reasons to prevent some kinds of selection from happening (think of employee selection processes based on race or gender rather than merit).

It is instructive to consider at this point the examples of games and social norms (see Bicchieri 2006). Arguably, if the participants in a game treat certain moves as good or successful while playing the game, those performances count as good or successful as moves in that rule-governed game. There is no further, external standard that determines whether a certain move in the game is successful, beyond the responses and attitudes of the players of the game (at least if we are considering non-institutionalized games that are created from scratch by the players). Something analogous happens with many social norms, for instance norms of etiquette. Whether certain behaviors count as good table manners in a given social dining practice depends on whether the participants in the practice treat them as such. Indeed, what is good manners according to a certain dining practice can be bad manners in a different cultural context, where participants reinforce and sanction different behaviors. Of course, that some behaviors are good simpliciter or should be promoted. After all, the relevant dining practice could be sexist, classist, or bad in other respects.

In the same way that the normative standards internal to games and social practices are established by the attitudes and sanctioning dispositions of participants, the standards internal to selective processes would be generated by the pressures constitutive of the process. Given that selective processes are driven by the pressures introducing the relevant standards, these standards can be said to actively govern such selective processes.

3 Biological Selection Beyond Evolution

We are aware that the considerations in the previous section may not be universally convincing. For instance, some could insist, perhaps appealing to Moorean openquestion arguments, that a purely causal process like differential reinforcement cannot introduce the evaluative standards underlying selection (see Bedau 1991 for such an anti-reductionist view). While we are not moved by these strong anti-reductionist intuitions, in particular when dealing with the lightweight normativity characteristic of teleology, we leave that debate for another occasion. Our immediate target here is those who accept selected-effects theories, and in particular those who are willing to apply this type of theory to natural selection. So, in what follows we will take selected-effects theories for granted, as one of our assumptions, understanding selection in terms of differential reinforcement. We want to extend selected-effects theories beyond Darwinian evolution, arguing that natural selection is not the only plausible selective process in the biological world (see Garson (2017, 2019b) for a project in the same direction). More specifically, our claim is that biological regulation constitutes a form of selection, and therefore it deserves to be counted as a distinctive source of biological teleology.³

Thus, the argument put forward in this paper is conditional. If selected-effects theories are accepted, then biological regulation should be taken to introduce teleological standards of success. To be clear, we do not intend to attack etiological-evolutionary theories of biological teleology. The main contribution of this paper is constructive, not critical. Our goal is to draw attention to the possibility of considering biological regulation, in addition to natural selection, as a legitimate source of teleology. This is, we think, a substantial contribution, given how widespread biological regulation is in nature. Although the argumentative scope of the paper is restricted as specified above, the conclusions we will draw are still far-reaching and worth exploring. Arguably, selected-effects theories offer the dominant naturalistic account of biological teleology, so it is interesting to note that they allow us to consider biological regulation as introducing teleology in the natural world.

It is worth stressing that we are not claiming that selective processes introduce teleological standards to the extent that they resemble natural selection. Rather, according to the selected-effects theory we are putting forward, it is the other way around: natural selection is teleological insofar as it counts as a form of selection. There are selective processes associated with teleological standards despite the fact that they do not meet some of the conditions characteristic of natural selection, for instance processes in which selective pressures do not operate over past tokens of a type, but over the current performances of some item. Think, as an example, of a recruitment process in which candidates are selected according to their performance in an exam. Here, the relevant selective reinforcement targets the candidates' current performance in the exam, and not their past behavior, or the behavior of past individuals.

Are we stretching the notion of selection unduly? There is no reason to think so. Many central, paradigmatic types of selection do not resemble natural selection. If anything, it is natural selection that is a heterodox form of selection. In particular, stereotypical cases of selection involve identifiable systems or mechanisms that exert the relevant reinforcing pressures (that is, a selector). As we will see, in biological regulation there are regulatory sub-systems, integrated into the organism, that play this selecting role. By contrast, in natural selection the source of reinforcement is environmental forces, which usually do not constitute individuated mechanisms or systems. In this respect at least, biological regulation is closer to stereotypical selective processes than natural selection.

Of course, we are not the first to generalize selected-effects theories beyond natural selection. This generalization has already been suggested by Wimsatt (1972: 13), who claims that "the operation of selection processes is not only not special to biol-

³ Schroeder (2014) has defended the view that natural regulation generates functions, relying on the analogy with the way in which everyday forms of regulation confer functions to objects. We follow an alternative path here: we aim to integrate biological regulation into a general selected-effects theory of teleology, arguing that regulation constitutes a selective process.

ogy, but appears to be at the core of teleology and purposeful activity wherever they occur." Similarly, Neander (1991) notes that selected-effects theories could in principle be applied to any selective process, not just natural selection, although she does not develop this line of thought. Several authors, working from the perspective of selected-effects theories, have pointed out that trial and error learning can introduce purposes (for instance, Wimsatt 1972, 2002; Millikan, 1984; Griffiths, 1993).

In this way, our proposal should not be seen as conflicting with standard selectedeffects approaches, but rather as continuous with them. As we have just seen, many authors consider selected-effects theories to offer a general framework for accounting for teleology, not only in biology but also in relation to purposeful behavior in other domains. However, when applied to biology, selected-effects theories tend to focus overwhelmingly on natural selection. We want to resist this dominant tendency, and extend selected-effects approaches to other biological processes, in particular regulation. In this respect, Garson's work (2011, 2012, 2017, 2019b) is especially relevant for our purposes. Garson's claim is that selected-effects theories should not be restricted to processes driven by differential reproduction, such as natural selection, but should also allow for selective processes involving differential retention, in particular neural selection. In this way, Garson argues that selected-effects theories should be seen as disjunctive theories, covering both cases of differential reproduction and of differential retention.

We agree with the spirit of Garson's proposal, even if we prefer to think of the generalization of selected-effects theories as a unified view, rather than a disjunctive one, as Garson presents it. The unifying element in this generalized theory would be the idea of selection, characterized in terms of the notion of reinforcement. As we have pointed out, reinforcement can take different shapes, including differential reproduction and differential retention, but this does not mean that selection is a disjunctive kind. A more substantial difference between our proposal and Garson's is that our characterization of teleological selection is wider than his. In particular, the phenomenon we are going to focus on, biological regulation, does not typically meet the conditions for selective processes set by Garson's theory. According to Garson (2017), the relevant forms of selection involve either differential reproduction or retention in a population of tokens of a type engaged in fitness-relevant (competitive or cooperative) interactions. This is not what happens in most cases of biological regulation. Blood sugar regulation does not involve interactions within a population of different levels of blood sugar. But, again, there are many paradigmatic examples of teleological selection in which this condition is absent. Selection does not necessarily require interactions among the items undergoing the selective process. For instance, we can select which students pass a course, and which fail, by means of an individual exam, with no interactions among the students. Indeed, there can be selection with only one candidate. Think of the process of selecting candidates for an award by means of an exam. This process can take place even with a single candidate: if the candidate passes the exam, they will be selected for the award, otherwise they will not (none will get the award). Despite not involving a population of items with alternative traits, this is clearly a process of selection (even if not of selection over

existing alternative traits).⁴ So, although Garson surely discusses an interesting type of biological selection, processes that do not fit his account can nonetheless be close to paradigmatic forms of selection.

Garson introduces the conditions we have just discussed to avoid counterexamples that threaten to make selected-effects theories too liberal. We will show below that the type of selection associated with biological regulation is not affected by at least the most glaring of these counterexamples. We will also argue that allowing for regulatory teleology has explanatory and theoretical benefits analogous to those vindicating selected-effects theories in relation to natural selection (and to Garson's neural selection). However, before that, in the next section, we present the notion of biological regulation in more detail.

4 Biological Regulation

Biological organisms are able to regulate their behavior in the face of perturbations and to adapt it to environmental changes, so as to remain in configurations that allow the organism to keep existing (Rosen, 1970; Di Paolo, 2005; Bich et al., 2016). Think, for instance, of a bacterium that modulates its movement searching for nutrients in its environment, or a sick human that compensates for a feverish state through perspiration.

Living organisms are complex self-maintaining systems (see Moreno & Mossio 2015). This means that the activity of an organism contributes to the preservation of the conditions in which its existence is viable. In this way, organisms sustain their own existence and identity. Among other things, this involves repairing and regenerating their constituents, obtaining enough nutrients, disposing of waste, and avoiding toxic substances.⁵

Organisms are often threatened by external and internal perturbations that push them away from the conditions favorable to their existence (for instance, changes in the temperature of the environment, scarcity of nutrients, or the presence of predators). The self-maintenance of organisms will, therefore, be fragile unless they are able to react to these perturbations in ways that tend to keep the organism within its range of viability conditions. At first pass, biological regulation can be understood as the capacity of organisms to modulate their own behavior in response to perturba-

⁴ What is essential for selection is that it presents a suitable modal profile: traits are selected because they produce certain effects, and would not have been selected if they did not produce them. This modal profile may require the existence of a population with alternative traits, for instance in cases in which the competition among such alternative traits explains the differential reinforcement of traits with the relevant effects. But, as the example of the lone award candidate shows, there are selective processes with a suitable modal dimension despite not involving a population of traits. In this way, the lone candidate in the example above will not be selected for the award if they do not pass the exam, regardless of the absence of competitors.

⁵ We will flesh out the notion of regulation within an organizational framework, following, among others, Bich et al. (2016). However, the type of biological teleology we want to explore differs from that studied by organizational authors like Mossio, Saborido and Moreno (2009), who focus on purposes associated with the contribution of traits to the self-maintenance of organisms. We will examine instead the purposes that, according to a selected-effects approach, are introduced by self-regulation. We consider these two approaches to be complementary.

tions that endanger their maintenance. Of course, regulation is not infallible. Organisms will not always manage to counteract the effects of perturbations. Yet regulatory responses will at least have the tendency to prevent perturbations from undermining the organism's viability conditions.

It is important to note, however, that a notion of regulation that includes all compensatory reactions to perturbations would be too broad for our purposes (see Bich et al., 2016; Bich, 2018; Bich et al., 2020). For instance, reversible chemical reactions show a certain degree of robustness against perturbations, as encapsulated in Le Chatelier's principle. In general, physical systems near stable equilibrium states tend to oppose perturbations that try to take the system away from the equilibrium (think, for example, of a marble at the bottom of a bowl). We do not want to conflate the behavior of these simple physical systems near equilibrium with the more sophisticated forms of adaptation to perturbations characteristic of biological organisms. Thus, we will work with a restricted, regimented notion of regulation that does not count every system near stable equilibriums as self-regulated.⁶

More specifically, we reserve the (regimented) notion of regulation for complex systems in which there are specialized mechanisms that modulate the behavior of the system in response to the relevant perturbations (see Bich et al., 2016). In self-regulated organisms, therefore, there is a hierarchical distinction between higher-level regulating mechanisms and the lower-level mechanisms and processes regulated by them. This does not happen, for example, in the case of a marble moving around the bottom of a bowl. Higher-level regulatory sub-systems are also absent in other cases of simple differential retention—for instance, in the example of the beach rocks eroded differentially by the sea, discussed by Garson (2017). Thus, our account avoids potential charges of overgeneralization faced by proposals that associate teleology with equilibrium systems or mere differential retention.

To be clear, regulatory sub-systems are an integrated part of the organism, insofar as such sub-systems are sustained by the activity of the rest of the organism. Yet it is possible to differentiate these regulatory sub-systems from the other parts of the organism whose behavior they modulate. Bich et al. (2016) propose delineating this distinction in terms of what they call dynamical decoupling: this type of decoupling occurs when the relevant sub-systems work at "different intrinsic rates", so that there is a certain degree of independence between their activities (Bich et al., 2016: 254).

The conception of regulation that we will adopt here is nicely summarized by Bich, Mossio and Soto:

regulation consists of the capacity to selectively modulate the first-order selfmaintaining regime in response to specific variations of the internal and external environment, due to the action of a dynamically decoupled dedicated control subsystem that is sensitive to these variations. (Bich et al., 2020: 9).

⁶ Bedau (1992) argues against the idea that equilibrium systems can generally be taken to be goal-directed, objecting that it leads to overgeneralization. As we explain above, we do not consider systems near equilibrium as self-regulated. Indeed, self-regulated biological organisms are far-from-equilibrium systems (see Moreno & Mossio 2015).

Thus, biological regulation, as we understand it, involves specialized or dedicated sub-systems that modulate the behavior of other parts of the organism in response to internal or external perturbations. It should be stressed that this talk of dedication does not presuppose teleological notions. In particular, we are not assuming that dedicated regulatory mechanisms have the purpose of modulating the behavior of the system. Self-regulation involves dedicated mechanisms in the sense that there are sub-systems that contribute causally to the dynamics of the system by producing the pressures that generate the relevant differential reinforcement. We can characterize this contribution in purely causal terms, as one would do in Cummins's causal-role approach to functional explanations (1975).

Regulatory modulation may amount to modifying the rate or intensity at which some mechanism operates. For example, one way in which the secretion of insulin contributes to blood sugar regulation is by stimulating the uptake of glucose in muscle and fat tissue cells. However, as Bich et al. (2016) emphasize, in other cases the relevant modulation is a matter of switching the regime under which the regulated sub-system works—so that the regulated sub-system changes its mode of operation. For instance, in bacterial chemotaxis, bacteria control the direction of their movement by alternating between two modes of rotation of gene expression in the lac operon, which allows bacteria to switch from metabolizing glucose to metabolizing lactose (for details see Jacob & Monod 1961; Müller-Hill, 1996; Bich et al., 2016). The lac operon is a clear illustration of a regulatory mechanism that shifts between different metabolic regimes of the regulated sub-system.

Far from being a novel concept, or a mere speculative construct, regulation is a well-studied phenomenon in the biological sciences (e.g. Heinrich & Schuster 1996; Fell, 1997; Tsokolov, 2010). Homeostasis, the ability of organisms to maintain stability in their internal variables, is generally the result of the activity of regulatory sub-systems. This is what happens, for instance, in thermoregulation, or in glycemia regulation. In this latter case, the pancreas acts as a regulatory mechanism that keeps blood sugar levels stable, via the production of insulin and glucagon (see Bich et al., 2020). Insulin, which is released by beta cells in the pancreas when they detect an increase of blood sugar, contributes to reducing the levels of glucose by inducing the liver to transform glucose into glycogen, and by promoting cellular intake of glucose in muscle and adipose tissues. By contrast, glucagon, released by pancreatic alpha cells, has the opposite effect of increasing the levels of blood glucose.

Glycemia regulation is just an illustrative example of biological regulation, among many possible others (think, for instance, of the regulatory roles of the thyroid, or of adrenaline). It should be stressed that biological regulation is a widespread phenomenon, which takes place in virtually every biological system, and on all levels of biological organization. Most aspects of the behavior of organisms and their interactions with their environment are shaped to some extent by regulatory mechanisms. Thus, we can find regulation at the basic level of gene expression, as in the lac operon. The movement of organisms in their environment is also usually controlled by regulatory mechanisms, even in simple cases like bacterial chemotaxis. Bacteria like *E. Coli* can direct their movements toward higher concentrations of some chemical substances (attractants, e.g., nutrients), and away from others (repellents, e.g., toxic substances),

despite the fact that they only have two ways of moving: swimming in a straight line (when rotating their flagella counter-clockwise) and tumbling (when rotating the flagella clockwise). This can be achieved thanks to regulatory mechanisms that detect variations in the environmental concentration of the relevant substances. When a decrease in the concentration of attractants is sensed, the regulatory mechanism induces a switch to clockwise rotation of the flagella, as a result of which the bacterium tumbles and changes its direction of movement at random. By contrast, when the concentration of attractants increases, the bacterium keeps swimming in a straight direction, which tends to get it closer to the source of attractants. The key components in this regulatory system are a group of proteins called *Che proteins*. These proteins are sensitive to the activation of the transmembrane receptors in charge of detecting attractants/repellents, and also control the rotation of the flagella (for details see Eisenbach 2004; Wadhams & Armitage, 2004; Bich et al., 2016). This simple regulatory mechanism allows bacteria to effectively navigate chemical gradients in their environment.

The behaviors of more sophisticated organisms are also typically subject to regulatory controls. Consider, for instance, a predator following the trajectory of its prey (say, a cat hunting a mouse). In order to be able to track and replicate the changes in direction of the prey, the movements of the predator will be guided by complex regulatory mechanisms, involving its sensory organs and central nervous system. In general, flexible behaviors that show a high degree of adaptability require the engagement of regulatory systems.

5 Biological Regulation as a Selective Process

Our proposal is that biological regulation constitutes a selective process. Regulatory sub-systems tend to promote, retain, or reproduce certain behaviors in organisms, and inhibit others. The activity of regulatory sub-systems results, therefore, in the differential reinforcement of the behavior of the organism regulated. This fits the characterization of selection in terms of differential reinforcement put forward above. Thus, it makes sense to talk of regulatory selection. In this type of selection, the relevant selective pressures are generated by the constraints imposed by the regulatory sub-system on the behavior of the regulated system.

Remember that natural selection can be counted as a selective process because it is driven by differential reproduction, which is a type of differential reinforcement. Given the involvement of differential reinforcement in biological regulation, it should also be considered a form of selection, at least to the same extent that Darwinian natural selection is. Indeed, many examples of biological regulation can be described in terms of differential reproduction or repetition of certain behaviors. Let us go back to bacterial chemotaxis. In this case, the regulatory sub-system promotes the repetition of rotations of the flagella that direct the bacterium towards high concentrations of an attractant (e.g., nutrients), while movements that lead away from attractants tend to be interrupted. In virtue of this differential reinforcement of flagella rotation, it makes sense to think of chemotaxis as selective control of the movement of bacteria.

Other examples of biological regulation are perhaps better accounted for by appealing to forms of selective reinforcement beyond differential reproduction or repetition. For instance, in glycemia regulation, the release of insulin intensifies or fosters the absorption of glucose into muscle, adipose and liver cells, whereas it inhibits the production of glucose via glycogenolysis. In this example, rather than differential reproduction, we find differential stimulation and inhibition of certain cellular processes. However, there is no reason to think that these further forms of reinforcement cannot give rise to selective processes-a point already made by Garson (2017) when discussing selection via differential retention. Nothing in the notion of selection requires reproduction, as shown by paradigmatic examples like employee selection (which, obviously, can take place without the candidate employees reproducing). What is important is that there are selective pressures that lead to differential reinforcement, allowing for the distinction between items selected for and against. Our claim is that biological regulation can be counted as a selective process, insofar as it involves relevant forms of differential reinforcement (even if this reinforcement does not always take the shape of differential reproduction). Indeed, the language of selection is difficult to avoid when describing biological regulatory mechanisms. Just to present one example, Bich, Mossio and Soto talk of regulation as the "capacity to selectively modulate the first-order self-maintaining regime" (2020: 9, our emphasis).

Once it is granted that biological regulation is a selective process, it follows from selected-effects theories that regulation introduces teleological standards. As far as regulatory teleology is concerned, the behaviors of organisms have as their purpose producing those effects that explain their positive selection in some relevant regulatory regime. That is, purposive behavior is produced by traits that operate under the causal control of regulatory sub-systems. The (positive or negative) reinforcement of the regulated trait is explained causally by the pressures exerted by the relevant regulatory mechanism. Thus, the (positive and negative) reinforcing constraints generated by the regulatory sub-system define the teleological evaluative standards to which the behavior of the regulated traits is subject (of course, there could be further purposes introduced by other selective processes, for instance natural selection). In this way, behaviors that tend to be inhibited by a regulatory mechanism (that is, behaviors that tend to be regulated against) count as unsuccessful or inappropriate with respect to the standards set by that regulatory mechanism. Our proposal, in sum, is that a trait has the purpose of Φ if it has been reinforced by some regulatory mechanism because of its tendency to bring about Φ (in the case of positive reinforcement), or because of its tendency not to bring about Φ (in the case of negative reinforcement).

Take the example of chemotaxis. Movements that drive the bacterium away from high concentrations of an attractant tend to be interrupted by the regulatory mechanism, while movements towards high concentrations of the attractant tend to be continued. From the perspective of the regulatory mechanism governing chemotaxis, therefore, the purpose of the bacterium's movement is to go towards high concentrations of attractants.

It should be stressed that although we are developing our characterization of regulation in an organizational setting (following especially Bich et al., 2016), our proposal is intended to be an instance of selected-effects theories. Other organizational approaches account for purposes as contributions to the self-maintenance of organisms (for instance, Mossio et al., 2009). In this type of view, regulation is not in itself a source of teleology, but rather a way in which organisms become sensitive to the teleological standards set by self-maintenance. In this paper, our approach is different (even if compatible). Adopting the perspective of selective effects-theories, we argue that regulation introduces purposes by virtue of being a selective process. At any rate, the application of selected-effects theories to biological regulation vindicates the claim by organizational theorists (see Mossio & Saborido 2016) that etiological accounts of teleology do not need to appeal to the evolutionary history of traits.⁷ There can be etiological accounts that focus instead on the behavior of the current organism, be it on the causal contribution of a trait to self-maintenance, as in standard organizational proposals (Mossio Saborido and Moreno 2009), or on the effects that explain the preservation or reinforcement of a trait under a regulatory regime.

The view that regulation is a source of teleology has all the explanatory virtues that support selected-effects theories in general, and etiological-evolutionary accounts of biological teleology in particular. First, it allows us to distinguish purposes from non-purposive effects. The latter would be effects that are not under the control of regulatory mechanisms (to be sure, these effects could count as purposive with respect to other, non-regulatory, selective processes).

Second, like other selected-effects theories, the view we are presenting accounts for the normative dimension of teleology. More precisely, regulation, being a selective process, establishes evaluative standards, so that behaviors can be classified as appropriate or inappropriate with respect to the standards introduced by the relevant regulatory mechanism (remember, though, that this is just an internal evaluation relative to this regulatory process). In particular, it is perfectly possible for a trait to fail to fulfil the purpose conferred on it by some regulatory mechanism. This will happen when the trait behaves in ways that tend to be counteracted by the regulatory mechanism (note that the regulatory mechanism may fail to counteract effectively deviations in the regulated system).

Finally, the standards instituted by regulatory processes are teleological, because they ground explanations of the presence of behaviors by appeal to their effects. The fact that some behavior produces effects that tend to be promoted, rather than inhibited, by a regulatory mechanism provides a relevant causal explanation for the continued presence of the behavior. If the behavior had different effects, it would probably have been inhibited by the regulatory mechanism controlling it. Therefore, in order to explain why the behavior is being preserved (or somehow reinforced) rather than inhibited by the (present) action of the relevant regulatory mechanism, we have to appeal to the effects of that behavior. This is the characteristic structure of teleological explanations. Note that teleological explanations do not always explain

⁷ Authors such as Garson (2019a) or Artiga and Martínez (2016) have argued that the organizational approach is actually a version of etiological accounts. This is not disputed by defenders of organizational views, who argue that these views are perfectly compatible with the etiological characterization of teleological explanations proposed by Wright (Saborido, 2014). Organizational approaches to functions have not been developed as alternatives to etiological accounts in general, but to etiological-evolutionary approaches in particular. The main difference between these two approaches is not that one is etiological and the other is not (both are), but that the organizational framework does not focus on evolutionary history (Mossio & Saborido, 2016).

the proliferation of a trait. Explanations that account for the preservation or continued presence of a trait can be considered to be teleological, insofar as they do so by appeal to the effects of that trait (see Mossio & Saborido 2016). A way of explaining the persistence of a trait is to explain how it avoids being inhibited by a selective, regulatory mechanisms to which the trait is subject.

Garson (2017) argues that, since the satisfaction of these three explanatory desiderata constitutes the best argument for etiological-evolutionary theories of teleology, other selected-effects theories that satisfy those desiderata should, by parity, be considered equally justified. He resorts to this argumentative strategy to vindicate the idea that neural selection gives rise to functions; however, as we have seen, the same strategy can be used to defend the view that biological regulation is a source of teleology.

Moreover, our account captures two distinctive features of teleological behaviors: their persistence and plasticity—these features are highlighted, among others, by Nagel (1979) and McShea (2012). The behavior of regulated systems is persistent in the sense that deviations from the relevant behavioral trajectories tend to be counteracted by the regulatory mechanisms. Additionally, regulatory mechanisms are typically able to take the system back to the target behavioral trajectories from different deviations (in the face of different perturbations), which confers plasticity to the system's behavior.

Thanks to the richness of regulatory behavior, our account is less prone to accusations of liberality and overgeneralization than other selected-effects approaches. Regulatory selection is not exposed to prominent counterexamples to selected-effects theories discussed in the literature. For instance, Bedau (1991) considers a collection of clay crystals reproducing from crystal-seeds at different rates. Bedau argues that these crystals meet the conditions for natural selection, even if we would not attribute teleology to them. Garson (2017) discusses another example, proposed by Kingsbury (2008), in which a group of beach rocks are eroded by the sea at different rates depending on their hardness. This process can be seen as a form of differential retention, yet it does not involve teleology.⁸

None of these counterexamples affect our proposal, because they do not count as instances of regulation. More specifically, they do not feature a higher-order subsystem exercising the relevant reinforcing pressures on a regulated system. Biological self-regulation imposes quite stringent conditions, since it requires the presence of higher-order regulatory mechanisms integrated in the self-maintaining organization of the system. While this sophisticated form of organization is characteristic of biological organisms, it is difficult to think of examples elsewhere in the natural world, for instance in collections of rocks or clay crystals. Thus, counterexamples to regulatory teleology are hard to come by. Even if regulation can be a phenomenon with fuzzy limits, and difficult borderline cases are to be expected, a selected-effects theory in terms of self-regulation does not seem to overgeneralize in problematic ways. This is not surprising, given that the presence of a selector (in this case, in the

⁸ Garson's (2017: 536–549) response to these purported counterexamples is to require that the relevant forms of selection operate over a population of items engaged in fitness-relevant interactions. The collection of beach rocks does not satisfy this condition.

shape of a regulatory subsystem) is one of the distinctive features of stereotypical selective processes, which sets them apart from more basic forms of sorting or near equilibrium behavior.

It is worth noting that, in addition to sharing the central explanatory virtues of etiological-evolutionary theories, the view we are putting forward avoids some of their problematic features. According to etiological-evolutionary theories, in order to identify the purposes of some trait, we have to examine the evolutionary history of its ancestors (we have to figure out what its ancestors were naturally selected for). However, researchers are often interested in how functional traits contribute to the organization of current organisms. That is, when attributing purposes, researchers often want to study the actual organization and behavior of present-day organisms, regardless of their evolutionary history. It can be argued, therefore, that in many cases etiological-evolutionary theories do not fit well with the explanatory interests that underly the practice of ascribing purposes to organisms in biological research. This is sometimes regarded as a problem for etiological theories (Amundson & Lauder, 1994; Christensen & Bickhard, 2002), and an advantage of alternative systemic accounts of teleology, in which purposes are seen as current contributions of a trait to the organisms' organization (for instance, Cummins 1975; Craven 2001; Christensen & Bickhard 2002; Mossio et al., 2009).

The view of biological teleology presented here does not face this problem. Although, as a selected-effects theory, it is an etiological view, the focus is not on the evolutionary history of the ancestors of current organisms, but rather on how behaviors are produced under a certain regulatory regime in the actual organisms studied. In self-regulation, the relevant selective processes operate on the very same organisms to which the resulting purposes are attributed. Regulatory mechanisms shape the behavior of the system they regulate. In this way, the selective pressures created by regulatory mechanisms will be directly reflected by the behavior of the regulated system. Thus, the attribution of purposes arising from biological regulation will be immediately relevant for explaining the current behavior of organisms. Note as well that regulation is not a marginal phenomenon, affecting only a narrow range of behaviors. Quite the opposite, regulation is pervasive in biology. Indeed, regulatory processes are crucial to explain phenomena as important as functional integration, the emergence of the complexity of organic bauplans, and even the origins of cognition (Bich, 2018). The idea that regulation is a source of biological teleology has, therefore, great explanatory potential.

All we have said is compatible with granting that the purposes introduced by natural selection can play a significant role in scientific explanations (for instance, if one wants to investigate the origin and evolution of some trait). The considerations in this paper lead naturally to a pluralistic selected-effects theory in which different teleological standards are instituted by different selective processes, including natural selection but also neural selection and, as we have argued, biological regulation (and we have also not ruled out the possibility that purposes may be established in further ways that do not involve selection). Depending on the interests of researchers on each occasion, some of these selective processes will be more relevant than others.

It is to be expected that, in many cases, the purposes introduced by biological regulation will align with those instituted by natural selection, since, in general, regu-

latory mechanisms have themselves been naturally selected. However, natural selection and regulation constitute distinct sources of teleology. The purposes generated by biological regulation are independent of the evolutionary history of the organism exhibiting the relevant regulatory mechanisms. Indeed, conflicts and divergences between these two sources of teleology are, in principle, possible. Imagine, as a hypothetical example, bacteria whose chemoreceptors treat as attractants substances that were not present in the environment where they evolved, and which are not beneficial for their fitness. In this case, bacterial chemotaxis would have a purpose (navigating towards the non-beneficial attractant) that clashes with evolutionary goals. When these misalignments occur, the purposes associated with regulation remain particularly useful for explaining the actual behavior of organisms and the way in which they are expected to react to perturbations.⁹

Before concluding, let us mention a possible objection to our account. According to the view we have presented, regulatory sub-systems set teleological standards for the systems they regulate, but not for their own regulatory behavior (see Schroeder 2014: 122). It seems, therefore, that regulatory mechanisms are not, themselves, subject to teleological standards. So, it would not be possible to attribute purposes to regulatory mechanisms, and to identify cases of regulatory malfunction (at least, if we are focusing just on teleological standards derived from regulation). This is certainly an implication of our view when dealing with systems controlled by a single regulatory mechanism. However, in sufficiently sophisticated organisms, regulatory processes may be themselves regulated by further regulatory mechanisms, creating a complex hierarchical network of regulatory sub-systems (Bich et al., 2020: 10). This makes room for the possibility that a regulatory mechanism malfunctions with respect to the standards instituted by another regulatory mechanism that controls its behavior. Although the purposes arising from regulation are ultimately established by the regulatory activity of the organism, particular regulatory mechanisms can be subject to teleological standards set by other parts of the regulatory network. In any case, we leave the study of how different regulatory mechanisms are integrated hierarchically in organisms for another occasion.

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⁹ Fagerberg (2022) criticises Garson's generalised theory, arguing that it counts some traits as both functional and dysfunctional. We do not find this to be problematic, but rather an interesting implication of the view. The important point is that the different, sometimes conflicting, purposes are introduced by different selective processes. As far as each selective process is concerned, the purpose of the trait is well defined.

References

Amundson, R., & Lauder, G. V. (1994). Function without purpose. *Biology and philosophy*, 9(4), 443–469. Artiga, M., & Martínez, M. (2016). The organizational account of function is an etiological account of

function. Acta Biolheoretica, 64, 105–117. Bedau, M. (1991). Can Biological Teleology be naturalized? The Journal of Philosophy, 88(11), 647–655.

Bedau, M. (1992). Goal-Directed Systems and the good. The Monist, 75, 34-49.

- Bicchieri, C. (2006). *The grammar of society: The nature and dynamics of social norms*. Cambridge: Cambridge University Press.
- Bich, L. (2018). Robustness and autonomy in biological systems: How regulatory mechanisms enable functional integration, complexity and minimal cognition through the action of second-order control constraints. In M. Bertolaso, S. Caianiello, & E. Serrelli (Eds.), *Biological Robustness. Emerging perspectives from within the Life Sciences* (pp. 123–147). New York: Springer.
- Bich, L., Mossio, M., Ruiz-Mirazo, K., & Moreno, A. (2016). Biological regulation: Controlling the system from within. *Biology & Philosophy*, 31(2), 237–265.
- Bich, L., Mossio, M., & Soto, A. M. (2020). Glycemia regulation: from feedback loops to organizational closure. *Frontiers in Physiology*, 11.
- Boorse, C. (2002). A rebuttal on functions. In A. Ariew, R. Cummins, & M. Perlman (Eds.), *Functions: New essays in the philosophy of psychology and biology*. Oxford: Oxford University Press.
- Campbell, D. T. (1960). Blind variation and selective retentions in creative thought as in other knowledge processes. *Psychological review*, 67(6), 380.
- Christensen, W. D., & Bickhard, M. H. (2002). The process Dynamics of normative function. *The Monist*, 85, 3–28.
- Craver, C. F. (2001). Role functions, mechanisms, and Hierarchy. Philosophy of Science, 68, 53-74.
- Cummins, R. (1975). Functional analysis. Journal of Philosophy, 72, 741-765.
- Darden, L., & Cain, J. A. (1989). Selection type theories. Philosophy of Science, 56(1), 106-129.
- Di Paolo, E. A. (2005). Autopoiesis, adaptivity, teleology, agency. *Phenomenology and the cognitive sciences*, 4(4), 429–452.
- Eisenbach, M. (2004). Chemotaxis. London: Imperial College Press.
- Fagerberg, H. (2022). Against the generalised theory of function. Biology & Philosophy, 37(4), 30.
- Fell, D. (1997). Understanding the control of metabolism. London: Portland press.
- Garson, J. (2011). Selected effects and causal role functions in the brain: The case for an etiological approach to neuroscience. *Biology & Philosophy*, 26(4), 547–565.
- Garson, J. (2012). Function, selection, and construction in the brain. Synthese, 189(3), 451-481.
- Garson, J. (2017). A generalized selected effects theory of function. Philosophy of Science, 84(3), 523-543.
- Garson, J. (2019a). There are no ahistorical theories of function. Philosophy of Science, 86(5), 1146-1156.
- Garson, J. (2019b). What biological functions are and why they matter. Cambridge: Cambridge University Press.
- Geach, P. T. (1956). Good and evil. Analysis, 17(2), 33-42.
- Godfrey-Smith, P. (1994). A modern history theory of functions. Noûs, 28(3), 344-362.
- Griffiths, P. E. (1993). Functional analysis and proper functions. *The British Journal for the Philosophy of Science*, *44*(3), 409–422.
- Heinrich, R., & Schuster, S. (1996). The regulation of cellular systems. New York: Champman & Hall.
- Hull, D. L., Langman, R. E., & Glenn, S. S. (2001). A general account of selection: Biology, immunology, and behavior. *Behavioral and brain sciences*, 24(3), 511–528.
- Jacob, F., & Monod, J. (1961). Genetic regulatory mechanisms in the synthesis of proteins. *Journal of Molecular Biology*, 3, 318–356.
- Kitcher, P. (1993). Function and design. Midwest Studies in Philosophy, 18, 379-397.
- McLaughlin, P. (2009). Functions and norms. In U. Krohs, & P. Kroes (Eds.), Functions in biological and artificial worlds: Comparative philosophical perspectives (pp. 93–102). Cambridge, MA: MIT Press.
- McShea, D. W. (2012). Upper-directed systems: A new approach to teleology in biology. *Biology & Philosophy*, 27(5), 663–684.
- Millikan, R. G. (1984). Language, thought, and other biological categories: New foundations for realism. Cambridge, MA: MIT press.
- Millikan, R. G. (1989). In defense of proper functions. Philosophy of science, 56(2), 288-302.
- Moreno, A., & Mossio, M. (2015). Biological autonomy: A philosophical and theoretical enquiry. New York: Springer.

- Mossio, M., & Saborido, C. (2016). Functions, organization and etiology: A reply to Artiga and Martinez. Acta Biotheoretica, 64(3), 263–275.
- Mossio, M., Saborido, C., & Moreno, A. (2009). An organizational account of biological functions. The British Journal for the Philosophy of Science, 60(4), 813–841.

Müller-Hill, B. (1996). The lac operon: A short history of a genetic paradigm. New York: de Gruyter.

- Nagel, E. (1979). *Teleology revisited and other essays in the philosophy and history of science*. New York: Columbia University Press.
- Neander, K. (1991). Functions as selected effects: The conceptual analyst's defense. *Philosophy of science*, 58(2), 168–184.
- Rosen, R. (1970). Dynamical system theory in biology. Stability theory and its applications. New York: Wiley.
- Saborido, C. (2014). New directions in the Philosophy of Biology: A new taxonomy of functions. In C. Galavotti, S. Hartmann, M. Weber, W. Gonzalez, D. Dieks, & T. Uebel (Eds.), *New directions in the philosophy of Science* (pp. 235–251). Dordrecht: Springer.
- Schroeder, T. (2014). Functions from regulation. The Monist, 87(1), 115–135.
- Kingsbury, J. (2008). Learning and Selection. Biology and Philosophy, 23, 493-507.
- Thomson, J. J. (2008). Normativity. Chicago: Open Court.
- Tsokolov, S. (2010). A theory of circular organization and negative feedback: Defining life in a cybernetic context. *Astrobiology*, *10*(10), 1031–1042.
- Wadhams, G. H., & Armitage, J. P. (2004). Making sense of it all: Bacterial chemotaxis. Nature reviews Molecular cell biology, 5(12), 1024–1037.
- Walsh, D. M. (2008). Teleology. In M. Ruse (Ed.), *The Oxford handbook of philosophy of biology* (pp. 113–137). Oxford: Oxford University Press.
- Wimsatt, W. C. (1972). Teleology and the logical structure of function statements. *Studies in the History and Philosophy of Science*, 3, 1–80.
- Wimsatt, W. C. (2002). Functional organization, analogy, and inference. In A. Ariew, R. Cummins, & M. Perlman (Eds.), *Functions: New essays in the philosophy of psychology and biology* (pp. 173–221). Oxford: Oxford University Press.
- Wright, L. (1976). Teleological explanations: An etiological analysis of goals and functions. Berkeley: University of California Press.

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