APhEx 26, 2022 (ed. Vera Tripodi)
Ricevuto il: 16/06/2022
Accettato il: 31/08/2022
Redattori: Andrea Borghini, Silvia De Toffoli, Matteo Morganti, Eugenio Orlandelli

APhEx
PORTALE ITALIANO DI FILOSOFIA ANALITICA
GIORNALE DI FILOSOFIA NETWORK
N° 26, 2022

OPEN PROBLEMS

Function Pluralism in Biology. An Open Problem

Claudio Davini

This article aims to deal with the problem of function pluralism in biology. The debate on function pluralism involves two conflicting sides: between-discipline pluralism and within-discipline pluralism. The majority of philosophers of biology are between-discipline pluralists. According to them, different theories of biological function – the selected effects theory and the causal role theory – are appropriate to different branches of biology; the selected effects theory is the most appropriate theory for evolutionary biology, while the causal role theory is the most appropriate theory for physiology – e.g., anatomy, neuroscience, and developmental genetics. On the contrary, within-discipline pluralism holds that we should seek out a plurality of functions inside any branch of biology. More precisely, according to within-discipline pluralists, selected effects functions and causal role functions can coexist within the same *field. In this paper, I will introduce arguments both in favour and against between-discipline pluralism. Afterwards, I will exhibit how the arguments against between-discipline pluralism motivate within-discipline pluralism. Finally, I will develop an argument that may be of help to prove the case of within-discipline pluralism.*

TABLE OF CONTENTS

1. Introduction. Function Pluralism in Biology

Function-talk is ubiquitous. Everyone uses the term "function" – whether directly or indirectly – probably every day of their life. So, when it comes to biology, it is not surprising at all that function attributions are widespread in the studies concerning the living world too. For example, even though Darwin himself dismissed the idea that zebra stripes can afford protection (1871: 302), biologists are still debating on what is the function of zebra stripes (Caro et al. 2014; Larison et al. 2015). Nowadays, the vast majority of philosophers of biology are pluralists about functions. But what is it meant by function pluralism in biology? In a general sense, function pluralism is the fact that both philosophers of biology and biologists employ the term function in different ways. This means that there can be more than just one single sense of biological function, and that different senses of biological function can capture different strands of biological usage. For example, some use the selected effects theory (Millikan 1984, 1989; Neander 1991a, 1991b, 2017a, 2017b; Garson 2016, 2019), which is also referred to as the strong etiological theory in contrast with the weak etiological theory (Buller 1998), some others use the causal role theory (Cummins 1975, 1983; Amundson and Lauder 1994; Hardcastle 1999, 2002; Davies 2001; Craver 2013; Šustar 2007; Šustar and Brzović 2014), and still others use the fitness-contribution theory (Canfield 1964; Ruse 1971;

Boorse 1976; Bechtel 1986; Bigelow and Pargetter 1987; Horan 1989; Wouters 1995, 2005, 2013; Walsh 1996; Walsh and Ariew 1996; Lewens 2004; Kraemer 2013). In a more limited sense, function pluralism indicates two different strategies for bringing order into such a plurality of functions: between-discipline and within-discipline pluralism. This more limited sense of function pluralism is the topic of this paper, since between-discipline pluralism has been severely contested in recent years and the alternative that has been proposed to it is indeed within-discipline pluralism. The idea behind between-discipline pluralism is that different theories of biological functions – that is, the selected effects theory and the causal role theory – are appropriate for different sub-disciplines, meaning that one may group different sub-disciplines of biology by the notion of function that its practitioners appeal to. On the contrary, the idea behind within-discipline pluralism is that one can make use of different theories of biological functions – once again, the selected effects theory and the causal role theory – inside any branch of biology.[1] In the next section, I will exhibit that function pluralism has a growing significance and I will deepen between-discipline pluralism's state of the art.

2. Between-Discipline Pluralism. An Attractive View

Biological functions are central to many discussions in both philosophy and science. In philosophy, they play a role in debates on the nature of teleological reasoning, normativity, health, disease, and artifacts. In science, they play a role in debates concerning genetics, neuroscience, and ecology. Therefore, it is straightforward that function pluralism has an important significance as well. Indeed, debates on function pluralism are becoming increasingly important in biology. As an illustration of the growing importance of function pluralism, consider the rivalry between the Human Genome Project and the consortium ENCODE – Encyclopedia of DNA Elements –, which has become a canonical

[1] I will introduce the selected effects theory and the causal role theory below. Regarding instead the fitness-contribution theory – which holds, briefly put, that a trait's function has to do with its present-day contribution to fitness –, I will not deepen it any further, since it has currently no part in the debate between the two above mentioned strategies. As an introduction to the fitness-contribution theory, see Garson 2016 (67-79).

example in the literature on biological functions (see for instance Garson 2016: 1-2; Garson 2017: 5; Garson 2019: 143-144). Notwithstanding their shared purpose, that is, sequencing the functional elements of the human genome, the proponents of these two projects do not agree about the percentage of the human genome to be considered functional. While ENCODE assigns function to 80% of the genome, the Human Genome Project's estimates amount to less than 15%. Scientific critics of ENCODE claim that the 80% estimate is a mistake because it rests, they charge, on an extremely liberal construal of the concept of function (Doolittle 2013; Graur et al. 2013).[2] Furthermore, those critics add that ENCODE even conflates the selected effects theory and the causal role theory (Brunet and Doolittle 2014; Elliott et al. 2014). On the contrary, the scientists leading ENCODE contend that there are multiple meanings of function in biology, and they responded to the criticism mentioned above precisely by arguing that all these meanings are legitimate and that we should therefore embrace function pluralism (Kellis et al. 2014).[3] However, they did not deepen their claim any further. This is indeed a good reason to demand clarification. That is why I will now introduce and discuss the most

[2] To understand in what such a liberal construal consists, consider the following explanation. One way in which practicing biologists attribute function to a certain biological item is through this experimental procedure: in case an organism-level effect E does not occur anymore after deleting or blocking the expression of a region R of DNA, then that same effect E is taken to be the function of that region R. Many biologists contend that such a procedure points, indirectly at least, to the selected effects theory; indeed, «they believe that effect E could, under suitable conditions, be shown to have contributed to the past fitness of organisms and most importantly, that R exists as it does because of E» (Doolittle 2013: 5296; cf. Garson 2019: 25-29). However, there is also another method to infer function, namely, mere existence. Critics of ENCODE hold that this method is exactly the one employed by ENCODE's members. According to it, the presence of a given structure or process or detectable interaction is considered to represent adequate evidence for its being currently under selection (Doolittle 2013: 5296). In short, the fact that a region R of the DNA is transcribed is thought of as being a sufficient condition for that region R to provide some fitness benefit representing its own function. In other words, for ENCODE's proponents this means that there must be some selection-based explanation for the existence of region R, even if it cannot be demonstrated that such a region is currently under selection. This is why ENCODE's opponents hold that members of ENCODE are too liberal (cf. Doolittle 2013: 5297).

[3] This example aims to show that function pluralism is a concept to which even scientists – in the above mentioned case, ENCODE's advocates – appeal to when pondering over the notion of biological function within the context of a specific scientific debate.

popular version of function pluralism concerning biological functions, namely, between-discipline pluralism.

According to the proponents of between-discipline pluralism, different theories of biological function are appropriate for different branches of biology. The theories to which this kind of function pluralism appeals are the selected effects theory and the causal role theory, which are two of the most respected philosophical analyses of function-talk in biology. The core idea behind the selected effects theory is that talking of a trait's biological function amounts to saying something about why natural selection led that very trait to evolve.[4] As Neander puts it, «in my view, the central element of the [selected effects] approach should be seen as the simple idea that a function of a trait is the effect for which that trait was selected» (Neander 1991b: 459). To put it otherwise:

> The problem is to discover what exactly is attributed when we attribute a proper function (or more loosely a function) in sentences of the form 'The/a proper function of X is Z'. My claim is that the proper function of a trait is to do whatever it was selected for. In so far as our organismic structures and processes are the result of selection they are the result of natural selection, so I claim that the biological proper function of such an item is to do whatever items of that type did that caused them to be favored by natural selection[5] (Neander 1991a: 173-174).

[4] The first philosophers who explicitly defined biological functions in terms of natural selection are Neander (1983) and Millikan (1984). However, given that Millikan is not always crystal-clear in recognizing that a selected effects theory should involve natural selection (1989: 288), in what follows I will only refer to Neander's formulation of the selected effects theory. This will allow us to better understand Garson's objection against between-discipline pluralism – an objection whose starting point is indeed a criticism of those who understand the selected effects theory just in a strict evolutionary sense (see also footnote 6).

[5] By equating selection and natural selection, Neander seems to commit herself to a position that is known as empirical adaptationism, according to which «[to] a large degree, it is possible to predict and explain the outcome of evolutionary processes by attending only to the role played by [natural] selection» (Godfrey-Smith 2001: 336; see also Godfrey-Smith and Wilkins 2007). However, given that the issue of adaptationism is not the focus of this paper, I will not examine it any further. For a detailed introduction to this a topic, see Orzack and Forber (2017).

Such functional attributions are therefore meant to answer why-is-it-there questions. Consider the polar bear's white coat. This trait has many effects, including reflecting sunlight, making children amazed, and camouflaging the bear itself when hunting. Given what we know about the environment in which polar bears evolved, it is very likely that the third of these effects is the reason why natural selection led the polar bear to evolve a white coat. A bear that is well-camouflaged has indeed an obvious selective advantage over one that is not; thus, on average, it will leave more offspring. If this is correct, then the selected effects theory implies that camouflaging is the genuine function of the polar bear's coat, while reflecting sunlight and amazing children are not (cf. Okasha 2019: 32-35). As Neander writes, «[a selected effects] theory of function claims what counts as a function of a trait is determined by that trait's [evolutionary] history» (Neander 1991b: 459), that is, evolutionary history in the sense of natural selection taking place over evolutionary time scales by altering the genetic composition of the population:[6]

> It is the/a proper function of an item (X) of an organism (O) to do that which items of X's type did to contribute to the inclusive fitness of O's ancestors, and which caused the genotype, of which X is the phenotypic expression, to be selected by natural selection (Neander 1991a: 174).

On the contrary, the causal role theory of functions contends that «[the] concept of function [refers] to contemporary causal powers of a trait rather than the causal origins of that trait, [and that] a trait's function amounts to identifying the causal role played by the trait in the organism's ability to achieve a contemporary goal» (Amundson and Lauder 1994: 447). As Cummins recommends (1975: 757), causal role functions are to be seen as

[6] Neander's version of the selected effects theory of biological functions is particularly strong since it holds that the only sort of selection process to be taken into consideration is natural selection between organisms over evolutionary time scales. As I will show later, Garson claims that one of the reasons why between-discipline pluralists tend to restrict the scope of application of the selected effects theory to the field of evolutionary biology is exactly that they have in mind Neander's formulation of that theory. According to Garson, the selected effects theory should instead be understood in a broader way. In the rest of the paper, I will introduce some examples of selection processes that are not processes of natural selection acting between organisms over evolutionary time scales.

dispositions. To say that a given trait has the function X is equivalent to say that such a trait has the disposition to do X under such-and-such conditions.

> If something functions as a pump in a system s or if the function of something in a system s is to pump, then it must be capable of pumping in s. Thus, function-ascribing statements imply disposition statements; to attribute a function to something is, in part, to attribute a disposition to it. If the function of x in s to ϕ, then x has a disposition to ϕ in s (Cummins 1975: 757-758).

In addition, according to the causal role theory, functional attributions are often made in the context of a particular sort of scientific investigation, that is, trying to understand how a complex biological system or process works. To put it otherwise, such functional attributions are meant to answer how-does-it-work questions. In order to answer similar questions, causal role theorists analyse organisms into a number of different systems – e.g., the circulatory system or the digestive system –, and then analyze the capacities of these systems by studying the capacities of their component organs and structures (see Cummins 1975: 760-761). As a brief example, consider thermoregulation in humans. To understand how the thermoregulatory system works, we need to know the contribution that each part makes. It is here that the notion of function comes in according to the causal role theory. Indeed, the function of some part is simply its contribution to the operation of the overall system, which enables the system itself to do what it does. Hence, as example, the function of the thermoreceptors in the hypothalamus is that of detecting blood temperature, while the function of the sweat glands is to secrete sweat onto the skin's surface.

Between-discipline pluralists hold that the selected effects theory is the most suitable theory for evolutionary biology, where why-is-it-there questions are asked, and that the causal role theory is the most appropriate theory of for physiology – e.g., anatomy, neuroscience and developmental genetics –, where how-does-it-work questions are asked. Forthright proponents of between-discipline pluralism include Godfrey-Smith (1993: 200), Amundson and Lauder (1994: 446), Maclaurin and Sterelny (2008: 114), and Bouchard (2013: 86-93). For Godfrey-Smith, there are entire realms of functional discourse that do not make any references at all to either evolution or selection. In those fields, the most attractive account of functions is the causal role theory.

Amundson and Lauder's remarks echo Godfrey-Smith's view, because they say that functional morphology generally reject the use of the selected effects theory. Maclaurin and Sterelny make similar claims about ecology, where according to them the causal role theory is the norm. Finally, Bouchard also emphasizes the idea that there are many biological disciplines that do not employ the selected effects theory. In other words, function pluralists of this stripe endorse the view that, as a practical rule, different branches of biology «can be sorted into two main categories depending on which theory of function its practitioners typically invoke» (Garson 2017b: 6).

The most important arguments in favor of between-discipline pluralism are the sociolinguistic argument and the ontological argument. As the term suggests, the sociolinguistic argument rests on an evident appeal to the way biologists talk and write. One of the clearest versions of such an argument comes up in the following quote from Godfrey-Smith:

> [...] There [are] realms of functional discourse, in fields such as biochemistry, developmental biology, and much of the neurosciences, which are hard to fit into the [the mold of the selected effects theory], as functional claims in these fields often appear to make no reference to evolution or selection. These are areas in which the attractive account of function has always been that of Robert Cummins (Godfrey-Smith 1993: 200).

Analogous arguments are present in the works of Amundson and Lauder (1994: 446), Walsh (1996: 558), Schlosser (1998: 304), Wouters (2003: 658), Sarkar (2005: 18), and Bouchard (2013: 93). They all make a sociolinguistic argument since they argue that biologists do not always appeal to evolution or natural selection, namely, they do not always employ the selected effects theory. According to these scholars, the contemporary scientific literature tells us a simple thing: biologists generally appeal to the selected effects theory in evolutionary biology, whereas they usually appeal to the causal role theory in other fields – e.g., neuroscience, biochemistry, and developmental genetics. Furthermore, the sociolinguistic argument makes between-discipline pluralism an attractive view; in case it is correct, it indeed provides a great way to make immediate inferences about which sense of biological function a scientist is employing just by knowing which branch of biology that scientist is working in.

The ontological argument is different from the sociolinguistic argument because it is not simply committed to answering the question of what notion of function biologists appeal to; in fact, it focuses on the reasons why biologists appeal to certain notions of function rather than others. The ontological argument rests on the following idea: there are certain branches of biology within which scientists commonly attribute functions to items that do not have the right sort of selection history, namely, items that did not undergo a process of natural selection (cf. Garson 2017b: 9). Thus, it is crystal-clear that the selected effects theory cannot be deemed as the most appropriate theory of biological function for those branches. This point is made in a very effective way by Maclaurin and Sterelny:

> Function in ecology is not like function in evolutionary biology or functional morphology. In those fields, functions derive from selective history [...]. The ponyfish has a light-emitting organ, and the function of the light the organ generates is to prevent the ponyfish from being visible from below, silhouetted darkly against a lighter background. [...] In making this claim about the function of the light-emitting organ, we make a claim about selective history. Ancestral ponyfish with such organs survived better than those without them (or with less well-tuned organs) because they were less often seen from below [...]. It is not likely that we can explain functional roles in local communities in a parallel way (Maclaurin and Sterelny 2008: 114).

As the authors point out, we cannot employ the selected effects theory of biological function when coping with local communities. But why is that? The exact reason is that local communities are not elements of a population made up of competing communities, and there is nothing like daughter communities resembling their parents. Therefore, we cannot talk of local communities as being part of lineages. In other words, ecologists attribute functions to entire groups of organisms. But groups of organisms do not usually have their own selection histories. So, Maclaurin and Sterelny's argument goes, the theory to be employed in the field of ecology is Cummins's theory, that is, the causal role theory of biological function (see Maclaurin and Sterelny 2008: 115). Long story short, according to the ontological argument it is the specific object of a certain biological discipline that determines what theory of biological function practitioners should appeal to (see also Bouchard 2013: 92).[7]

3. Between-Discipline Pluralism vs. Within-Discipline Pluralism

In this section, I will introduce Garson's objection against between-discipline pluralism. According to Garson, the reason why between-discipline pluralists believe that the selected effects theory is the best theory for evolutionary biology is that they rest on an overly narrow understanding of what that theory really holds. In their opinion, «[such a] theory holds that a function of a trait is whatever it was selected for by natural selection [acting between organism over evolutionary time scales]» (Garson 2017b: 11). Hence, they follow Neander in claiming that «[...] selection between organisms is the only way new functions are created» (Garson 2019: 66). Therefore, it is clear why they tend to confine the selected effects theory to the realm of evolutionary biology. However, in Garson's opinion we should not assume that the selected effects theory only assigns functions to biological traits that evolved by natural selection acting between organisms over evolutionary time scales. As he puts it:

> There are many function-bestowing selection processes in nature other than natural selection in the evolutionary sense. Some of these processes operate over ontogenetic time scales [...]. [However, the sociolinguistic argument and

[7] The distinction between the sociolinguistic argument and the ontological argument, as I presented it above, is found in the extant literature on function pluralism. Nonetheless, I believe that a similar distinction may be slightly confusing; it may indeed give the impression that there is a strong separation between scientists' linguistic claims and the object of their disciplines. As far as I am concerned, however, the way biologists talk is instead precisely meant to reflect a real difference in the object of different biological disciplines. As an example, consider those ecologists studying functional roles in local assemblages (Maclaurin and Sterelny 2008: 114). Indeed, they do not talk about natural selection since one of the many objects of their discipline – that is, local assemblages – has no selective history in the evolutionary sense. In other words, the way ecologists talk about functions in the context of local assemblages shows that those functions are not the same functions to which evolutionary biologists refer; there is in fact a difference between the object studied by these two disciplines, and such a difference is reflected in the way ecologists and evolutionary biologists talk.

> the ontological argument] for between-discipline pluralism assume that the only relevant sort of selection process is natural selection (Garson 2017b: 11).

Such considerations led Garson to develop a new theory of biological functions, which is known as the generalized selected effects theory. Briefly put, this theory contends that the function of a trait is whatever that same trait did in the past that caused its differential reproduction, or its differential retention, within a certain population. The first part – that is, differential reproduction – captures everything that the selected effects theory does. The second part – that is, differential retention – captures selection processes over things that do not reproduce but nonetheless persist better or worse than others.[8] This means that for Garson the selected effects theory applies more broadly than evolutionary natural selection in Neander's sense; indeed, functions can be created through different sorts of selection processes.[9]

First, Garson takes into consideration group selection (Garson 2019: 66; Garson 2022: 23-36). According to him – even if biologists may disagree about what group selection requires –, if a group is selected over another due to group-level trait, then that very trait acquires a function of its own. As an example, he mentions reduced sexual aggression in water striders (Garson 2019: 66; see also Eldakar et al. 2010). The second reason why biological functions do not always need to be the result of a process of selection understood in Neander's terms is gene selection. Garson alludes to meiotic drive, whereby, contrary to what usually happens in meiosis, one chromosome sabotages the other and enters the gamete pool for the next generation (see Garson 2019: 67). Third, Garson refers to ontogenetic selection processes. Such processes do not involve the transmission of genetic material from organism to organism; they simply occur in the span of a single life. But this does not mean

[8] In other words, whereas according to the traditional selected effects theory functions pertain to things that reproduce, according to Garson's theory – that is, the generalized selected effects theory – functions can be assigned both to things that reproduce and to things that, despite not reproducing, persist better than others. For reasons of space, I cannot delve into such a theory. In order to examine it, see Garson 2012, 2016, 2017a, 2017b, 2019, 2022.
[9] This means that, contrary to the selected effects theory, the generalized selected effects theory does not assume that all biological functions should ultimately be grounded in phylogenetic processes of natural selection.

that they cannot yield new functions. One of the clearest examples that Garson drills down through is antibody selection (Garson 2019: 67), a two-stage process that shapes the mature immune system. I will briefly describe it building on Alberts et al. (chap. 25). At birth, billions of genetically distinct B cells are generated in the bone marrow by means of a mechanism of genetic recombination. Each B cell is covered with antibodies, which are "Y"-shaped proteins characterised by slightly different molecular textures. When an antibody meets an antigen – which is a foreign particle with a similar shape –, the B cell corresponding to that antibody starts being heavily replicated. But such a process is not completely faithful; in fact, B cells are endowed with activation-induced deaminase (AID), an enzyme whose function is to bring about somatic hypermutation, that is, to cause mutations in the B cells' genetic code. This means that when a B cell is replicated, the result is nothing but a group of daughter cells genetically differing both from each other and from the original B cell. At this stage, a second round of selection occurs. Some of these daughter cells' antibodies will indeed be slightly better than their B cell parent's antibodies at matching their antigen and will themselves be replicated for that very reason, while those with lower affinity will self-destruct. Now consider an imaginary B cell producing an antibody with a specific "Y"-shape, Y_{n1}, and imagine that such a B cell comes into contact with its corresponding antigen – e.g., a surface protein of the parasite *Trypanosoma brucei rhodesiense* –, thus getting massively replicated. Suppose also that, after this replication process, we find daughter B cells with slightly different "Y"-shapes, Y_{n2} and Y_{n3}, and that daughter B cells' Y_{n2}-shaped antibody is better than original B cells' Y_{n1}-shaped antibody and daughter B cells' Y_{n3}-shaped antibody at matching its antigen. Therefore, B cells with a Y_{n2}-shaped antibody will be massively replicated for that very reason, while B cells with a Y_{n3}-shaped antibody will self-destruct. This means that the function of B cells' Y_{n2}-shaped antibody is to bind one of *Trypanosoma brucei rhodesiense*'s surface proteins because that is precisely what caused B cells with a Y_{n2}-shaped antibody to be massively replicated in the lymph node. As Garson would say, the fact that Y_{n2} binds one of *Trypanosoma brucei rhodesiense*'s surface proteins explain why B cells with a Y_{n2}-shaped antibody exist or, more precisely, why they are there with a frequency greater than zero (cf. Garson 2019: 71).[10] Therefore, there can be

[10] One may object that the reason why there are B cells with a Y_{n2}-shaped antibody having as a function that of binding one of *Trypanosoma brucei rhodesiense*'s surface proteins is the

functions in the selected effects sense even if they are not the result of a process of natural selection acting between organisms over evolutionary time scales. This consequently means that selected effect functions can be also found outside the field of evolutionary biology. There are indeed other selection processes than just natural selection in the evolutionary sense, and they take place in different domains of biology – as I showed, for example, antibody selection in immunology – and are associated with the production of novel functions.[11] In short, the argument provided above against between-discipline pluralism is the following:

1) There are many kinds of selection processes in nature other than natural selection in the ordinary evolutionary sense, meaning that a process of natural selection acting between organisms over evolutionary time scales is not the only function-bestowing process to be found in nature.

2) All these different kinds of selection processes that take place in various domains of biology are plausibly associated with the production of novel functions.

---

process of hypermutation. However, hypermutation causes mutations in the original B cells' genetic code and thus brings about daughter B cells with new antibody shapes, while it is selection that works on daughter B cells, favouring those having antibodies that are better at matching their antigen. Indeed, those daughter B cells having antibodies that match their antigen in a more effective way with respect to the original B cells will be consequently replicated. Given that in the example mentioned above B cells' Y_{n2}-shaped antibody is slightly better than the original B cells' Y_{n1}-shaped antibody and daughter B cells' Y_{n3}-shaped antibody at matching its antigen – that is, a surface protein of the parasite *Trypanosoma brucei rhodesiense* – B cells with a Y_{n2}-shaped antibody will be massively replicated, whereas B cells with a Y_{n3}-shaped antibody will self-destruct. Therefore, when advocates of the selected effects theory contend that the function of B cells' Y_{n2}-shaped antibody – namely, to bind one of *Trypanosoma brucei rhodesiense*'s surface proteins, and to do so better than B cells having a Y_{n3}-shaped antibody – explains why B cells with a Y_{n2}-shaped antibody are there, they do not mean to deny that it is the process of hypermutation that led a B cell having a Y_{n2}-shaped antibody to come into existence for the very first time; they simply intend to say that the function of B cells' Y_{n2}-shaped antibody is what caused its mass-production in the lymph node.

[11] Garson's idea that natural selection is just one single type of selection process has been anticipated, at least, by Hull, Langman, and Glenn (2001).

3) So, selected effect functions can be discovered outside the domain of evolutionary biology too, contrary to what between-discipline pluralists hold.

To put it otherwise, between-discipline pluralists cannot claim anymore that the selected effects theory is the most appropriate theory just for the field of evolutionary biology, because such a theory can apply indeed to different sorts of selection processes. However, if between-discipline pluralism is not justified at all in confining the selected effects theory to evolutionary biology, then what do we have to do with it? As Garson writes:

> A better way to think about function pluralism is within-discipline pluralism. [...] In my view [selected effects] functions are appropriate not just when evolutionary questions are being asked, but whenever function statements are used in a causal-explanatory sense, that is, whenever they are meant to answer a why-is-it-there question, in whichever discipline that question arises. [Causal role] functions are probably most appropriate as answers to the how-does-it-work questions (Garson 2017b: 17).

While between-discipline pluralism simply emphasises the plurality of functions in so far as they pertain to different branches of biology – that is, selected effects functions in evolutionary biology and causal role functions in the realm of physiology –, within-discipline pluralism seeks out such a plurality of functions inside any branch of biology. Indeed, selected effects functions and causal role functions can coexist within the same field; it just depends on what we are asking, whether we are asking why-is-it-there questions or how-does-it-work questions.[12]

Unfortunately, Garson has not yet dedicated a specific publication – be it a monograph or a paper – to extensively giving positive reasons for accepting this new kind of function pluralism in biology. As I showed, he mainly focused on why philosophers of biology should reject between-discipline pluralism –

[12] See also Mayr 1961 and Sober 1984.

roughly put, they should reject it given that there are many examples of selected effect functions outside the domain of evolutionary biology, contrary to what between-discipline pluralists themselves hold. For the time being, Garson has only hinted at two positive arguments. First, he claims that if we agree to reject between-discipline pluralism and still want to remain pluralists about biological functions, then within-discipline pluralism seems the only viable option. Second, within-discipline pluralism can provide biologists with heuristic value. The reason is that, if we hold that selected effect functions are appropriate only in the field of evolutionary biology, it can be extremely harsh to recognise the existence of different kind of selection processes as they are represented and studied in other biological disciplines. As Garson puts it:

> Within-discipline pluralism seeks out and acknowledges the diversity of functions within any particular [biological] discipline rather than between them.[13] [Thus], within-discipline pluralism has a major advantage when it comes to scientific discovery. It encourages us keep looking for selection processes, even where we might not have initially expected to see them. It broadens our scientific horizons and helps us see new thins. A good theory of function should do that, too (Garson 2019: 151).

I believe that further research is still needed to prove the case of within-discipline pluralism; indeed, at the present time there is a lack of detailed positive arguments. However, in the next section I will present an argument that may be of help to prove the case of within-discipline pluralism.

---

[13] As this statement suggests, the fact that Garson mainly focuses on the selected effects theory and on those selection processes that can be found outside the field of evolutionary biology does not absolutely mean that causal role functions cannot be found outside the field of physiology. In principle, indeed, within-discipline pluralism can surely allow for such a possibility. To the best of my knowledge, this possibility has been somewhat anticipated by Griffiths, if I am right in taking it that this is what he had in mind when he asserted that «[...] anatomy, physiology, molecular biology, developmental biology, and so forth [can even] turn their attention to specifically evolutionary questions [...]» (Griffiths 2006: 3). As a recent example of the possibility of employing the causal role theory when facing issues concerning evolution, see Cusimano and Sterner 2019, whereby the authors show that some causal models that biologists have developed to explain changes in the evolutionary functions of proteins integrate selected effects and causal role senses of function in order to provide explanations for how gene duplications become fixed in a population.

4. Conclusion. Normal Functioning and Within-Discipline Pluralism

As I said in Section 2., both the selected effects theory and the causal role theory acknowledge that the concept of biological function has an explanatory role. However, they diverge from the first step on what explanation means. Indeed, according to the selected effects theory, the function of X being Y accounts for the existence of X, that is, why X is there, whereas according to the causal role theory the function of X being Y contributes to explain the general proper activity of a biological system within which X is included. Based on the difference between these theories, between-discipline pluralists hold that the selected effects theory is appropriate for evolutionary biology – where why-is-it-there questions are asked – and that the causal role theory is instead befitting to physiology – where practitioners generally face how-does-it-work questions. In Section 3., I showed Garson's argument against between-discipline pluralism. I will now introduce another argument – one built upon the biological function/dysfunction distinction.

Such a distinction entails that it is possible for a trait token to have a function that, in fact, it cannot currently perform. As a quick example, consider the stomach. The function of the stomach is that of digesting food. However, owing to a serious ulcer, one's stomach may not perform its function at present, namely, it may be dysfunctional. In that case, then, the stomach has the function of digesting food, but it cannot perform it. Physiologists have in mind similar distinctions when they explain how complex living systems work and operate. As Neander puts it:

> In case readers doubt that physiologists [...] speak of normal-proper function in their serious journal articles, let me add that a quick read of the titles and abstracts of papers in the *American Journal of Physiology*, for example, would soon make the prevalence of talk of normal-proper functions clear. Reference to disease, dysfunction, abnormal, impaired, or pathological functioning is commonplace in titles and abstracts, as well as in the main text of the papers (Neander 2017a: 57).

But why do physiologists ascribe malfunction-permitting functions when talking about the overall operation of complex organic systems? This is due to a generalization issue that they usually face while performing their research. Indeed, living systems exhibit extreme complexity and great variety, and this is in fact the case even between organisms pertaining to the same species. Nonetheless, physiologists are able to provide useful, general descriptions of how organisms of various types operate. This is possible since they describe idealized systems that function normally or properly or correctly. To put it otherwise, physiologists cannot carry out a separate functional analysis of every individual body; they cannot but make generalizations, and they make them by describing systems in which all of the components can perform their proper functions (cf. Neander 2017a: 58-60). In this respect, the selected effects theory seems to be our best way to make sense of such generalizations.

To grasp this claim, consider once again the example of thermoregulation in humans. In humans, thermoregulation involves a complex control system in which a specific brain region, the hypothalamus, monitors body temperature and sends certain impulses to cause appropriate physiological responses – e.g., sweating. This system is of course made up of many specialized parts and sub-systems, each of which does a precise job. In order to understand how this system works, according to the causal role theory of biological functions we should look at the contribution that each part makes (see Section 2.). The function of each of these parts is merely its contribution to the operation of the system as a whole, which enables the system to do what it does. In this regard, the function of sweat glands is that of secreting sweat onto the skin's surface, while the function of thermoreceptors within the hypothalamus is that of detecting blood temperature. Therefore, the thermoregulatory system is able to perform its function, namely, keeping body temperature constant, since its parts enable it to do so by performing their own functions. However, what possibly could the causal role theory tell us in case the thermoregulatory system does not work, that is, if it is malfunctioning? As I showed in Section 2., on Cummins's view, causal role functions are to be seen as dispositions; this means that when we say that a certain biological trait has the function X, we are saying nothing but that such a trait has the disposition to do X under certain conditions. In other words, having a function X is equivalent to having the disposition to perform that function X under such-and-such conditions. Hence, in case one's thermoregulatory system is damaged so that it cannot keep body temperature constant anymore, then, according to Cummins's view, that system loses the disposition to keep body temperature constant, meaning that it loses its own function. To put it otherwise, the attribution of a causal role function requires satisfaction of the condition that a given trait be able of performing its task; but if that very trait has lost its requisite capacity, it has thereby lost the associated causal role function – in which case malfunction cannot occur. So, the problem with Cummins's version of the causal role theory is that, based on the way it is formulated, we could not even properly talk of malfunctioning (cf. Davies 2001: 28-29; Garson 2016: 87; Neander 2017a: 54). A more effective way to account for the normative dimension of biological functions is to make an appeal to natural selection, that is, an appeal to the selected effects theory. In fact, according to this theory, the proper function of a given trait is the effect in virtue of which that trait was favoured by natural selection, and this helps to explain abnormal as well as normal functioning (cf. Neander 2017a: 61-62); we can indeed affirm that the thermoregulatory system is working properly in case it is currently performing the function in virtue of which it was selected, and not working properly in case it is not currently performing the function in virtue of which it was selected (cf. Neander 2017b). Let me summarise. As Neander observed, physiologists cannot describe all of the actual functioning and malfunctioning of organisms; that would indeed require a *sui generis* functional analysis of each organism, which is impossible to carry out in practice. So, in order to alleviate this problem, physiologists need a notion of normal or proper function allowing them to account for functions and dysfunctions in an efficient way. As previously shown, this notion cannot be provided by the causal role theory, since its formulation leads to the counterintuitive conclusion that losing a functional capacity cannot be considered equivalent to malfunctioning. As far as I am concerned, I think that the selected effects theory represents a more straightforward way to characterise the notion of proper function. On the selected effects account of function, indeed, the proper function of a biological item is «[...] to do whatever items of that type did that caused them to be favoured by natural selection» (Neander 1991a: 174), and this leads us to easily define the notion of dysfunction; a given biological trait is dysfunctional when it cannot perform the function in virtue of which it was favoured by natural selection. This means that even if physiologists may not be explicitly referring to selection when attributing functions to biological traits, they may be doing so implicitly (Garson 2016: 50; Garson 2017a: 9-11); in fact, physiologists use the notion of function with normative connotations, and the selected effects theory is able to represent a straightforward account of such connotations.[14] Therefore, the key point of this argument is that we have no *a priori* right to expunge selected effect functions from the field of physiology without further ado.[15]

[14] As one of the anonymous reviewers argued, it may not be immediately clear why we should refer to history – that is, to selected effects functions – when talking about dysfunctional traits. In order to make their point, the reviewer gives the interesting example of an electric lawn mower that has been constructed to perform the function of cutting grass and asks: in case the blade breaks down, or in case the electric wire is cut by mistake, in what sense should it be useful for us to be appealing to the history of the electric lawn mower's manufacturing process so as to explain such dysfunctions? First, I would say that the case of the blade breaking down and the case of the electric wire being cut are not analogous. In the former case, a mechanism within the electric lawn mower itself is broken – e.g., something is going wrong with the motor drive, which consequently cannot transfer engine power to the blade. Hence, this kind of dysfunction can be deemed as a mechanistic failure; indeed, the electric lawn mower cannot perform its function – namely, that of cutting grass – because one of its mechanisms is not anymore able to do what it ought to do according to the purpose for which it has been constructed. This means that if the owner of the electric lawn mower wants to repair it, they implicitly take into account history – that is, the reason why the electric lawn mower itself has been constructed – since they want to repair the lawn mower in order for it to continue working according to its original purpose. However, we cannot even exclude that such a history be taken explicitly into account; indeed, the owner may need to be acquainted with some peculiarities of the manufacturing process to fix the broken mechanism effectively. This way of going wrong does not merely concern artifacts. It is in fact familiar from the literature on selected effect functions, where a given biological trait is said to fail in performing its functions if it is unable to fulfil the causal role for which it has been selected (Godfrey-Smith 1994). As an example, consider the db/db mouse, that has a genetic mutation leading to faulty receptors for the hormone leptin and therefore to gross obesity (Friedman 2002; Matthewson and Griffiths 2017: 7). In the latter case, instead, the normal functioning circumstances for the electric lawn mower have been disturbed; these circumstances require indeed that the electric lawn mower be hooked up to a certain power source – which is not the case of the example, given that the electric wire has been accidentally cut. In other words, the lawn mower cannot perform its function due to abnormal circumstances. As Millikan puts it, «when a device does not perform some proper function only because the necessary background conditions are absent, we do not consider that to be a malfunction [...]. Malfunction results only from abnormalities in the constitution of the device itself» (Millikan 2013: 40). The distinction between the former and the latter case might seem unnecessarily picky at first glance, but it is instead of great value. Take as an example the scenario in which a man is blindfolded and therefore cannot see anything. Thanks to the above mentioned distinction, we can account for the fact that in such a case there is no dysfunction involved, even if that man cannot see anything.

[15] Some scholars would not be willing to accept this argument. For example, Lewens (2007: 536-539) aims to downplay the theoretical interest in the category of dysfunction from the point

What are the consequences of this argument for the debate on function pluralism? As illustrated in Section 2., between-discipline pluralists hold that biology can be sorted into two main categories: that in which practitioners typically invoke the selected effects theory – namely, evolutionary biology – and that in which practitioners generally use the causal role theory – that is, for example, anatomy, neuroscience, and developmental genetics. Nevertheless, as shown in Section 3., Garson objected to between-discipline pluralists that there are many sorts of selection processes other than natural selection in Neander's sense, namely, natural selection acting between organisms over evolutionary time scales. This means that, his argument goes, selected effect functions can also be found outside the realm of evolutionary biology – as a consequence, between-discipline pluralists' claim that selected effect functions and causal role functions cannot coexist within the same field is nothing but undermined. For its part, the alternative theoretical position suggested by Garson – within-discipline pluralism – does not rule out the possibility that one can employ the selected effects theory outside the field of evolutionary biology and the causal role theory outside the realms of neuroscience, biochemistry, developmental genetics, physiology, and so on. Taking into account this context, the argument that I introduced in Section 4. may be of some help to prove the case of within-discipline pluralism. Indeed, it states that physiologists may implicitly refer to the selected effects theory when they employ the concept of function with normative connotations. Once again, then, it appears that we have no right at all to conclude – as between-discipline pluralists do – that the field of physiology only makes use of the cause role theory and therefore completely rules out the selected effects theory.

References

Alberts et al., 2012, *Molecular Biology of the Cell*, 5th ed., New York, Garland.

Amundson R., Lauder G. V., 1994, «Function Without Purpose: The Uses of Causal Role Function in Evolutionary Biology", *Biology & Philosophy*, 9, 4, pp. 443-469.

---

of view of evolutionary biology, and Davies (2000, 2001) argues against the idea that the selected effects theory can account for the distinction between function and malfunction in an effective way. For reasons of space I will not deepen any of these interesting counterarguments.

Bechtel W., 1986, «Teleological Function Analyses and the Hierarchical Organization of Nature», in Rescher N. (ed.), *Current Issues in Teleology*, pp. 26-48, Lanham (MD), University Press of America.

Bigelow J., Pargetter R., 1987, «Functions», *Journal of Philosophy*, 84, 4, pp. 181-196.

Boorse C., 1976, «Wright on Functions», *Philosophical Review*, 85, 1, pp. 70-86.

Bouchard F., 2013, «How Ecosystem Evolution Strengthens the Case for Function Pluralism», in Huneman P. (ed.), *Function: Selection and Mechanisms*, pp. 83-95, Dordrecht, Springer.

Brunet T. D. P., Doolittle W. F., 2014, «Getting "Function" Right», *Proceedings of the National Academy of Sciences of the United States of America*, 111, 33, E3365.

Buller, D. J., 1998, «Etiological Theories of Function: A Geographical Survey», *Biology & Philosophy*, 13, 4, pp. 505-527.

Canfield J., 1964, «Teleological Explanation in Biology», *British Journal for the Philosophy of Science*, 14, 56, pp. 285-295.

Caro T. et al., 2014, «The Function of Zebra Stripes», *Nature Communications*, 5, 1, 3535.

Craver C., 2013, «Functions and Mechanisms: A Perspectivalist View», in Huneman P. (ed.), *Function: Selection and Mechanisms*, pp. 133-158, Dordrecht, Springer.

Cummins R., 1975, «Functional Analysis», *Journal of Philosophy*, 72, 20, pp. 741-765.

Cusimano S., Sterner B., 2019, «Integrative Pluralism for Biological Function», *Biology & Philosophy*, 34, 6, 1-21.

Darwin C., 1871, *The Descent of Man, and Selection in Relation to Sex*, vol. 2, London, John Murray.

Davies P. S., 2000, «Malfunctions», *Biology & Philosophy*, 15, 1, pp. 19-38.

Davies P. S., 2001, *Norms of Nature: Naturalism and the Nature of Functions,* Cambridge (MA), MIT Press.

Doolittle W. F., 2013, «Is Junk DNA Bunk? A Critique of ENCODE», *Proceedings of the National Academy of Sciences*, 110, 14, pp. 5294-5300.

Eldakar O. T., 2010, «The Role of Multilevel Selection in the Evolution of Sexual Conflict in the Water Strider Aquarius remigis», *Evolution*, 64, 11, pp. 3183-3189.

Elliott T. A., et al., 2014, «Conceptual and Empirical Challenges to Ascribing Functions to Transposable Elements», *American Naturalist*, 184, 1, pp. 14-24.

Friedman J. M., 2002, «The Function of Leptin in Nutrition, Weight, and Physiology», *Nutrition Reviews*, 60, 10, pp. 1-14.

Garson J., 2012, «Function, Selection, and Construction in the Brain», *Synthese*, 189, 3, pp. 451-481.

Garson J., 2016, *A Critical Overview of Biological Functions*, Dordrecht, Springer.

Garson J., 2017a, «A Generalized Selected Effects Theory of Function», *Philosophy of Science*, 84, 3, pp. 523-543.

Garson J., 2017b, «How to Be Function Pluralist», *British Journal for the Philosophy of Science*, 69, 4, pp. 1101-1122.

Garson J., 2019, *What Biological Functions Are and Why They Matter*, Cambridge, Cambridge University Press

Garson J., 2022, *The Biological Mind. A Philosophical Introduction*, London, Routledge (2nd edition; 1st edition 2015).

Godfrey-Smith P., 1993, «Functions: Consensus Without Unity», *Pacific Philosophical Quarterly*, 74, 3, pp. 196-208.

Godfrey-Smith P., 1994, «A Modern History Theory of Functions», *Nous*, 28, 3, pp. 344-362.

Godfrey-Smith P., 2001, «Three Kinds of Adaptationism», in Orzack S. H. and Sober E. (eds.), *Adaptationism and Optimality*, pp. 335-357, Cambridge, Cambridge University Press.

Godfrey-Smith P. and Wilkins J. F., 2007, «Adaptationism», in Sarkar S. and Plutynski A. (eds.), *A Companion to the Philosophy of Biolog*y, pp. 186-201, Hoboken (NJ), Wiley-Blackwell.

Graur et al., 2013, «On the Immortality of Television Sets: "Function" in the Human Genome According to the Evolution-Free Gospel of ENCODE», *Genome Biology and Evolution*, 5, 3, pp. 504-513.

Griffiths P. E., 2006, «Function, Homology, and Character Individuation», *Philosophy of Science*, 73, 1, pp. 1-25.

Hardcastle V. G., 1999, «Understanding Functions: A Pragmatic Approach», in Hardcastle V. G. (ed.), Where Biology Meets Psychology: Philosophical Essays, Cambridge (MA), MIT Press, pp. 27-43.

Hardcastle V. G., 2002, «On the Normativity of Functions», in Ariew A., Cummins R., and Perlman M. (eds.), Functions: New Essays in the Philosophy of Psychology and Biology, Oxford, Oxford University Press, pp. 144-156.

Horan B., 1989, «Functional Explanations in Sociobiology», *Biology & Philosophy*, 4, 2, pp. 131-158.

Hull D. L., Langman R., and Glenn S., 2001, «A General Account of Selection: Biology, Immunology and Behavior», *Behavioral and Brain Sciences*, 24, 3, 511-528.

Kellis M. et al., 2014, «Reply to Brunet and Doolittle: Both Selected Effect and Causal Role Elements Can Influence Human Biology and Disease», *Proceeding of the National Academy of Sciences of the United States of America*, 111, 33, E3366.

Kraemer D. M., 2013, «Statistical Theories of Functions and the Problem of Epidemic Disease», *Biology & Philosophy*, 28, 3, pp. 423-438.

Larison B. et al., 2015, «How the Zebra Got Its Stripes: A Problem With Too Many Solutions», *Royal Society Open Scienc*e. On-line: https://doi.org/10.1098/rsos.140452.

Lewens T., 2004, *Organisms and Artifact: Design in Nature and Elsewhere*, Cambridge (MA), MIT Press.

Lewens T., 2007, «Functions», in Matthen M. and Stephens C. (eds.), *Philosophy of Biology*, pp. 525-547, Amsterdam, North Holland.

Maclaurin J., Sterelny K, 2008, *What Is Biodiversity?*, Chicago, Chicago University Press.

Matthewson J., Griffiths P. E., 2017, «Biological Criteria of Disease: Four Ways of Going Wrong», *Journal of Medicine and Philosophy*, 42, 4, pp. 447-466.

Mayr E., 1961, «Cause and Effect in Biology: Kinds of Causes, Predictability, and Teleology are Viewed by a Practicing Biologist», *Science*, 134, 3489, pp. 1501-1506.

Millikan R. G., 1984, *Language, Thought, and other Biological Categories*, Cambridge (MA), MIT Press.

Millikan R. G., 1989, «In Defense of Proper Functions», *Philosophy of Science*, 56, 2, pp. 288-302.

Millikan R. G., 2013, «Reply to Neander», in Ryder D., Kingsbury J., and Williford K. (eds.), *Millikan and Her Critics*, Malden (MA), Wiley-Blackwell, pp. 37-40.

Neander K., 1983. *Abnormal Psychobiology*, LaTrobe University (unpublished Ph.D. dissertation).

Neander K., 1991a, «Functions as Selected Effects: The Conceptual Analyst's Defense», *Philosophy of Science*, 58, 2, pp. 168-184.

Neander K., 1991b, «The Teleological Notion of "Function"», *Australasian Journal of Philosophy*, 69, 4, pp. 454-468.

Neander K., 2017a, *A Mark of the Mental: In Defense of Informational Teleosemantics*, Cambridge (MA), Cambridge University Press.

Neander K., 2017b, «Functional Analysis and the Species Design», *Synthese*, 194, 4, pp. 1147-1168.

Okasha S., 2019, *Philosophy of Biology. A Very Short Introduction*, Oxford, Oxford University Press.

Orzack S. H. and Forber P., 2017, «Adaptationism», In Zalta E. N. (ed.), *Stanford Encyclopedia of Philosophy*. On-line: https://plato.stanford.edu/archives/spr2017/entries/adaptationism/.

Ruse M. E., 1971, «Functional Statements in Biology», *Philosophy of Science*, 38, 1, pp. 87-95.

Sarkar S., 2005, *Molecular Models of Life*, Cambridge (MA), MIT Press.

Schlosser G., 1998, «Self-Re-Production and Functionality: A Systems-Theoretical Approach to Teleological Explanation», *Synthese*, 116, 3, pp. 303-354.

Sober E., 1984, *The Nature of Selection: Evolutionary Theory in Philosophical Focus*, Cambridge (MA), MIT Press.

Šustar P., 2007, «Neo-functional Analysis: Phylogenetical Restrictions on Causal Role Functions», *Philosophy of Science*, 74, 5, pp. 601-615.

Šustar P., Brzović Z., 2014, «The Function Debate: Between "Cheap Tricks" and Evolutionary Neutrality», *Synthese*, 191, 12, pp. 2653-2671.

Walsh D. M., 1996, «Fitness and Function», *British Journal for the Philosophy of Science*, 47, 4, pp. 553-574.

Walsh D. M., Ariew A., 1996, «A Taxonomy of Functions», *Canadian Journal of Philosophy*, 26, 4, pp. 493-514.

Wouters A., 1995, «Viability Explanation», *Biology & Philosophy*, 10, 4, pp. 435-457.

Wouters A., 2003, «Four Notions of Biological Function», *Studies in the History and Philosophy of Biological and Biomedical Sciences*, 34, 4, pp. 633-668.

Wouters A., 2005, «The Function Debate in Biology», *Acta Biotheoretica*, 53, 2, pp. 123-151.

Wouters A., 2013, «Biology's Functional Perspective: Roles, Advantage, and Organization», in Kampourakis K. (ed.), *The Philosophy of Biology: A Companion for Educators*, pp. 455-486, Dordrecht, Springer.