



# Biological functions and dysfunctions: a selected dispositions approach

Fabian Hundertmark<sup>1</sup> · Marlene van den Bos<sup>1</sup>

Received: 18 April 2023 / Accepted: 23 February 2024  
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## Abstract

Justin Garson has recently argued that proper functions are proximal activities of traits selected by phylogenetic or ontogenetic selection processes, and that traits are dysfunctional only if they cannot perform their proper functions for constitutional reasons. We partially agree with Garson, but reject the view that functions are proximal activities, as well as his account of dysfunctions. Instead, we propose our own theory that biological functions are selected dispositions and that a trait is dysfunctional in virtue of not having the dispositions for which it was selected. This account can explain both defects (or dysfunctions in Garson's sense) and dysfunctions due to environmental factors. Moreover, it offers a neat way to explain the graduality of dysfunction.

**Keywords** Biological functions · Dysfunctions · Defects · Selected effects theory · Dispositions

## Introduction

Biological functions and dysfunctions play a significant role in the philosophy of biology, mind and medicine. Some philosophers argue that the presence of a dysfunction is necessary for mental disorders (Boorse 1976; Neander 1983; Wakefield 1992) or somatic diseases (Boorse 1977). Others argue that biological functions play a central role for naturalistically acceptable explanations of the representational contents of perceptual states (Neander 2017, 2012), desires (Papineau 1998), or even all representations (Millikan 2006, 1984). Biological functions and dysfunctions also play a role in explaining how there can be miscomputation (Coelho Mollo 2018; Piccinini 2015) or mechanisms for a certain purpose (Garson 2019 ch. 10, 2013).

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✉ Fabian Hundertmark  
fhundertmark@uni-bielefeld.de

Marlene van den Bos  
marlene.vandenbos@uni-bielefeld.de

<sup>1</sup> Department of Philosophy, University of Bielefeld, Bielefeld, Germany

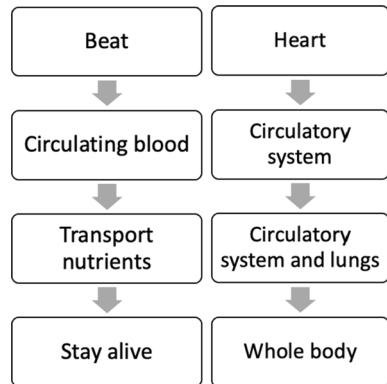
All of these philosophical theories require a robust notion of biological functions (sometimes called “proper functions”) in contrast to mere effects (Neander 2017). Such a notion of is required to fulfill three criteria. Firstly, it needs to be able to distinguish between functions and mere effects. Secondly, it needs to provide an adequate account of dysfunctions. Thirdly, it needs to be truly useful for biology.

In this paper, we will address the related questions of what biological proper functions and dysfunctions are. So, if not specified otherwise, we will use the word “function” to refer to biological proper functions. In Sect. “[Garson on functions and dysfunctions](#)”, we will introduce Justin Garson’s well-developed theory of functions and dysfunctions. Garson starts with the assumption that functions are activities or effects of traits selected by phylogenetic or ontogenetic selection processes. But he argues that not all such selected effects are proper functions. Garson restricts functions to selected proximal effects to solve the so-called “indeterminacy problem”. Moreover, he argues that dysfunctional traits are those that cannot perform their functions for constitutional reasons. In Sect. “[The case for distal functions](#)”, we will argue against Garson’s restriction of functions to selected proximal effects. We will show that Garson’s reasons for this restriction are made superfluous by his theory of dysfunctions. Additionally, we will provide examples of non-proximal proper functions from philosophy and biology. In Sect. “[The case for contextual dysfunctions](#)”, we will argue against Garson’s thesis that dysfunctions always involve constitutional defects by taking a closer look at his arguments and by arguing that some dysfunctional traits fail to perform their function because of their environment rather than their constitution. In Sect. “[The selected dispositions theory of functions](#)”, we will present our own theory of functions, starting with the idea that functions are selected dispositions rather than selected effects or selected activities. We will show that this position, among other advantages, can capture distal functions. In Sect. “[The selected dispositions theory of dysfunctions](#)”, we will introduce the selected disposition theory of dysfunctions. According to this theory, dysfunctions simply consist of a trait not having the disposition for which it was selected. As we will show, this allows it to explain both environmental dysfunctions and defects. Furthermore, we show how this theory provides an account of the graduality of dysfunctions. In Sect. “[Conclusion](#)”, we conclude.

## Garson on functions and dysfunctions

Justin Garson’s General Selected Effects Theory (GSE) of functions and dysfunctions is based on the Selected Effects Theory (SE), an etiological theory of function, developed mainly by Ruth Millikan and Karen Neander (Millikan 1989; Neander 1991; Odenbaugh and Griffiths 2020, p. 3). The SE theory states that functions are the effects or activities of traits for which those traits were selected—where a trait was selected for a particular effect or activity if that effect or activity caused the trait to be positively selected. By incorporating selection, the theory can distinguish functions from mere effects. Our noses, for example, have plausibly been selected because they warm and moisten the air we breathe and enable us to smell. They have not been selected to carry glasses. Hence,

**Fig. 1** Hierarchies of systems and their functions (c.f. Garson 2019, p. 120)

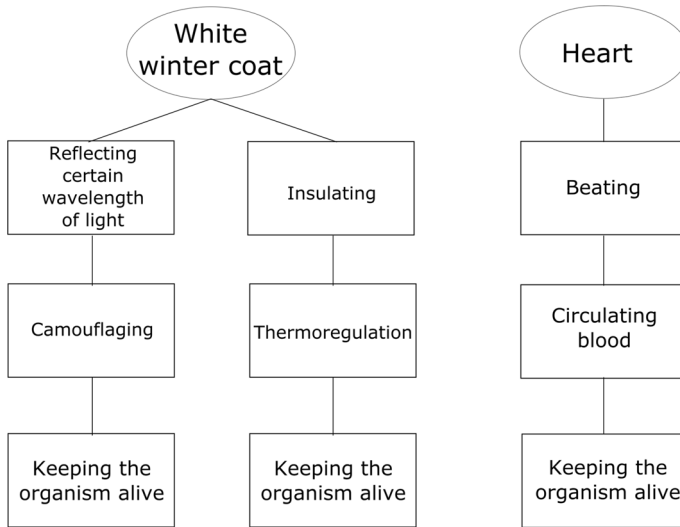


warming and moistening the air, as well as enabling us to smell, are functions of the nose, while being able to carry glasses is just a helpful effect. Furthermore, the SE theory can account for dysfunctions. Noses might not be able to warm and moisten the air, even if they have been selected for having this effect.

Garson argues that differential retention is another form of selection. His GSE states that functions are activities that led to the trait's differential reproduction or its differential retention in a population (Garson 2019, p. 93). Thus, a trait may have a function by virtue of the fact that it persisted because it did certain things. Accordingly, GSE can ascribe functions to things such as neural structures and behavioral dispositions without any need for reproduction.

Furthermore, Garson defends the proximal-function thesis (this label comes from Wakefield 2021a, p. 338). This thesis says that only the activity or effect closest to the trait (i.e., one that is exclusive to that trait) is the trait's proper function. According to Garson, we can find the function of a trait by using functional analysis. We choose a high-level capacity of a system, for example, an organism's ability to survive. This capacity can, in a second step, be explained by dividing it into several sub-capacities—e.g. breathing, digestion and heat retention. The chosen sub-capacity is then explained by also dividing it further into sub-sub-capacities. This can then be continued until the function is only performed by a single mechanism. By applying functional analysis to the problem of function indeterminacy, a hierarchical form is achieved which shows the most proximal activity and therefore the function of a trait (Garson 2019, pp. 118–121).

Garson combines functional analysis with mechanistic explanations to define the specific notion of function (Garson 2019, pp. 121–123). It results in the characterization of “[...] the function of an item is its (historical) contribution to the activity of the mechanism in which it is immediately contained, when this hierarchy of activities has been identified by GSE” (Garson 2019, p. 122). Figure 1 shows the hierarchy of activities and the corresponding system and its capacities. The heart beats which is part of the circulatory system and enables the circulation of blood (like Garson, we use “beating” to refer to the rhythmic pumping motion of the heart and not to the production of a specific sound). This then leads



**Fig. 2** On the left-hand side is the trait of white winter coats which has two hierarchies of activity, hence two functions. On the right hand side we have the previously described hierarchy of activities of the heart

to nutrients being transported throughout the circulatory system and the lungs, which contributes to the overall goal of the whole body to stay alive.

This does not mean that traits cannot have multiple functions. On the contrary, traits can have an indefinite number of functions as long as these are not in the same hierarchy of activities. For example, species that occupy temperate and polar regions have developed different adaptations to the harsher climates and high seasonality. One of those adaptations is the seasonal coat color (SCC) where animals have brown-grayish coats in the summer months and almost entirely white coats during the winter months. In SCC species, however, the seasonal coat changes have multiple functions. One of them is thermoregulation and the other is for camouflage. In some SCC species the white hairs of the winter coat have a different microstructure that allows for more air to be trapped by the hairs and therefore increase the insulation. The second function of the seasonal coat color is camouflage which is one of the strongest evolutionary forces driving coloration. So, in the case of SCC species, we have a trait, i.e. the seasonal coat, that has two distinct functions. It has the function of thermoregulation, as do most winter coats, and it has the additional function of camouflage (Zimova et al. 2018).

In Fig. 2 two traits are depicted, the heart and the white winter coat, as described above. Two hierarchies branch off from the white winter coat. The left branch begins with the activity of *reflecting a certain wavelength of light* which is the most proximal activity and therefore, according to GSE, a proper function of the white winter coat. The hierarchy continues with the activities of *camouflaging*, and *keeping the organism alive* which are the distal activities. The right branch of the white winter coat trait starts with *insulating* because the white winter coat has different heat retention properties than the gray summer coat. The hierarchy continues with

*thermoregulation* and *keeping the organism alive*. This is to show that in a singular hierarchy of activities there can only be one proper function, according to the GSE. However, in traits with multiple hierarchies there can be multiple functions.

According to Garson (2019, p. 111f), solving the problem of function indeterminacy is important for two reasons. First, he thinks that such a resolution is required for teleosemantics where the contents of mental representations depend on the biological functions of the mechanisms that produce (Neander 2017, e.g., 2012) or use (Millikan 2006, e.g., 1984) these representations. Consequently, if the function of these mechanisms is indeterminate, so is the content of the mental representation (Garson 2019, pp. 111–114; see also Neander 1995). Let us, for example, consider the following simplified teleosemantic theory: A mental state represents a state of affairs  $p$ , in virtue of being used by a mechanism that requires that mental state covary with  $p$  to perform its function. For this theory, it matters a great deal whether the function of the mechanism is proximal or distal since both functions would yield very different representational contents. Consider, for example, the notorious case of the hunting frog. Whether a mental state of this frog represents flies or black dots depends, according to the aforementioned theory, on the function of the system that uses this state to regulate its behavior. If the system has the function of snapping at black dots in the environment, the mental state represents black dots. If, on the other hand, the system has the function of catching flies, it represents flies.

The other reason why Garson argues wants to resolve indeterminacy is for an adequate account of dysfunctions. In some cases, it seems clear when a trait is dysfunctional and when it is not. For example, if someone suffers from an arterial hemorrhage and loses too much blood, the heart does not seem to be dysfunctional. After all, it would still be able to beat, even though it is not able to pump blood. Another example Garson gives is the one of filial imprinting in goslings (Garson 2019, p. 112f). Goslings imprint on the first large moving object they see after hatching. In one case, the goslings imprinted on the scientist's boots instead of their mother. Was the imprinting mechanism of this gosling dysfunctional? If the specific function of imprinting is to follow the mother, then the imprinting mechanism was dysfunctional. However, if the specific function is to follow the first moving object the gosling sees, the imprinting mechanism functions perfectly.

Garson justifies the proximal-function thesis with three arguments. The arguments of intuition, intervention, and informativeness. Beginning with the first argument, Garson presents Dretske's (1986) magnetosome example. Magnetosomes are organelles of bacteria that consist of membrane-enveloped crystals of a magnetic iron mineral. They are organized in intracellular chains that allow the bacterium to align and swim along geomagnetic fields, which is called "magnetotaxis". All of the magnetotactic species of bacteria are highly motile and either live a microoxic or anoxic lifestyle. They do this with the help of the magnetotaxis where the magnetosome aligns them with geomagnetic north or south, depending on the hemisphere they are in, which leads them into oxygen-poorer waters (e.g. Blakemore 1975, 1982; Faivre and Schüller 2008; Stolz 1993; Uebe and Schüller 2016). The question Garson poses is whether the proper alignment with the magnetic field (proximal) or the leading away from oxygen-rich waters (distal) is the proper function of the magnetosome. Garson suggests following

the intuition that the function is aligning with the geomagnetic field (proximal). He further supports this intuition with the example of manipulating the magnetosome with a magnet. Due to the added magnet, the magnetosome cannot align the bacterium to the geomagnetic field and potentially lead to oxygen-rich instead of oxygen-poor waters. However, the magnetosome is still fulfilling its function by aligning the bacterium with a magnetic field—in this case the field of a magnet and not the geomagnetic field of the earth. Now, on the other hand, if the magnetosome does not direct the bacterium northward even though it is located in the northern hemisphere and it is not being manipulated, the magnetosome would not be fulfilling its function and therefore would be dysfunctional (Garson 2019, pp. 115–116).

Garson's second argument for the proximal-function thesis is the argument of intervention, based on Buller (1997; c.f. Garson 2019, p. 116). Garson argues that the dysfunctioning trait should be an appropriate target of medical intervention. This means that if you cannot breathe properly because you have a broken rib, it is the rib that should be treated and not the lungs because your lungs are not dysfunctioning. The rib is where the intervention would take place because of its dysfunction.

The final argument for the proximal-function thesis is the one of informativeness which says that statements about some trait being dysfunctional should be highly informative. For example, if the heart cannot circulate the blood properly throughout the body, this could be caused by several different parts of the cardiovascular system. It could be due to the heart not beating correctly, or it could be due to an extensive hemorrhage leaving the heart unable to circulate blood through the damaged cardiovascular system. If dysfunctions were only failures to carry out the most proximal selected activities, saying that the heart is dysfunctional implies that the heart but not other parts of the cardiovascular system are dysfunctioning (Garson 2019, pp. 114–117).

Given the proximal-function thesis, one might think that a trait is dysfunctional iff it cannot perform its proper function. Garson, however, disagrees. If a trait is dysfunctional as soon as it cannot perform its most proximal selected activity, then traits that simply lack the resources necessary to perform their function would also be dysfunctional. Garson illustrates this with an example of an unplugged toaster. This toaster simply does not have the electricity it needs to perform its function even though it is not dysfunctional. As soon as it's plugged in, it is capable of toasting again and can therefore fulfill its function (Garson 2019, pp. 124–125). Thus, the inability to perform its function can be due to two reasons: the current constitution of the trait or the current circumstances. The second reason is an uncooperative environment, i.e. an environment in which the trait does not have access to the normal conditions and resources necessary to fulfill its function. More specifically, a trait's normal environment to fulfill its function is that in which it has historically performed its function, which then supported its relative fitness (Garson 2019, p. 128). This view has also been defended Millikan, who argues that a trait is not dysfunctional if it cannot perform its function because it is lacking the necessary background conditions. Accordingly, a dysfunction only occurs if the constitution of the trait is the reason for it not being able to perform its function (Millikan 2013, p. 40). Let us call this "the constitutional-dysfunction thesis".

To summarize, Garson advocates the proximal-function and constitutional-dysfunction theses. While the former identifies the proper functions with the most proximal selected effects or activities, the latter states that a trait is only dysfunctional if it cannot fulfill its function due to its constitution and not due to its circumstances.

## The case for distal functions

In this section, we will argue against Garson's assumption that functions are only proximal effects or activities. First, we will show that this proximal-function thesis is not necessary to explain dysfunction, and second, we will present philosophical and biological examples of activities that have been accepted as proper functions even though they are not proximate.

First, we will argue that Garson does not need a solution to the indeterminacy problem to account for dysfunctions. We will do so by taking a closer look at two examples. The first is about a trait in an uncooperative environment, while the second example is a dysfunction in Garson's sense. For both examples, we will show-case a function hierarchy and will be looking at activities on different hierarchical levels to see whether the proximate function is necessary for determining their dysfunction.

**The hemorrhage example** This first example is a trait in an uncooperative environment, namely a heart without enough blood. According to Garson, the function hierarchy of the heart is the following: (1) the heart beats, (2) it circulates blood, (3) it transports nutrients and oxygen, and (4) it keeps the organism alive. Now if someone were to suffer from a severe hemorrhage and their heart would not be able to beat properly anymore. The proximal approach to this would be that the person has lost too much blood for the heart to continue beating normally (1) even though it would be able to do so in its normal environment, a body that has not lost too much blood. Therefore, the constitution of the heart is not the reason for its inability to fulfill its function and is therefore not dysfunctioning. The same is true when looking at a more distal function of the heart e.g., circulating the blood (2). The heart is unable to circulate the blood (2) because the body has lost a lot of blood. Under normal conditions or in its normal environment, a healthy and unharmed body, the heart would be able to circulate blood. Therefore, the heart's constitution is not the reason for its failure, and it is not dysfunctioning. This analysis of the constitution can be done at any step of the trait's chain of activities and, if done properly, will always lead to the result that the heart is not dysfunctioning.

**The magnetosome example** This second example is about a dysfunctional trait, specifically a bacterium with a dysfunctioning magnetosome. The hierarchy of selected activities for the magnetosome is the following: (1) the magnet aligns with the geomagnetic north, (2) it leads the bacterium away from oxygen-rich water, and (3) it keeps the bacterium alive. Now unlike the hemorrhage example, here we assume that the magnet is dysfunctioning because it does not align with the geomagnetic north. Starting again with the proximal function, we have the magnetosome, which

does not align with geomagnetic north (1), therefore not leading the bacterium away from oxygen-rich water and potentially killing it. The magnet is not being manipulated, nor has geomagnetic north changed, which means that the magnetosome is in its normal environment. Thus, the constitution of the magnetosome is wrong, and it is dysfunctioning. Now turning towards a distal function on the chain of activities, the magnetosome is not leading the bacterium away from the oxygen-rich water (2) even though it is in its normal environment therefore, the constitution of the magnetosome must be wrong. The magnetosome is dysfunctional whether we start from the most proximal activity of the trait or a more distal one.

In both examples, the functionality or dysfunctionality of the trait does not depend on the function being the most proximal activity to the trait. It only depends on the trait's constitution being such that a selected activity cannot be carried out. Consequently, this dependence on the constitution renders the solution of the indeterminacy problem superfluous for the definition of dysfunction because as long as the constitution is false, the trait cannot perform any of its activities, whether they are proximal or distal.

But what happens when we have two dysfunctioning traits that counteract each other? In this case, it might be intuitive to assume that the proximal function is required to determine whether or not the traits are dysfunctioning. However, that intuition is wrong, as can be seen in the following example. Let us say we have hormonal gland *A* and hormonal gland *B*. *A* produces hormone *a*, which increases insulin production, and *B* produces hormone *b*, which blocks the cell intake of insulin. For this case, we assume that these glands work entirely independently of one another and are not connected through any feedback loops. Now, hormonal gland *A* is dysfunctioning, and the production of hormone *a* has come to a halt. Therefore, insulin production remains steady or even drops. Simultaneously, hormonal gland *B* is dysfunctioning therefore, the insulin is not being blocked from the cells. Therefore, the insulin that is still being produced, even though it is less than before, has free passage into the cell. If only *A* were dysfunctional, the insulin levels in the cells would decrease. If only *B* were dysfunctional, the insulin levels would keep on increasing. Both scenarios would lead to drastic effects on the metabolism while if both hormonal glands dysfunction, they counteract each other, and the effects would be more in the realm of insulin fluctuations decreasing and the cell intake becoming more stable. So overall, the organism might not experience the effects of the glands dysfunctioning. Is the proximal function of these glands necessary to determine whether or not they are dysfunctioning? No, it is not. Even though both dysfunctions cancel each other out, Garson's definition still only requires the constitution of the traits. Both glands are dysfunctioning because their constitutions are wrong and not because of their environment. It might be more difficult to notice the dysfunction; however, this does not change the fact that a solution to the indeterminacy problem is essentially irrelevant to the question of whether a trait is dysfunctional.

Garson's other reason for solving the indeterminacy problem was teleosemantics. According to teleosemantics, the content of a mental representation depends on the function of its producer or consumer. Consequently, one might think that the indeterminacy of function automatically leads to the indeterminacy of content. This is not true. Even though Karen Neander (1995) argues for the position that proximal



selected effects are the ones relevant for teleosemantics—and also for malfunctions—she considers all activities in the hierarchy as functions since “all of these are correct descriptions of what the trait did which caused it to be selected.” (Neander 1995, p. 115) So, even if function indeterminacy is not resolved in a principled way, this does not automatically result in content indeterminacy.

What is even more, most teleosemantic theories *prima facie* require distal functions to account for the fact that mental representations represent distal states of affairs. According to David Papineau (1998, 1993, 1984), for example, the content of desires is determined by what they have the function to bring about. Since most desires are directed at the outside world, this requires that the relevant functions are distal. According to Millikan (2006, 1989, 1984), the content of descriptive mental representations roughly depends on what these representations must correspond to for the system using these representations to fulfill their functions. Since descriptive mental representations usually represent the world outside the organism to be such-and-such, the functions of the consumer also need to be distal. Let us, for example, consider the famous case of the frog that represents flies in its environment. If Millikan is correct, a certain brain state of the frog represents the presence of a fly roughly in virtue of the following facts. First, this brain state causes a tongue-snapping mechanism to let the tongue shoot out. And second, this mechanism has the function of catching flies, which only can be fulfilled if the brain state actually corresponds with the presence of flies. So, while Garson argues that a solution to the indeterminacy problem is required by teleosemantics, most teleosemantic theories are incompatible with his preferred solution, according to which proper functions need to be proximate. This, of course, is only a *prima facie* worry. On the one hand, one can formulate teleosemantic theories even if one accepts the proximal-function thesis. This is, for example, done by Garson (2019, p. 205f.) who appeals to distal “normal causes” in his version of Neander’s (2017) informational-teleosemantics. On the other hand, one might, of course, reject the whole teleosemantic project as misguided.

But ascriptions of distal functions are not restricted to philosophy. Let us, for example, consider the function of zebra stripes. Some hypotheses have been that they have the function of camouflaging, confusing predators, cooling the body temperature, and avoiding biting flies. Caro and colleagues (2014) argue that the latter hypothesis seems to be the case which has found further support in Tombak et al. (2022), who compared landings of *Stomoxys* flies on striped and uniform tan pelts. Garson picks up this example of a biological function to introduce and explain why it is necessary to have a clear concept of biological functions. However, the zebra stripes and their potential functions may argue against Garson’s thesis, because deterring biting flies is not a proximal activity of the stripes. Rather, their proximal selective activity would be to reflect light in a certain way. This shows that in biology, not all proper functions of interest are the most proximate ones.

Garson (2019, p. 117f.) accepts that biologists and even regular people routinely refer to distal selected effects as “functions”, but dismisses this as “loose talk”. In our opinion, however, this does not do justice to biological practice. In evolutionary biology, distal functions are regularly appealed to in order to explain the adaptive significance of a trait. For instance, the distal function of the beak of a bird is to aid

in the acquisition of food. However, this distal selected effect is achieved by different proximal means in different birds. The sharp, pointed beaks of sparrows, for example, have the proximal function of breaking up objects. The large, broad beak of a pelican, on the other hand, has the proximal function of scooping up objects. Similarly, in ecology, distal functions are used to understand the role of a species in an ecosystem. For example, the distal function of predators in an ecosystem is to control the population of their prey. Still, the specific proximal mechanisms by which they do this vary widely among different predator species. A snake and a pack of wolves are both predators, however, the snake lies in wait for its prey and attacks it alone while the pack of wolves stalks and attacks its prey as a group.

To sum up, we think that there are no reasons to accept the proximal-function thesis. There are, however, good reasons to allow for proximal as well as for distal functions to allow a variety of different explanatory aims and projects that might be pursued by using function talk. Mechanistically oriented fields, such as genetics, biochemistry, molecular biology, cellular biology, physiology, and neuroscience, are more likely to use proximal functions—as Neander (1995) and Garson (2019) correctly recognized. Other fields such as ecology, evolutionary biology, psychology, and psychiatry are less mechanistically oriented as they tend to focus more on understanding the interactions and relationships between different organisms and their environment, as well as the processes that shape these interactions over time, rather than on understanding the specific mechanisms behind these interactions. Consequently, these fields are more likely to use distal functions.

## The case for contextual dysfunctions

In this section, we will argue against the constitutional-dysfunction thesis—that dysfunctions are inability to perform proper functions for constitutional reasons. We do so in two steps. First, we present Garson's case against contextual dysfunctions (dysfunctions due to environmental reasons), which rests on two examples in which a trait cannot fulfill its function due to internal circumstances even though it is not dysfunctional. We argue that these examples do not show what they are supposed to show. Second, we give examples of contextual dysfunctions from medicine, psychiatry, and ecology.

Garson argues for the constitutional-dysfunction thesis by appealing to our intuitions in two cases. In the first part of this section, we discard these intuitions by taking a closer look at them. Garson's first example has been previously mentioned in Sect. "[Garson on functions and dysfunctions](#)". He asks us to consider an unplugged toaster (2019, p. 126). This toaster is not dysfunctional, even though it cannot perform its proximal function (to heat some coils when a lever is pressed). From this observation, Garson infers that external circumstances are not relevant to the question of whether a toaster is dysfunctional.

With regard to this argument, there are three things to note. First of all, toasters and their parts do not have biological functions, according to Garson's own theory, simply because they are not biological entities. Consequently, Garson appeals to our

intuitions concerning *artifact* dysfunctions, and there is no guarantee that conclusions drawn also hold for biological dysfunctions. Secondly, the specific function ascribed to the toaster is not simply an innocent assumption. After all, the function of the toaster may also be *to heat the coils when the lever is pressed and the toaster is plugged into a functioning outlet*. If this were the correct function ascription, there would be no reason to believe that the toaster cannot fulfil it. After all, the toaster would heat the coils when the lever is pressed, and the toaster is plugged into a functioning outlet. Third, even if we accept that the right function ascription does not explicitly mention the presence of electricity, the step from “the fact that the toaster is not plugged in does not make it dysfunctional” to “external factors cannot make the toaster dysfunctional” is not valid. After all, the fact that the toaster is not plugged in is not only an external circumstance but also a very contingent one insofar as the toaster could easily be plugged in. However, these intuitions can falter as soon as the external circumstances that prevent the toaster from fulfilling its function are more stable. Let us, for example, imagine a toaster with a very unusual plug, a toaster that requires an outlet with an unusual voltage level (e.g., 634 V), a toaster that does not work when oxygen is present, or a modern toaster 300 years ago. In these cases, it is not obvious anymore that the toaster is not dysfunctional, even though it would perform its function in its normal operating circumstances. In our view, it is generally true that only stable conditions make systems or traits dysfunctional, but circumstances that can be easily changed do not. The difference between internal and external conditions is of secondary importance. A toaster in which an easily removable bread crumb obstructs the ejection mechanism may not be able to fulfill its function due to internal circumstances, but it is not dysfunctional. However, if the heating coils of the toaster are burnt out, this stable internal condition ensures that the toaster is dysfunctional.

In his second example, Garson asks us to consider blindfolded eyes. These are not dysfunctional, even though they cannot perform their function (to see or to process information about light). From this example, Garson infers that “[t]he eye is only dysfunctional when it cannot perform its function in its normal operating circumstances—it’s hooked up to a light source.” (Garson 2019, p. 127).

The eyes clearly have biological and not artifact functions. Consequently, our first concern regarding the toaster example does not apply here. However, the other two problems remain. On the one hand, it is not all but obvious that eyes have the function *to process information about light* rather than the function *to process information about light when light reaches it*. If this were the correct attribution of function, the blindfold does not ensure that the eyes cannot perform it. Consequently, there would also be no reason to believe that the eyes were dysfunctional in the first place. Furthermore, our judgment that blindfolded eyes are not dysfunctional may also be guided by the fact that a blindfold can very easily be removed. Stable external circumstances that prevent the eyes from fulfilling their function (oversized eyelids, a permanently attached iron blindfold, complete lack of light in the stable environment), on the other hand, ground the dysfunctionality of the eyes.

To make our point clear, it is valuable to introduce a distinction that is often overlooked. That is the distinction between dysfunction and mere malfunction. A trait malfunctions if it fails to perform its proper function, while a (fully) dysfunctional

trait is not even capable of doing so. In general, we agree with Garson that traits can malfunction due to external circumstances without these traits being dysfunctional. However, this is not because these circumstances are external but because they are unstable. The same is true for similarly unstable internal circumstances. For example, a vestibular system malfunctions when one gets off a rapidly spinning merry-go-round because it does not immediately accommodate for the change of movement leading to a brief loss of balance. However, it is not dysfunctional, even if the vestibular system does not enable equilibrium due to internal factors (the continuous movement of the fluid in the arcades).

So far, we have only argued that Garson's arguments against contextual dysfunctions are not convincing. In the second part of this section, we will give two examples to show that there are actual contextual dysfunctions. According to Caro et al. (2014), the function of zebra stripes is to deter biting flies that carry a parasite responsible for African trypanosomiasis (sleeping sickness). Plausibly, zebra stripes that cannot deter biting flies with this parasite are dysfunctional. However, stripes could only be unable to fulfil their function in virtue of biting flies adapting to the striped pattern. This, however, is an external change that prevents zebra stripes from fulfilling their distal function. Consequently, if zebra stripes can be dysfunctional at all, there are contextual dysfunctions.

Our second type of example comes from evolutionary psychiatry. According to the DSM 5, “[a] mental disorder is a syndrome characterized by clinically significant disturbance in an individual’s cognition, emotion regulation, or behavior that reflects a *dysfunction* in the psychological, biological, or developmental processes underlying mental functioning.” (American Psychiatric Association 2013, p. 20; our emphasis). According to the DSM, the so-called “seasonal affective disorder” (SAD) is a subtype of major depressive disorder (specifier: “with seasonal pattern”, American Psychiatric Association 2013, p. 187). Consequently, the DSM implies that SAD reflects a dysfunction in the processes underlying mental functioning. There are, however, theories, according to which SAD does not imply that any system cannot fulfill its function *due to its constitution*. According to Randolph Nesse (2019, 2000), low mood has been selected for limiting resource expenditure in situations where expending one’s resources is likely to do more harm than good (e.g., a situation in which hunting for food will burn more calories than you will gain from the hunt). This is, of course, a distal function. The proximal function of these mechanisms is to bring about low mood in response to certain environmental cues (e.g., diminished sunlight in the winter). However, in people with seasonal affective disorder, this function is perfectly fulfilled. If this hypothesis is right, however, the most charitable interpretation of the DSM must imply the existence of contextual dysfunctions. According to this interpretation, the dysfunctionality in the case of seasonal affective disorder is a consequence of the fact that in contemporary Western societies, it is not adaptive anymore to limit resource consumption in winter.

At this point, one may object that allowing for contextual dysfunctions blurs a vital distinction drawn by psychiatrists themselves (Wakefield 2021b, p. 146f; thanks to one of the reviewers for pointing this out). However, we believe that a similar distinction can be maintained without accepting the constitutional-dysfunction thesis. This is the distinction between constitutional dysfunctions (defects) and

contextual dysfunctions, which we will introduce in Sect. “[The selected dispositions theory of dysfunctions](#)”.

## The selected dispositions theory of functions

We hold the view that functions are selected dispositions (see also Godfrey-Smith 1994, p. 356; Leahy 2016; Neander 2017, p. 127ff; Hundertmark, 2021). Dispositions are properties of objects characterized by the fact that they would manifest themselves in certain ways under certain conditions. Here are some examples. A sugar cube is water-soluble because it would dissolve if it was exposed to water. A butterfly wing is sensitive, as it would be easily damaged if touched. A person is psychologically resilient because they would maintain or restore their mental health even under adverse conditions.

Taking functions to be selected dispositions rather than selected effects or selected activities has several advantages. First, since traits can have dispositions to respond to circumstances in certain ways, it allows for response functions (Neander 2017, p. 127ff). The pineal glands, for example, have the function of producing melatonin *in response to the dimming of light*. This function cannot be accounted for if we take the requirement that functions have to be selected *effects* seriously. After all, producing melatonin *in response to the dimming of light* is an activity but not an effect. Consequently, one can either think that functions are selected activities or selected dispositions. According to the first option, the function of the pineal gland is determined by the fact that it has been selected for its activity of producing melatonin in response to the dimming of light. According to the second option, the function depends on the fact that the disposition to produce melatonin in response to the dimming of light has been selected. Both options are suitable for allowing response functions—especially since dispositions can, of course, only contribute to selection if they manifest and produce the corresponding activities. However, the advantages presented below show that the functions are selected dispositions and not activities.

Second, it is widely accepted that some dispositions are multi-track (e.g., Ryle 1949; Vetter 2013) insofar as they can manifest in multiple different ways depending on the circumstances that trigger them. Hardness, for example, manifests by the hard object resisting deformation or by causing pain (Ryle 1949, p. 44). Similarly, some genotypes’ phenotypic plasticity manifests by the genotype producing different phenotypes when exposed to different environmental conditions. This fact can be used by a selected dispositions theory of functions to explain how traits can have functions that have never been manifested before (see Hundertmark, 2021, sec. 5).

As we will show in this section, a third reason for taking functions to be selected dispositions is that this theory allows distal functions (sect. “[The case for distal functions](#)”). Let us take a look at our proposal, beginning with our theory of functions:

**Selected dispositions theory of functions** Trait  $T$  has the biological proper function of  $\varphi$ -ing iff  $T$  has been selected due to having the disposition to  $\varphi$ .

So, the main idea is that functions are selected dispositions in contrast to selected effects or selected activities. Before showing how the selected dispositions theory

solves the problems of Garson's theory, two clarifications are in order. First, a trait has been selected due to one of its dispositions iff the fact that this trait has this disposition is causally relevant for its selection.<sup>1</sup> This, of course, presupposes that the traits in question have produced the effects or activities in which the dispositions manifest themselves.<sup>2</sup> However, it does not require that every possible manifestation of a multi-track disposition occurred—just as the redness of a triangle can be causally relevant for the pecking of a pigeon, even if the triangle had only one specific shade of red (Yablo 1992, p. 257). Second, the selected dispositions theory of functions is compatible with different accounts on what constitutes positive selection—e.g., whether differential retention is enough or whether differential reproduction is required.

Let us take a closer look at how the selected dispositions theory accounts for the distal functions listed in Sect. “[The case for distal functions](#)”. We argued that various teleosemantic theories (like Papineau's theory of desire content or Millikan's theory of descriptive content) require distal functions. Millikan's biosemantics, for example, says that a certain brain state of the frog represents the presence of a fly partly in virtue of being used by a tongue-snapping mechanism with the function of catching flies. According to our theory, this means that the mechanism of tongue-snapping has been selected because of its disposition to catch flies. First, tongue-snapping mechanisms certainly had this disposition in the past. Moreover, they would not have been selected if they did not have it. The same reasoning applies to the case of the zebra stripes. If Caro et al. (2014) are correct, zebra stripes have the function of distracting tsetse flies. According to our theory, this means that they have been selected for the disposition to do so. It is plausible that zebra stripes had the disposition to distract tsetse flies, and they would not have been selected for if they did not have it. Similarly, the beaks of birds have been selected for their disposition to aid the acquisition of food.

In short, the selected disposition theory can account for distal functions since dispositions with distal manifestation (like catching flies, distracting tsetse flies or acquiring food) can be selected for. Of course, this does not mean that all functions are distal. All cases above also come with proximal functions, which can be understood as selected dispositions with proximal manifestations. For example, the tongue-snapping mechanism also has the function of letting the tongue shoot out in response to the brain state, and the Zebra stripes have the function of reflecting light in a certain way. Consequently, we embrace a pluralism with regard to selected disposition functions which reflects the different explanatory aims and projects that might be pursued by using function talk (sect. “[The case for distal functions](#)”).

<sup>1</sup> See McKittrick (2018, chaps. 9 and 10) for a comprehensive defense of the causal relevance of dispositions and Hundertmark (2021, sec. 5) for a detailed account of how this helps to explain the selection of multi-track dispositions.

<sup>2</sup> This is at least true in the context of our paper, which is concerned with biological functions. One might argue that this restriction does not hold when it comes to artificial selection processes. However, this line of thought is beyond the scope of our paper.

## The selected dispositions theory of dysfunctions

In this section, we introduce the corresponding theory of dysfunctions and argue that it gives us a comprehensive account of dysfunctions. It is compatible with the existence of contextual dysfunctions (sect. “[The case for contextual dysfunctions](#)”), and it gives us a plausible explanation for the graduality of dysfunctionality.

By taking functions to be selected dispositions, our theory is tailor-made to yield a simple but powerful theory of dysfunctions:

**Selected dispositions theory of dysfunctions** An instantiation of  $T$  ( $t$ ) is dysfunctional (w.r.t. its function to  $\varphi$ ) iff traits of type  $T$  have been selected for  $\varphi$ -ing and  $t$  does not have the disposition to  $\varphi$ .

The main thing to note about this account is that it rejects the question of whether some trait is dysfunctional or not as too simple. As we have seen in Sect. “[Garson on functions and dysfunctions](#)”, traits can have different functions, even if we abstract from problems of hierarchical indeterminacy (think of the white winter coat). If our arguments from the last sections hold, however, functions can be proximal as well as distal selected dispositions.

One might think that a trait has a constitutional dysfunction if it lacks a proximal selected disposition, while a trait has a contextual dysfunction, if it lacks a distal selected disposition. Unfortunately, things are not quite as simple. To clarify this, we need to introduce the distinction between intrinsic and extrinsic dispositions. Intrinsic dispositions are instantiated by objects only because of their intrinsic features, while external dispositions are instantiated by objects partly because of features of the object’s environment (McKittrick 2018, 2003, chap. 8). To account for contextual dysfunctions, it must be possible for traits to be selected for their extrinsic dispositions. However, it is not obvious that this is possible, nor does it follow from the fact that traits can be selected for distal dispositions. A disposition that manifests itself in distal activities (such as fly catching or prey population control) need not be an extrinsic disposition. The reason for this is that dispositions can be masked (under circumstances that prevent manifestation) without ceasing to be instantiated. Consequently, distal dispositions can still be intrinsic if their instantiation depends on whether they *would manifest under external circumstances favorable to their manifestation*. For example, the selected distal disposition of the tongue-snapping mechanism to catch flies may be an intrinsic disposition if the mechanism has it because it would catch flies if it were under favorable external circumstances (e.g., if the rest of the frog’s body is normal, if the frog is in its natural environment, and if flies are present).

Because “has the disposition to pump blood”, “has the disposition to distract tsetse flies”, and “has the disposition to control prey populations” are not conventional predicates, there is no fact of the matter, whether they refer to intrinsic or extrinsic dispositions. We can, however, make progress by taking another look at Garson’s examples of the unplugged toaster and the blindfolded eyes. In these examples, we had malfunctions without the traits in question being dysfunctional.

Consequently, the selected disposition theory has to say that the toaster, as well as the eyes still possess the dispositions for which they have been selected. As we argued, the reason for this does not lie in the fact that the presence of electricity or the presence of light are external circumstances but, in the fact, that both factors are very unstable. Dispositions, in contrast, are stable properties of objects and even if this would not apply generally, we can safely assume that traits are only selected for their stable dispositions. Consequently, whether light reaches the eye or whether electricity reaches the toaster should not make a difference for whether these objects possess the dispositions in question. Generalizing from these examples, we may say that some factor which is causally relevant for the manifestation of some selected disposition is also relevant for its possession if this factor has been stable during the selection process. This answer can account for our judgments with regard to unplugged toasters, and blindfolded eyes as well as for the fact that the vestibular system is not dysfunctional directly after leaving a rapidly spinning merry-go-round (sect. “[The case for contextual dysfunctions](#)”).

In the light of these clarifications, let us take another look at contextual dysfunctions. In Sect. “[The case for contextual dysfunctions](#)”, we argued that zebra stripes can only be dysfunctional due to environmental factors. Let us, for example, assume that the neurophysiology of tsetse flies changes in such a way that they do not get irritated by the striped pattern anymore. In this case, a stable factor relevant to the manifestation of the zebra stripes’ disposition to distract tsetse flies changed. As a result, the zebra stripes lost their disposition to distract tsetse flies and became dysfunctional. The same reasoning applies to seasonal affective disorder. In this case, the mechanisms of mood regulation still have the (intrinsic) disposition to limit resource expenditure in the winter, but in modern societies, they have lost their selected disposition to limit expenditure *in circumstances where doing so is likely to do more harm than good*. After all, stable factors that have been relevant for this disposition (lack of food and greater dangers in winter) are absent in industrialized societies. Consequently, the mood regulation mechanisms are dysfunctional with regard to this function.

But, of course, the selected dispositions theory of functions also recognizes that some functions are selected intrinsic dispositions. If a trait fails to perform one of these functions, this can be called “constitutional dysfunction”. An already established term for this phenomenon, however, is “defect”. In our view, the arguments from intuition, intervention, and informativeness concern *defects* rather than the more encompassing class, which we call “dysfunctions”. The intuitions to which the first argument refers thus come from the fact that dysfunctions are not distinguished from defects. Furthermore, defects and not dysfunctions are appropriate targets of interventions and statements about defects should be maximally informative, whereas statements about dysfunctions may include contextual factors.

We have argued that the selected dispositions theory can account for contextual dysfunctions (dysfunctions due to external circumstances) as well as for defects (dysfunctions due to internal circumstances). This is the first reason for preferring the selected dispositions theory of dysfunctions over Garson’s alternative. But there is another one. As we have seen, our theory rejects the idea that traits are functional or dysfunctional simpliciter. Rather, functionality and dysfunctionality have to be



indexed to one of the functions of the trait. However, there is another complexity a selected dispositions theory can easily account for.

Dysfunctions come in degrees. For example, a keyboard can exhibit a level of dysfunctionality. The keys responsible for the characters “1” and “q” are not functioning reliably. In order for them to send the correct signal to the computer and produce a single digit or letter, they have to be pressed much more lightly compared to the other keys. So, the keys are somewhat dysfunctional and functional at the same time. Similarly, swollen noses are somewhat dysfunctional insofar as they are less able to warm and moisten the air and less able to smell compared to a nose that is not swollen.

Neither the SE nor the GSE theory of functions can capture this graduality of dysfunctions. The reason for this lies in the fact that this kind of graduality is a matter of modality. SE and GSE, however, do not capture modality. Consequently, they have to bring it in again when it comes to dysfunctionality. Garson does this, when he says that a dysfunctional trait *cannot* perform its most proximal selected effect for constitutional reasons. If Garson would want to capture the graduality of dysfunctions, he would have to make this modality a gradual matter.

The selected dispositions theory, in contrast, can easily account for the graduality of dysfunctions. Here is a sketch. The first thing to note is that dispositions are also a gradual matter (Manley and Wasserman 2007; Vetter 2015, p. 36). Wine glasses can be more or less fragile, roughly in virtue of breaking in many or fewer counterfactual situations. Furthermore, dispositions can be selected for, even if they do not manifest in all relevant situations. They just have to be reliable enough to confer an advantage in reproduction or retention. Let us, for example, assume that some trait has been selected for a disposition to  $\varphi$ . During the selection processes, tokens of this type possessed this disposition to a degree of  $X$  (where “ $X=1$ ” would mean that the trait  $\varphi$ -s in all relevant counterfactual situations and where “ $X=0$ ” means that the trait  $\varphi$ -s in no relevant counterfactual situation).  $X$  can now be used as a standard against which to measure the degree of dysfunction tokens of this trait have.

Accordingly, a trait is not dysfunctional at all if it possesses the selected disposition to  $\varphi$  to a degree of at least  $X$ . This explains how traits that are not dysfunctional can be malfunctioning in certain situations. After all, a trait does not need to be completely reliable in order to not be dysfunctional. Traits that possess the selected disposition to a degree between less than  $X$  and greater than 0 are somewhat dysfunctional, while traits that do not possess the disposition at all (grade=0) are completely dysfunctional.

## Conclusion

The selected dispositions theory of functions and dysfunctions provides a more robust and comprehensive framework for understanding the complex relationship between traits, their functions, and their environment. Unlike Garson’s theory, which argues that functions are proximal selected effects and that dysfunctions are always defects, our theory posits that functions are selected dispositions and that

dysfunctions are simply the absence of these dispositions. This approach allows for a more nuanced understanding of dysfunctionality, including both intrinsic and extrinsic factors, and also provides an account of how dysfunctionality can be gradual.

**Acknowledgements** We would like to thank the participants and members of the Bielefeld Colloquium in Philosophy of Psychiatry, of the ThUMB 2022 Meeting on Functions in Biology and the Biomedical Sciences, Rijeka, of the PhilBio Meeting, of the Empirical Philosophy Workshop in Bielefeld for their valuable comments on previous versions and presentations of this paper. Special thanks go out to Dr. Katie Morrow and Pablo Hubacher Haerle for their helpful and constructive feedback.

**Funding** Open Access funding enabled and organized by Projekt DEAL. Fabian Hundertmark's research was supported by the German Research Foundation (DFG) as part of the project "Inductive Metaphysics" (Grant No. FOR 2495). Marlene van den Bos' research was supported by the German Research Foundation (DFG) as part of the project "Individual-based Research: Concepts, Epistemology and Integration" (project number: 396781820) in the CRC TRR 212 "A Novel Synthesis of Individualisation across Behaviour, Ecology and Evolution: Niche Choice, Niche Conformance, Niche Construction (NC<sup>3</sup>)" (project number 31609922).

## Declarations

**Conflict of interest** All authors declare that they have no conflicts of interest.

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