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Function

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Organs, tissues, cells as well as biochemical components of living beings are ascribed functions. When talking about functional limitations and malfunctions, functions are referred to a norm. In such normative assessments of the performance of components of a system, biology differs fundamentally from physics, which has dispensed with this since the Renaissance. Understanding this feature of biology requires a more detailed explanation of the concept of function. Conceptions of this range from approaches that ground the functional status on the evolutionary emergence of a trait, to those that take the contribution to the integrity of an organism as the sole criterion for functionality, to approaches that see the reason for the use of functional statements in the peculiarity of biology *to consider* living beings *as organisms* and not merely as physical-chemical systems. At different phases of biological theorising and in different sub-disciplines, however, this consideration is justified in different ways. This raises the question of whether the concept of function can be unified or must be explained in theory-relative terms.

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1. Demarcation of the biological concept of function

In the Middle Ages, 'functio' was understood to mean the exercise of a public office. The biological concept of function that emerged in the 16th century (Toepfer 2011: I, 644) is linked to this original meaning. Just as a public office is always an office in a community and contributes to it, the function of a biological trait is related to a superordinate system. It is a role in a system. Wings, legs and hearts are not solely identified morphologically, but are determined by their functions in locomotion or in pumping blood or haemolymph. And just as an office bearer can be characterised or classified by her or his office, as judge, mayor or secretary, the function can also serve to classify the function bearer.

The linking of the biological concept of function to the exercise of an office emphasises an aspect that makes it both interesting and problematic: If the function is a role, expectations can be attached to its fulfilment. Measured against these, the function can be performed in a better or worse way. An ascription of a function of this kind thus implicitly or explicitly refers to a norm that may often be vague, but whose fulfilment is fundamentally expected of the function bearer. Functions are thus not only demarcated from other things that are not functions, but also from dysfunctions. A function bearer who does not fulfil his or her function does not lose his or her status as a function bearer, which would mean that the norm would no longer apply; rather, he or she fails to fulfil this norm. For gaining scientific knowledge, such dysfunctions are even particularly important, as they often make it possible to grasp and explore functions in the first place (Krohs 2010; 2023; Roux 2018; Schweitzer 2019).

In even stronger terms, it is said that the function bearer serves the purpose or has the purpose of performing a certain task. The concept of function is thus, at least according to its origin, a teleological concept (gr. *telos* = purpose, goal). A considerable part of the contemporary debate on the biological concept of function deals with this teleological aspect (cf. Allen/Neal 2020), which is problematic in the context of a descriptive natural science. The teleological view was eliminated from physics during the Renaissance without any loss of the explanatory power of physical theories (Woodfield 1998). Attempts at elimination were also made in biology. Thus, classical and radical behaviourism attempted to completely bypass functional considerations and merely describe regular input-output connections (Watson 1913). Reactions to stimuli were to be understood not as purposive but as behaviour whose probability of occurrence in certain situations was increased by conditioning (Skinner 1953: chapter 5, section “Goals, purposes, and other final causes”). However, the complete renunciation of any teleological language was unconvincing and was subsequently abandoned in biology. But why does talk of purposes in biology, in contrast to physics, appear illuminating and perhaps even conducive to knowledge, and how, in light of this, can we retain the scientificity of biological disciplines such as physiology which work with ascriptions of function? To solve this problem, various proposals for naturalising the teleological element of the concept of function have been formulated. Naturalisations explain what must be the case in a physical world in order for a normatively understood function to be justifiably ascribed. For instance, it is claimed requiring a certain constitution or a certain ontogenetic or phylogenetic prehistory of the system to whose performance the function contributes. Today, there is a multitude both of diverse concepts of function and approaches to unifying them.

The biological concept is to be distinguished from the mathematical concept of function. The latter refers to formal properties of certain so-called mappings, i.e. unambiguous assignments of an element y of one set to an element x of another set. As in all mathematised sciences, it also plays a role in biology, but has only the historical roots of the word “function” in common with the biological concept of function.

2. Historical positions

Although the term “function” has its origins in the Latin Middle Ages, the philosophical idea of the purposefulness of processes in living nature, which is often unquestioningly accepted as obvious, dates back to Greek antiquity (cf. Sorabji 1964). In the following, the focus will be on certain approaches that are particularly important as precursors for the current debate.

2.1 Aristotle

The application of the concept of purpose to the organs – from the Greek *organon* (= tool) – of living beings is not only unproblematic for Aristotle, but required. This, however, is not because living beings have a special status, but because for him every thing can be traced back to four kinds of causes or must be explained in four ways (Aristotle, Physics II, 3, 194b). These include stating “for what sake” (*hou heneka*) something is there. Aristotle thus identifies a final or purposive cause, in addition to the cause of action, by which something is brought about, the “whence of the beginning of motion” (*hothen hē archē tēs kinēseōs*), which comes close to, but does not anticipate, a modern understanding of causality. The quartet of causes is completed by the material cause and the formal cause. The latter is itself closely related to purpose. Thus, for example, the purpose of the eye for Aristotle is vision, its form is sight (Aristotle, De Anima 412b). The existence and performance of an organ is explained with reference to its purpose. Similarly, for Aristotle, the falling of a stone has a purposive cause: the stone falls to reach its natural place on the ground (cf. Woodfield 1998). This is by no means to be understood as “backward causation”, as is sometimes misinterpreted. For Aristotle, the purposive cause is not a cause effective *per tractionem* (“by pulling”), which resembled, apart from the direction of time, “regular” causation *per actionem*, as was discussed in scholasticism, but the purpose of the thing under consideration (cf. Kullmann 1998: 261–272; Woodfield 1998).

2.2 The Modern Age

Descartes and Leibniz

In modern natural science, which began with the Renaissance, no explanatory value is attributed to the ascription of purposive causes or purposes with regard to inanimate natural objects. If purposes or, as they are now called, functions continue to be ascribed to the organs of living beings, this must be justified in a different way than by means of purposive causes.

René Descartes advocates a machine model of the organism. It seems obvious to consider functions in machines as assigned by the designer to their components. However, Descartes’ reconstruction of biological functions does not exploit this aspect of the metaphor. Explanations in terms of purposes could at best cite God’s purposes in relation to living beings. However, these are not accessible to us, so a form of explanation based on them is not applicable to animate nature. Instead, Descartes uses the machine metaphor in a different way: He emphasises the reciprocal relation of the components to each other. Like the wheels of a clockwork, which are predisposed to interact in a certain way, the organs of a living being are interdependent. He thus understands their function as the natural disposition of the parts of an organism (Descartes, Meditations IV.7; Toepfer 2004: 10).

Gottfried Wilhelm Leibniz, by contrast, allows explanations of nature of a teleological-functional kind. He places them alongside mechanistic explanations, without seeking to combine the two (Leibniz, Monadology § 79). However, he cannot give a criterion that would limit the attribution of purposes. This gives functional explanations a certain arbitrariness, against which Voltaire polemicises: if one were only skilful enough in identifying purposes, one could invent an almost inexhaustible variety of alleged functions, e.g. the nose exists for the wearing of glasses (Voltaire, Candide).

Kant

Like Descartes, Immanuel Kant sees the reciprocal relationship of the organs as a distinctive feature of living beings. He captures this with his concept of the *organised being*. Although he thereby adopts a concept of organism that later authors see as justifying statements of purpose or function, Kant does not ascribe purposes to the organisation of living beings or the organism's parts (this, however, for different reasons than Descartes, which will be discussed in a moment). Unlike Descartes, Kant recognises the explanatory value of teleological statements in relation to living beings. True, we cannot say anything about a purpose of the organisation of living beings; we cannot say that an organ *has* the purpose of bringing about something specific in the living being or of interacting in a certain way with another organ. Yet we can *ascribe purposiveness* to it: we can state that the organisation *fits* an (envisaged) purpose. Considerations of purposiveness have an as-if character for Kant (see, however, Gambarotto/Nahas 2022). They help us to explain the organisation of living beings. They form an indispensable complement to physical-mechanistic explanations of life processes. Even if life processes could one day be explained completely mechanistically, they would not become superfluous (Bartuschat 1972: 195; Teufel 2011).

The reason why, according to Kant, we cannot ascribe purposes to parts of living beings is due to the fact that for him the concept of purpose is not a *constitutive* concept under which the objects of experience fall or by which they are determined, as is the case with the concept of causality and the other categories. Our limited reason is thus not even able to grasp a potential orientation towards ends (Kant, Critique of Judgment: § 67). Instead, the concept of purpose is a *regulative* idea of our understanding with which we can explain the mutual dependence of the parts of an organism upon each other. Despite their as-if character, considerations of purpose are necessary according to Kant, since our reason cannot otherwise make sense of the interdependence of the components of organised beings. For this represents a circular dependence, whereas causality is essentially linear. The concept of causality can therefore only be applied to interdependence under the assumption of purposiveness. From the perspective of human understanding, living beings are thus purposefully organised wholes (ibid.: §§ 64–65).

2.3 Functional concepts in biology up to Darwin

The origin of the discipline of biology is often taken to be the study of the circulation of blood by William Harvey in the early 17th century. Like his contemporary Descartes, Harvey held a physical-mechanistic view of living beings. A biology that regards organisms as objects of a unique kind and therefore claims independent modes of knowledge vis-à-vis physics only emerges around 1800, i.e. in the period in which Kant's reflections on purposiveness are also located (Toepfer 2011: I, 258). Harvey does use the concept of function to describe the circulation of blood, but not at all in the way suggested by later philosophers (prominently, for example, by Wright 1973), who assume that Harvey's use of the concept of function means that he wanted to explain what the heart is for. In a few places Harvey does speak of "*functio*", but nowhere does he refer to it as the reason for the heart's existence or as its purpose. Instead, he seems to take into account that there is no difference between "*actio*" and "*functio*" (and also "*officium*"). He even equates the two and speaks of "action or function of the heart" – "*et hanc esse actionem sive functionem cordis*" (Harvey 1628: 58; cf. Krohs 2004: 55–56).

The concept of function only takes on a central role with the work of Georges Cuvier, who explains the structure of biological traits on the basis of their function. This view is an expression of a physico-theological worldview that, assuming a divine plan, sees no difficulty in aligning functions with purposes that a Creator has provided for the respective traits (Toepfer 2011: I, 646). The purely physical mechanism of the early modern period becomes the design of a divine engineer. Étienne Geoffroy St.-Hilaire, who argued against Cuvier that it was not functions but the morphological organisation of basic body plans that determined the anatomy of a species, also spoke of functions, but saw their necessity as rooted in the organism's construction (ibid.; for a detailed discussion, see Cheung 2000).

Finally, with his theory of evolution, Charles Darwin offers an explanation for the emergence of the complex morphology of organisms which at the same time explains the emergence of their body plans. He speaks impartially about functions, functional differences and functional relations between organisms. For him, they can be read from the structure of traits, the construction of the organisms and their interaction with their habitat. There are often formulations that even explicitly refer to purposes or to the lack of purposes (Lennox 1993). For Darwin, these are reflected in the fit between an organism or a trait with its environment (Krohs 2022). Darwin contrasts formulations such as "specialised for particular functions" with "serve for one special purpose alone" (Darwin 1859: 149), talks about adaptations to "specific purposes" (158) and also explicitly mentions a case in which there is no purpose: the Apteryx uses its wings "functionally for no purpose" (182). He also describes the evolutionary change of such functions or purposes with formulations like the following: "the swimbladder in fishes […] shows us clearly the highly important fact that an organ originally constructed for one purpose, namely flotation, may be converted into one for a wholly different purpose, namely respiration" (190).

3. 20th century debates

In the second half of the 20th century, the philosophy of science, which initially focused strongly on physics, also turned to biology and led to an extensive discussion about an adequate explanation of the biological concept of function. This discussion was thematically dominated by the problem of teleology. With one important exception, both, Descartes' approach to understand functions as natural dispositions and the Kantian subject-dependence of the mere *ascription of* purposiveness were felt to be too weak to be able to grasp the meaning of statements about function in biological explanations.

3.1 Functional explanation

Initially, so-called functional explanation was in the foreground, the explanation of the existence of a functional agent with recourse to its effect: hearts *exist because* they pump blood. Carl Gustav Hempel (1959) examined whether this could be a valid explanation by linking the statement to the schema of deductive-nomological explanation. According to this schema, a state of affairs is explained if it can be deduced from general laws, taking into account the specific circumstances according to schemata of logical reasoning.

Applied to the explanation of the existence of a heart, this schema could generate the following syllogism:

All normal vertebrates have circulating blood.
All hearts cause blood circulation.
Fido is a normal vertebrate.

Fido has a heart.

However, as Hempel states, this is not a valid inference since blood circulation could also be produced in another way. At best, one could conclude that there is an element of the class of entities that cause blood circulation, but this is not very informative and does not explain the existence of a heart.

Ernest Nagel (1961) takes up the problem in a similar way. His approach is to identify the trait to be explained as a necessary condition for the occurrence of the observed phenomenon. The presence of chlorophyll is a necessary condition for the process of photosynthesis, which is why the presence of chlorophyll can be inferred from the presence of photosynthesis. However, functions can in principle be realised in different ways, so that the assumed necessity exists neither logically nor physically. And indeed, the antenna complex, to which the largest part of chlorophyll belongs, is realised in e.g. cyanobacteria by means of other pigments. Even the reaction centre can consist of a pair of bacteriochlorophyll molecules instead of a pair of chlorophyll *a* molecules (Niel 1932).

3.2 Etiological concepts of function

After the failure of attempts to justify functional explanations, philosophical interest shifts to explicating the concept of function according to the intended use of the entity in question. An explication replaces the broad spectrum of meanings and connotations of an originally imprecise and enigmatic concept with an exact concept of lesser scope. There is no one correct explication to set alongside wrong or misguided ones; rather, different ideas of what is to be understood by a function manifest themselves in different explications. Thus, the same explication can be considered appropriate or inappropriate depending on the philosophical position.

The greatest influence on the debate has been developed by approaches that consider a certain causal history (etiology) as a condition for functionality. In these, the notion of functional explanation continues to play a role. This is particularly clear in Larry Wright's work (1973), which is considered the archetype of etiological approaches. Wright explicates the meaning of the statement "The function of X is Z" with a two-part definition of the concept of function, in which the functional explanation appears in modified form as the first condition.

> The function of X is Z *means*:
> (W1) X is there because it does Z;
> (W2) Z is a consequence (or result) of X's being there (Wright 1973: 161).

In the connection between the two conditions a cyclical causal structure becomes clear which Kant had already pointed out: X causes Z (W2) and Z causes X to exist (W1). X thus apparently causes itself or brings itself about. This requires explanation. For example, the following evolutionary description is considered a plausible interpretation: hearts move blood around the body, and hearts are present today because they also moved blood in earlier organisms. According to this evolutionary-biological interpretation, the "it" in (W1) cannot refer to the concrete X that is currently being considered. At most, predecessors of the same type can have causally contributed to the existence of the feature currently under consideration. The accomplishment of Z, on the other hand, is a consequence of both the earlier X and the X currently under consideration.

Karen Neander (1991) develops Wright's approach by clearly distinguishing – with the help of Peter Strawson's (1959: 231) generalisation of an idea of Charles S. Peirce (1906: CP 4,537) – between trait types ('type') and the occurrence or instantiation of a trait ('token') and clarifying the causal relations at hand with explicit reference to a mechanism of evolutionary adaptation. An effect of a trait is, according to Neander, precisely its function or one of its functions if, due to this effect, it is an instantiation ('token') of a trait ('type') that has been positively selected in the evolutionary process. The selection of a type, which is an abstraction, is of course based on causal interactions of *concrete* traits, i.e., of earlier instantiations of the type. Neander thus succeeds in resolving the ambiguity that was left by Wright: a given instantiation of a certain trait exists because traits of this type produce effects of a certain type, and because these have contributed to the survival of individuals that had instantiations of this type.

Ruth Millikan (1984) chooses a different way to resolve the type-token problem. She transforms the etiological approach entirely to the level of tokens and describes the connection between past and present concrete traits without recourse to the affiliation to a common type. She does this – closely following what has been described as Darwin's 'population thinking' (Mayr 1959) – by looking at populations and lineage relationships. Concrete organisms descend from other concrete organisms, so that a population in its temporal development can be viewed as a reproductive family. Belonging to the same reproductive family replaces in population thinking the classification of organisms by types defined in terms of properties. Millikan transfers this idea to traits. She considers as functions those effects of the respective biological traits of a reproductive family on account of which these traits have been selected, i.e., have been preserved in the evolutionary process. In short, functions are selected effects or selected roles of components of a system.

However, traits of organisms arise from other traits only indirectly by reproduction. There are no families of reproducing hearts or kidneys. In order to make her specification of Wright's approach rigorous, Millikan therefore goes to some conceptual lengths. Crucially, she introduces the concept of the reproductively established family (REF): Although the hearts of the animals of a given species do not form a reproductive family, their family membership is reproductively *established*. It is established via the reproduction of the animals that carry that trait.

In contrast to Neander's approach, the structural sameness of hearts, for example, is thus not a classification criterion that could be used to justify functional statements but merely a consequence of lineage relationships (Millikan 1984: 20). Accordingly, Millikan defines a notion of 'proper function': The proper function of a member *m* of a REF is that effect or systemic role of the members of a REF that was exercised by ancestors of *m*, and the exercise of which had a causal influence on *m* being produced (simplified after Millikan 1984: 28).

A major advantage of etiological approaches is that they can explain the normativity of the concept of function: Selection history sets the norm against which to measure whether a trait is functional or dysfunctional. Sometimes, however, it has been disputed that this goal is actually achieved (Prior 1985; Davies 2000).

The etiological approaches have been modified in different ways. According to the "recent history approach" (e.g., Peter Godfrey-Smith 1994), only the recent selection history is relevant for a function. A former role of a trait that no longer contributes to selection loses its status as a function. According to Millikan, the trait would become dysfunctional. However, in the "forward looking view" the evolutionary future of a trait is considered instead of its evolutionary past. A function would then be such a contribution of a trait to an organismal capacity that contributes to the reproductive success of the organism and to its genetic contribution to future generations (Bigelow/Pargetter 1987). This allows a new trait to be considered functional at its first appearance, even though it has not yet contributed to selection at that time.

The problem with etiological theories of function is that only adaptive processes are accepted as generating functions. While this corresponds to the long-prevailing picture of evolutionary processes, it ignores more recent developments in evolutionary theory. The sole relevance of adaptive processes has already been disputed by the neutral theory of evolution, which emphasizes the relevance of genetic drift for evolutionary processes (Kimura 1955). However, neutral drift alone can probably not explain the establishment of functions. More important is that the "Extended Evolutionary Synthesis" questions, with good arguments, that reproduction of traits is due to an organism's genome alone. It abandons gene-centrism in favour of a consideration of organism-environment interaction and a consideration of epigenetic and, where appropriate, environmentally and culturally mediated inheritance (Odling-Smee 1988; Odling-Smee et al. 2003; Laland et al. 2014; Sultan 2015; see below, section 3.5). Therefore, a family of traits cannot be established reproductively alone, provided that reproduction is understood as a copying process in Millikan's sense.

3.3 Functional analysis

Robert Cummins (1975) explicates the concept of function by recourse to the role that a component plays in a system. The organism is viewed as a system of interacting subsystems that perform specific services and are themselves made up of components. To explain a system or subsystem capacity, it is usually necessary to examine the interaction of several components and their respective contributions to the overall capacity. Cummins refers to such a contribution to a system capacity as functions of the components under consideration. In contrast to etiological approaches, in this systems analysis approach the function thus results solely from the embedding in a system, without its causal history playing a role:

> *x* functions as a *Φ* in *s* (or: the function of *x* in *s* is to *Φ*) relative to an analytical account *A* of *s*'s capacity to *ψ* just in case *x* is capable of *Φ*-ing in *s* and *A* appropriately and adequately accounts for *s*'s capacity to *ψ* by, in part, appealing to the capacity of *x* to *Φ* in *s* (Cummins 1975: 762).

To explain Cummins' formula using the standard example: in a given dog, the heart functions as a blood pump (i.e., one function of the heart in that dog is to pump blood) relative to a physiological analysis of the dog's capacity to supply oxygen and nutrients to its peripheral tissues if and only if it can pump blood in that dog and the physiological analysis of the supply to the peripheral tissues appeals to the heart's ability to pump blood to appropriately and adequately account for this capacity.

The instrumentalist aspect of Cummins' approach, that functions are not out there in the world, but rather depend on our analyses of the world, is often seen as problematic, but secondary. In contrast to the representatives of etiological approaches, Cummins is thus not a function realist. Regardless of whether instrumentalism with regard to functions is fundamentally welcomed or rejected, it is important for Cummins' approach because it compensates for a shortcoming of the systems analysis approach: its lack of selectivity. Physical and chemical systems can be analysed functionally, as can technical artefacts and organisms. The sun can be said to have the function of forcing the earth into an elliptical orbit and supplying it with light, a stone in a streambed the function of eddying water. Cummins tempers this arbitrariness precisely through his instrumentalism – although this seems at first to add to the arbitrariness. For in cases where functional analysis does not yield any additional knowledge, as in the case of the solar system, no one will propose such an analysis. However, this is not ruled out. For this reason, Amundson and Lauder (1994) modify Cummins' approach and remove the arbitrariness of the ascription of function. As function realists, they assume that system capacities in organisms exist objectively and independently of the existence of an analysis. However, unlike Cummins' approach, this presupposes that organisms can be shown to be ontologically distinct from other systems.

It is true for every concept of function in systems analysis that they are non-normative. This means that the concept of function escapes the suspicion of teleology. However, the possibility of talking about dysfunctions is thereby lost.

3.4 Cybernetic and organisational concepts of function

A third class of philosophical concepts of function has its roots in 20th century debates, although the most thorough elaboration of this is more recent. Here, too, the criterion for functionality is not the history of a trait, but its integration into the organism. Thus, these organisational or cybernetic concepts of function are close to the concept used in functional analysis. Unlike in the latter, however, strict requirements are placed on the system in order for it to be considered functionally organised. Its components must be mutually dependent on each other in the sense that they produce and maintain each other reciprocally (without a heartbeat there is no formation of the liver and without a liver there is no continuous heartbeat), i.e. they are subject to the cyclical causality thematised by Kant (see section 2.3). However, in contrast to Kant's approach of a regulative idea and to the instrumentalist status of functions in the functional analysis approach, many cybernetic and the organisational approaches consider functions to be real.

According to these approaches, functionally organised entities must be causally closed. Exactly this is what makes an organism. Causal closure includes regulating loops, especially feedback loops, as described by cybernetics (Rosenblueth et al. 1943; Weaver 1948). However, the cybernetic approach alone does not provide a sufficient basis for modelling living organisms (Collier 2011). To this must be added the aforementioned reciprocal production, which was emphasised as a central aspect of "living beings" by Aleksandr Ivanovich Oparin (1956) as well as Eduardo H. Rapoport and Osvaldo Rapoport (1958: 24). Rapoport and Rapoport refer to living beings as "bio-regenerative systems" (ibid.: 6–7 et passim), Gerhard Schlosser (1998) and Peter McLaughlin (2001) call them "self-reproducing systems". This term takes up the view of the organism as a system that maintains its integrity itself to a considerable extent and can also restore it after a disturbance (Maturana/Varela 1987). Robert Rosen models these systems with the concept of (M,R)-systems (Rosen 1966; 1971), which aims at a formal description of such self-maintenance (Letelier et al. 2006).

In the currently most prominent approach of this kind, developed by Matteo Mossio, Cristian Saborido and Alvaro Moreno (Mossio et al. 2009; Moreno/Mossio 2015), the integrity of an organism is referred to as "organisational closure". In an organisationally closed system, every component plays a role in the maintenance of the whole, and at the same time the whole is necessary for the existence of the components. This approach can be read as a resolution of Wright's conditions for functionality, which is an alternative to Millikan's and Neander's specifications. (W1) "X is there because it does Z" and (W2) "Z is a consequence (or result) of X's being there" are here interpreted organisationally rather than historically. Functions are then precisely those effects of traits that contribute to the organisational closure of an organism.

One consequence of the reference to closure is that components of a living being that do not serve its self-maintenance do not belong to the organism and have no function. In particular, the reproductive organs would be considered functionless. This applies to the organisational approach as well as to Kantian-influenced approaches in general (Toepfer 2004; 2012). To avoid this criticism, the proponents of the organisational approach understand functions not as a contribution to the self-preservation of a *system*, but to the perpetuation of the *organisation* of the system. If one considers small time steps, the vital organs of an organism contribute to new instantiations of its organisation at each new point in time. If one chooses larger time steps, the reproductive organs contribute to new instantiations of the closed organisation of the parent organisms in the descendants. Therefore, they are functional in the same sense as the organs maintaining an organism (Saborido et al. 2011).

However, discussing this issue at the level of instantiations obscures the fact that vital organs and reproductive organs play different roles with respect to organisational closure. Closure *consists in the interplay* of life- or system-maintaining functions. In the quasi-stroboscopic view of the organism proposed by the authors, this merely *results in new instantiations* of the organisation at each new point in time. Reproduction, on the other hand, *consists in newly instantiating* the organisation. *Only if* the organisation of the predecessors is closed, the reproduction *results in* closedness of the reproduced organisation.

3.5 Concepts of function in 20th century biology

The physiological disciplines within biology, from molecular genetics and biochemistry to the classical physiology of tissues and organs and functional anatomy to behavioural physiology, each investigate the functions of structures and processes. Central to this research are the questions of what a structure does and what a process contributes to. If an effect is found that can be understood as a contribution to a broader process such as a metabolic pathway or to a higher-level capacity of the organism or one of its subsystems, it is designated as a function. This concept of function, which is predominant in the physiological literature, is thus similar to the concept used in systems analysis (Krohs 2004: 8–11; Wouters 2013). However, in contrast to Cummins' approach, it also allows for the ascription of dysfunctions (Krohs 2004: 195–196). Usually this does not require reference to the evolutionary origin of the structure or even generally investigating it. The evolutionary origin is assumed, but can at best claim heuristic value in the search for physiological functions and pathophysiological states. Conceptually, it is irrelevant. In palaeontology, too, ascribing functions is a matter of the inferred interaction of morphological traits. Here, likewise, the selection process is not used to explain function, but selection is seen as dependent on functions.

Similarly in the classical evolutionary biology of an adaptationist sort and in the classical behavioural biology committed to it, functions are attributed according to physiological criteria. The preoccupation with the central question of the adaptive value of a trait, which, according to Niko Tinbergen, seeks to determine its function (Tinbergen 1963: 8), asks, like the etiological approaches, about the conditions of selection. In contrast to etiological theories, however, functionality is not based on selection, but rather the opposite is assumed, i.e. that anything that has a function is evolutionarily selected. The explanatory direction of the answer to Tinbergen's question thus runs counter to that of the etiological concept of function: The function adopted by a structure is considered to precede its selection history. The trait morphologically adapts to its function in the processes of mutation and selection and thus improves its performance. Nevertheless, Tinbergen sees the teleological aspect of an ascription of function as justified by the history of selection. Selection determines what a trait is for (ibid.).

Newer approaches emphasise that, in addition to mutation and selection, other mechanisms contribute to evolution. On the one hand, there are exaptations. These are traits that initially have no function, but then take on a function in a new environment to which they happen to fit, without being adapted to it (Gould/Vrba 1982). On the other hand, as representatives of the Extended Synthetic Theory of Evolution emphasise, the development of an organism can be systematically modified by environmental influences and these new ontogenetic pathways can also lead to new functions. Through the organism's influence on the environment (so-called "niche construction") these influences can even be generated by the organism itself and maintained for subsequent generations (Odling-Smee et al. 2003; Laland et al. 2014; Sultan 2015; cf. section 3.2). Accordingly, the evolutionary history of a trait need not be exhausted in its selection history.

4. Recent developments: return of the concept of function in biological theories

The explications of the biological concept of function presented in sections 3.2 to 3.4 are each committed to a particular understanding of biology. Etiological concepts of function are committed to the image of adaptationist evolutionary biology. The systems-analytic approach focuses on the analysis of physiological capacities of the organism. Cybernetic and organisational approaches consider the contribution to the self-preservation of the organism (or even: of its organization) as the criterion for functionality. Biology, however, is multifaceted and biological theories change and evolve. Therefore, there has been a call to reconstruct the concept of function in such a way that its respective uses in different biological theories can be captured. Etiological accounts serve as a starting point for such expansions. They had temporarily found such wide acceptance that there was talk of a “near consensus” (Godfrey-Smith 1993). Alternatives have since been developed that consider Millikan’s proper functions to be at best a special case of the concept of function that is influential in the specific theoretical context of adaptationism, but which inappropriately entrenches the basic assumptions of what has come to be regarded by many as a one-sided approach. The following three approaches or classes of approach each contradict Millikan in different respects.

4.1 Generalised etiology: from selection in evolution to mechanisms of selection in general – and further to mechanisms of retention

The dependence of etiological functions on cross-generational criteria prevents individual elements of ensembles of similar components (such as nerve cells or synapses), each of which plays a different role in the organism, from being ascribed their respective specific role as a function. A particular synapse may have the proper function of transmitting signals, but not the specific function of, e.g., enabling the detection of vertical edges in the visual field through feedback or contributing to the detection mechanism for yawning in a mirror neuron network. It is true that the existence of a concrete synapse can also be described as the result of a selection process that takes place during the development of the brain: During this development all possible synapses are initially formed and only the functionally relevant ones remain. However, the concept of proper function does not apply here, because its applicability would require the synapse under consideration to belong to a REF whose members all take on the same role. Yet the roles of neurons and those of their synapses in the cases considered here are specific. Synapses contributing to a particular capacity are recruited anew in each brain; so the neuronal realisation of the capacity and thus the functional contributions to it differ individually. There are no REFs for synapses of these different specific functions. Although the synapses as a whole form a REF and have (activating or inhibiting) signal transmission as their general proper function, ascribing their respective specific functions within Millikan’s approach therefore fails.

For this reason, Justin Garson (2019) extends the theory of selected effects to a “generalised selected effects theory” (GSE) and complements the requirement of differential reproduction with a second, alternative selection mechanism, that of selective retention: a synapse that has been selectively retained because it plays a specific role thus acquires the function of performing that role. This criterion captures neurophysiological (and, where appropriate, other) ascriptions of function within the framework of an etiological approach that has been somewhat expanded from Millikan’s and Neander’s model. The expanded definition of the concept of function is – leaving aside definitional stipulations about REFs or their analogues: “A function of a trait is an activity that led to its differential reproduction, or its differential retention, in a population” (Garson 2019: 93)

Different synapses may have been retained because of quite different roles they occupy in their respective contexts. Thus, Garson’s GSE can also attribute quite different functions to them, for example, the contributions to detection mechanisms already mentioned. GSE thus enables a differentiation of functions far beyond the realm of Millikan’s proper functions. In this way, it also does justice to the practice of function ascription in brain research and the cognitive sciences.

It should be borne in mind, however, that the definition cited above links two alternatives with an “or”, i.e. it is disjunctive. The desired extension of the concept of function may be achieved in this way. But the question arises, firstly, whether the two disjuncts actually describe a *uniform concept of function*, or whether two different, possibly related concepts are merely being taken as synonymous. Secondly, it remains open whether the definition is now complete or whether further disjuncts can always be added as needed. There would be a large number of candidates for further disjuncts: Should differential growth not also be considered as the basis of an ascription of function and does the differential elimination of some types of programmed cell death not also reveal a function?

The fact that we are dealing with *one* concept and not an amalgamation of two concepts under the same term would have to be ensured by a unification of the definition. In the case of the two disjuncts in Garson's definition, such a unification could be found by considering the differential reproduction of the carrier of a proper function at the type level. On this level, it is in fact a retention. This shows up already in Darwin's description of natural selection as a "principle by which each slight variation, if useful, is preserved" (Darwin 1876: 49). Abandoning Millikan's limitation to tokens, Garson's definition can thus be unified as follows: "A function of a trait is an activity that led to its differential retention in a population".

4.2 Instrumentalist and theory-relative notions of function: from metaphysical presupposition to recognition of theory change

The majority of philosophers dealing with the topic want to understand the concept of function both teleologically and realistically: It should be possible to distinguish between function and dysfunction, so that it can be meaningfully said that a trait *should* behave according to its function and that otherwise there is a dysfunction. This purposefulness should be understood as existing in the world and not as merely ascribed. The realists' endeavour is therefore to naturalise the teleological content, that is, to specify the conditions that must exist in the world in order for a teleological statement to be justified.

Some approaches, however, take a different path. They ask not about the realist content of the concept of function but about its epistemic role. When biologists ask about function they want to find out something about the organisation of a living being or even about the origin of its traits. The question "What is it for?" structures their research (Ratcliffe 2000). If a self-regulatory picture of the organism is assumed, it is heuristically valuable to ask what purpose a component serves in this system – even without presuming that something in nature corresponds to this "serving". The project has achieved its goal when it can be clarified what role a component plays and how it contributes to the integrity of the living being or to one of its capacities. The question of function is answered before we have to look at whether the function bearer actually *should* do this. The latter question cannot be answered biologically. The answers typically offered in fact transform the question: It does *f* and it has also been selected to do *f*; it is adapted to do *f*; only when it does *f* does the integrity of the organism remain intact; and so on. Matthew Ratcliffe (2000) rightly sees himself as close to Kant with his instrumentalist approach. Because like Kant, who instead of teleology only allows for a teleological *judgement* that facilitates the understanding of organised beings, Ratcliffe maintains that questions about functionality have a role in the research process, but are not answered by demonstrating real teleological functions.

However, biological theories are often not as neutral or purely descriptive as Ratcliffe's reconstruction of the language of functions implies. In many cases they refer to norms. In molecular genetics, we speak of "reading errors" and "correction functions". Neoplasms, among other things, are explained as being based on faulty regulation, while organs are regarded as dysfunctional in the case of clear deviation of their performance from statistical mean values. Biological theories underlying such normative characterisations are usually interpreted in realistic terms, especially in the field of molecular genetics (cf. Rosenberg 1993, who incidentally takes an instrumentalist view on large parts of biology).

However, this normative role of statements about function in biological theories can also be taken into account without making ontological commitments that are independent of theory. Indeed, if reference to trait types can be included in Cummins' instrumentalist approach, this approach can also account for the normative dimension of the concept of function (Godfrey-Smith 1993). In addition, the standard must also be set, for example in a design or a plan of the organism (Kitcher 1993).

Now, the question of what is the design on which an organism is based has been answered differently by different biological theories. First and foremost, the genome has been considered, but also regular interactions with the environment, including the social environment.

In some colony-building insects, for example, the diet, which may depend on the position of a honeycomb cell in the hive, is one of the factors that determines the development of the individual and is, as it were, part of the design. It is no longer a question of nature or nurture but of the interplay between them that is necessary for every developmental process (Keller 2010; Goldhaber 2012).

However, the plan-like nature of the genome or of larval feeding is not something that "by itself" has the character of a plan. Admittedly, adaptationism in the form of genetic determinism treats parts of the genome as a plan. But first of all, DNA is simply a macromolecule with a complex structure of recurring elements, the nucleotides. The metaphors of the plan and the template seem to fit very well. However, their epistemic value is not dependent on a realist interpretation, so that their use does not entail any ontological obligations (Krohs 2014: 95 f). Within the adaptationist approach, however, the DNA sequence is conceptualised as a plan. Thus, by tying her concept of function to this metaphor via reference to REFs, Millikan explains how adaptationism understands the design that determines the components of an organism. If, on the other hand, the contribution of the environment to the generation of form is emphasised, as in the Extended Synthetic Theory of Evolution, this approach can be seen as overly narrow. Ulrich Krohs (2009; 2011) therefore suggests that the concrete sort of design should not be fixed in the definition of the concept of function. According to him, the function of a trait is the role it plays according to the design of the organism. What exactly the design consists of, however, is not explained by the philosophical reconstruction of the concept but by the respective biological theory. Thus, the concept of function is defined in a theory-overarching manner, but its respective scope is nevertheless theory-dependent. Since the norm of a function is prescribed by the design while it depends on the respective biological theory what counts as design, the teleological part of the concept of function is theory-dependent. Therefore it cannot be understood in realist terms. The approach thus incorporates the possibility of theory change and in this sense remains instrumentalist or relativises ontological statements to the respective biological framework in the sense of a "metaphysics of scientific practice" (Ankeny et al. 2011). This specifies the view that the assumed normativity of functions merely expresses justified expectations of the functionally described biological processes (Franssen 2009) by making explicit that these expectations may depend on the respective theoretical framework.

Instead of such a unifying approach, a relativisation of biological functions to theoretical perspectives has also been developed in the form of a pluralism of the concept of function. The norms of function are construed as only being valid within each perspective, so that the overall picture only emerges from the integration of these perspectives, which are not necessarily compatible with each other (Cusimano/Sterner 2019). The approach allows for different perspectives to refer to their own reality without assuming a reality that transcends perspectives.

5. Relationship to non-biological concepts of function

Not just biological systems are described as being functionally organised, but also technical artefacts and social systems. Admittedly, with the understanding of function as a contribution to a higher-level performance there is an aspect of functionality that is relevant in each of these three fields, and the explanatory roles of the concept of function are largely analogous in each (Mahner/Bunge 2001). However, norms according to which function and dysfunction are demarcated from each other seem to be field-specific. Since hybrid forms such as biotechnical or socio-biotechnical systems located between the aforementioned fields are also analysed from the viewpoint of functionality, different sorts of norms can play a parallel role in such systems (Krohs/Kroes 2009).

5.1 Social and technical functions

Talk of the functions of social institutions was already established with structural functionalism in the first half of the 20th century. Here, a function is seen as a systemic role in its value for the stability and continued existence of the social system (e.g. Radcliffe-Brown 1940). The assumed goal of stability is established in social systems not as it is for Millikan in relation to organisms, through selection, but through the development and persistence of the system. The writings of the structural functionalists thus contain reflections on a normative concept of function that precede the debate in the philosophy of biology, though they are barely taken into account by the latter.

The technical concept of function, on the other hand, was long considered unproblematic (e.g. Wright 1973), so that it was referred to as an example in the debate on the biological concept of function (Millikan 1984; Kitcher 1993). In fact, however, with a few exceptions (Achinstein 1977: 350), it was scarcely addressed philosophically at this time (cf. Krohs/Kroes 2009; Artiga 2016). Later, reflections on the technical concept of function conversely took up proposals from the biological debate.

It turned out that Millikan's requirements for the etiology of function bearers are too strict and often inappropriate for the field of artefact functions. For example, in artefacts, often manufacturing processes rather than structures are copied, as in some techniques of basket weaving. Or users ascribe different functions to artefacts than the manufacturers do, without this needing to be relevant to selection (Preston 1998; Vermaas/Houkes 2003). Function in the sense of systemic role plays a part in each case. The differences relate to the normative aspect of functions (Preston 2000: 32).

Wybo Houkes and Pieter E. Vermaas (2004; 2010) develop an independent technical concept of function. Their approach takes up aspects of biological concepts of function, but places the intentions of designers and users at the centre of ascriptions of function via the concept of the "use plan": (i) The original function of a technical artefact is the role and purpose that the designers intended the artefact to have. However, a user can (ii) develop a new use plan. Thus, he or she can justifiably ascribe a new function to the artefact. Someone looking at the function from an analytical perspective may (iii) again recognise a different use plan in the use of the artefact and therefore justifiably ascribe yet another function. Thus, for example, mosquito traps that work with UV light may be attributed by designers and users with the function of reducing the number of mosquitoes at garden parties. From an analytical perspective, however, it may turn out that they do not fulfil this function at all and actually increase the density of mosquitoes. The latter would therefore be their – unintended – technical function. (Nevertheless, the traps could have the social function of reassuring partygoers about the risk of mosquito bites.) The dependence of function on intentions and use plans shows that technical functions are, according to this conception, ontologically subjective. However, this does not mean that ascriptions of function are arbitrary. In the so-called ICE theory of technical functions by Houkes and Vermaas, the conditions for ascription are precisely stated. Despite ontological subjectivity, they are thus epistemically objective (cf. Searle 1995).

In order to accommodate the three instances of ascription mentioned above, separate definitions must be drawn up in each case. These, in turn, have two or three parts: one definition each is given for (i) designers or justifiers, (ii) passive users and (iii) analysts, in which the (I) intentional, (C) causal and, in the case of passive users, (E) etiological conditions for a justified attribution of function are specified (Houkes/Vermaas 2010: 100).

Just one of the three definitions will be considered here by way of example. For the passive user, who does not develop his or her own use plan but takes over that of the designer, the following definition is given (ibid.): A passive user *u* justifiably ascribes the physicochemical capacity to *φ* as a function to an artefact *x* relative to a use plan *p* for *x*, and relative to testimony T, iff [if and only if]:

> (I.) *u* has the belief B_{cap} that *x* has the capacity to *φ*; *u* has the belief B_{con} that *p* leads to its goals due to, in part, *x*'s capacity to *φ*; *u* believes that a designer *d* or justifier *j* of *p* has B_{cap} and B_{con};
> (C.) *u* can justify B_{cap} and B_{con} on the basis of T; *u* can justify on the basis of T that *d*/*j* has B_{cap} and B_{con}; and
> (E.) *u* received T that *d*/*j* has B_{cap} and B_{con}.

The use plan is therefore applied by the user with the conviction that it will contribute to achieving a certain intended goal (I). This conviction of the user can be justified on the basis of a testimony that the developer has this very conviction (C), whereby the user has indeed received this testimony (for example in the form of an instruction manual) (E).

The authors assume that every case of ascription of technical functions falls under one of the three definitions and thus this three-case distinction fully captures the spectrum of such ascriptions.

5.2 Integration of biological, technical and social functions

In principle, the integration of biological and technical functions is possible by expanding the cumulative concept of technical functions (Vermaas 2009). However, it seems questionable whether such a formally integrated concept of function can be regarded as unified.

The approach of Riichiro Mizoguchi, Yoshinobu Kitamura and Stefano Borgo (2016) strives for a unification that goes beyond a sum of case distinctions, as offered by the ICE theory or as the sum of specific biological, technical and social concepts of function could offer. Unification is achieved here via the systems analysis approach, which represents the lowest common denominator, as it were, of concepts of function from all the disciplinary fields. Field-specific differences are considered as goals within the specific systemic context. Systemic functions should refer to the “needs of the systems to survive” (ibid.: 131) in the case of biology, and in the case of an artefact to the roles assigned to it and thus to the intentions of designers and users (ibid.: 152). The field-specific functions are thus dependent on goals of different kinds. The associated ontologisation of goals, however, raises once more the question of an appropriate naturalisation, here the naturalisation of goals. This naturalisation is neither achieved nor even addressed by the authors. Such an undertaking would doubtless be no less difficult than a naturalisation of functions, since the concept of function encompasses precisely the least demanding goals that can be attributed to living beings or their components. The attempt at unification via systemic functions thus at best captures a common basis of ascriptions of function in different fields, but cannot satisfactorily capture its normative aspect.

Instead of ontologising purposes, these can also be considered as – perhaps even necessary – presuppositions of the respective discipline or theoretical framework. In 4.2 it was shown that the commitment to type-fixing instances (templates, plans, regular environmental influences, intentions) can be reconstructed as a respective ontological presupposition internal to the theory.

5.3 Open questions

Some fundamental questions about biological functions are answered differently by the various approaches presented above:

(i) Are biological functions ontologically independent, i.e. do they “exist” in the world independently of our ascriptions, or are they ontologically dependent and rely on our conceptualisation of living beings, on how we structure the world for ourselves?

(ii) Do biological functions and other specific forms of functions fall under the same generic term, or are biological, technical and social functions so fundamentally different from each other that they are merely designated the same on the basis of superficial similarities?

(iii) Are biological functions teleological, i.e. do they “serve” something, or are they to be regarded merely as processes or as dispositions to enter into certain processes, but not related to a norm?

The points raised in these questions must be considered as still open. Higher-level arguments may come to different conclusions regarding each of the three questions, which is why it seems unlikely that the questions can be satisfactorily answered individually. It is more plausible to assume that the problem of biological functions will not be considered to be satisfactorily solved until an approach convincingly connects all three questions in such a way that they can be answered together. One such attempt has already been discussed in section 5.2, namely to identify functions as (ii) unified (namely systemic), (iii) teleological (namely related to field-specific goals), and (i) ontologically independent (Mizoguchi et al. 2016). This approach can capture the goals of technical and other intentional functions, but fails because it cannot explicate those of biological functions. In general, attempts at unification seem to fail as soon as the concept of function is regarded as ontologically objective (Weber 2017).

Approaches that (ii) assume a pluralism of concepts of function can (iii) answer the teleology question differently for each of the different disciplinary fields and, for example, as Preston (1998) does, reconstruct technical functions as teleological and biological functions as non-teleological. If unification within fields is abandoned, the teleology question can even be answered differently for different classes of biological functions (Wouters 2003; Cusimano/Sterner 2019). An even more flexible approach to the concept of function is permitted by the highly differentiated pluralism advocated by Mark Perlman (2004). For him, pluralism does not primarily consist in a distinction between disciplinary fields of application or subject areas, but rather in the nature of the concepts of function themselves, which exhibit numerous other differences than those discussed here. Perlman accepts all the reconstructible differences between the explications of the concept of function found in the debate, but at the same time does not commit himself to the idea that an ontologically definable class of phenomena corresponds to each of them. Thus, at least with regard to many of the distinctions, his position presupposes at best epistemic but not ontological objectivity. This view is nevertheless compatible with (i) the ontological independence of functions, insofar as the class boundaries, but not the phenomena themselves, are regarded as constructed.

Even the recognition of ontological subjectivity, however, does not rule out the possibility that there may be non-epistemic standards for the ascription of teleological functions that enable reliable strategies for such ascriptions to be pursued (Sullivan-Bisset 2017). This can be seen in the type-fixation approach (Krohs 2009; 2011) which is both (ii) unifying, and (iii) recognises the normativity of statements about function, while abstaining from ontological statements about these functions, assigning their respective theory-dependent answers to the metaphysics of scientific practice. The ontological presuppositions are regarded as field-dependent. However, it is precisely this that allows the concept of function to be explicated in a unified way: under the respective presuppositions, the unified concept of function as type-fixedness acquires its respective field-specific form. This approach identifies biological but also social and technical functions (since these depend on the intentions of agents) (i) as ontologically dependent. This is in contrast to the widespread attitude of function realism, but does not entail any epistemic disadvantages. Moreover, the position avoids the reproach of reconstructing the physical world teleologically, which function realism has to face.

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