Note on the individuation of biological traits

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In 2010 Bence Nanay has argued that we ought to abandon the etiological theory of teleological function, because it is circular. The etiological theory explains the function[1] of hearts in terms of hearts being selected for pumping blood; but hearts are only hearts because they have the very function to be explained. We can make the alleged circularity more explicit if we look at the following two explanations:

Explanandum 1 H has the function to pump blood. (where H is an individual heart)

Explanans 1 H is a heart, and hearts have been selected to pump blood.

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[1]For brevity this article will often refer to teleological functions simply as 'functions.' The article will not use the term 'function' in any of its other extant senses.

Explanandum 2 *H* is a heart.

Explanans 2 *H* has the function to pump blood.

Notice how Explanans 1 contains Explanandum 2, which is explained by Explanans 2, which in turn is identical to Explanandum 1. Thus Explanans 1 is partly explained by Explanandum 1, and the explanation is circular.

A similar argument is given by Paul Griffiths,[2] but to a different conclusion. Whereas Nanay concludes that the etiological theory is mistaken, Griffiths concludes instead that we should analyze teleological functions not in terms of teleo-functional categories such as 'heart,' but always in terms of homological categories such as 'vertebrate heart.' (Vertebrate hearts still have a function, of course, but Griffiths maintains that it is possible to identify them non-functionally.)

In 2012 Karen Neander and Alex Rosenberg have replied to Nanay along lines reminiscent of Griffiths' – though not quite identical. Neander and Rosenberg contend, in our terms, that Explanans 1 does not need to talk about hearts as such; instead, it only needs to talk about the homological lineages that particular hearts came from:

Explanandum 1 *H* has the function to pump blood.

Explanans 1' *H* comes from a lineage of organs that have (recently) been selected to pump blood.

Explanandum 1 is now free to explain Explanandum 2 without circularity.[3]

Nanay objects, to Neander and Rosenberg, that "lineages themselves could not be identified without talking about trait types" (2012:624). That is to say, my heart *H* is on the same lineage as my ancestors' hearts H_1, H_2, etc. precisely because H_1, H_2, etc. are my ancestors' *hearts*. Thus, according to Nanay's objection, we are back to circularity: function is explained

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[2] 1994, p. 213 and 2006, pp. 18–20.
[3] A similar reply to Nanay is given by Brian Leahy and Maximilian Huber in 2017.

by selection pressures on lineages, lineages are explained by trait types, and trait types are often explained by function.

Nanay's claim about lineages is not without precedent; it may seem, at first, to receive support from a series of arguments that stem, as it happens, from an earlier Neander and Rosenberg. These arguments are intended to show that (some) homological categories depend constitutively on teleological functions. As I will argue, however, even if the earlier Neander–Rosenberg arguments were right, we can still adopt and defend the 2012 Griffiths–Neander–Rosenberg reply to Nanay.

Let me first outline the principal Neander–Rosenberg arguments for the metaphysical dependence of (some) homologies on functions. To be sure, these are not the only arguments they give, but they do seem to be the most worrisome.

Argument 1. In 2002, Neander argues that many homological categories are partly functional. For instance, take the gill arches of jawless fishes, which are famously homologous to reptilian jaw bones and to mammalian ear bones. Neander concedes to earlier arguments by Ron Amundson and George Lauder (1994) that these three trait types are subsumed under an overarching, purely non-functional homological category. She replies, however, that the three subcategories themselves have an essential functional aspect: mammalian ear bones, for instance, are typed not only by their shared phylogeny (which is also shared with gill arches), but also by their function in hearing. So at least some homological categories are delineated by functions.

Argument 2. (At least some) homological categories are 'abnormality inclusive,' i. e., they admit malformed instances (Neander, 2002). But what is malformed can only be determined by a history of natural selection. Hence every abnormality-inclusive homological category is implicitly teleo-functional.

Argument 3. Rosenberg and Neander concede to Griffiths (2006:8–9) that two phenotypic traits can be homologous even when controlled by genes that have undergone whole-

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sale evolutionary replacement. The two argue, however, that such homologies can only be explained – constitutively – by the new genes taking over the functions of older ones:

> How, after all, can an underlying molecular developmental pathway be judged to remain the *same* pathway to the *same* morphological structure, during a substantial or even largely complete turnover of its nucleotide sequence foundation? Shades of the ship of Theseus! (Rosenberg and Neander, 2009:322-23)

This article does not attempt to evaluate the three preceding arguments. Rather, the article aims for something both smaller and more precise: to show that these arguments do not threaten the Griffiths–Neander–Rosenberg reply to the circularity argument. We will leave it open whether the three arguments show, or do not show, that certain homological categories depend on functions. As I will argue, however, the lineages required to explain functions do not depend on these functions.

The key observation is simple: Sameness of lineage is a transitive relation. If A is on the same lineage as B and B is on the same lineage as C, then A is on the same lineage as C. This applies, for one thing, to entire trait types: if mammalian ear bones are on the same lineage as early tetrapod jaw bones, and if early tetrapod jaw bones are on the same lineage as jawless fish gill arches, then, of course, our ear bones are on the same lineage as the gill arches. More importantly, however, the principle also applies to concrete, particular trait tokens: If my kidneys are on the same lineage as those of my parents, and if my parents' kidneys are on the same lineage as those of my grandparents, then my kidneys are on the same lineage as those of my grandparents.

Not only does this principle hold as a matter of entailment, but it is also explanatory; we can explain the fact that A and B are on the same lineage if we point out that A is on the same lineage as its immediate precursor A_1, A_1 on the same lineage as its own immediate precursor A_2, and so on until B. What this means is that we don't need to worry about securing function-free homologies that connect my kidneys directly to those of a ten million year old primate!

All we need is to connect my kidneys to my parents', my parents' to my grandparents', and so on until ten million years ago. We can thus build a long lineage out of an uninterrupted chain of generation-to-generation steps:
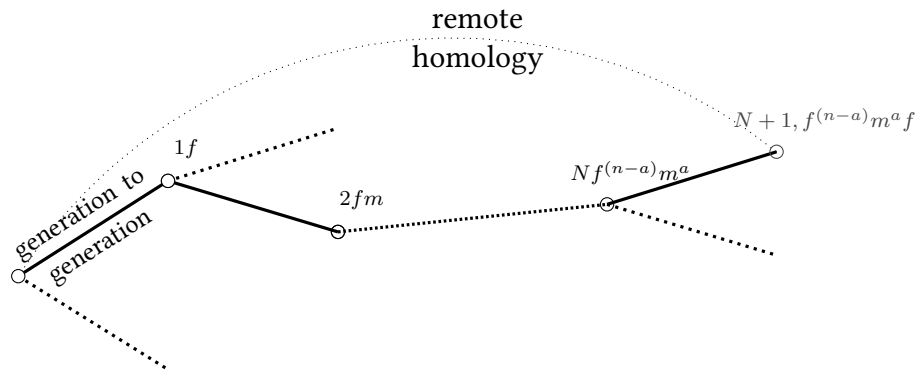
In the figure above, the leftmost node corresponds to my (left) kidney. The other nodes are labeled according to generation and maternal/paternal descent; for instance, node $2fm$ corresponds to the left kidney of my maternal grandfather. As we see, we can break down the remote homology between my left kidney and the one at $N + 1, f^{n-a}m^a f$,[4] into the generation-to-generation homologies between adjacent nodes. This is so even if generation N connects to $N + 1$ by virtue of a different explanation than the one by which, e. g., generation 100 connects to 101.

Let us now see whether these generation-to-generation steps are threatened by the three arguments we have seen above.

Neander's first argument concerns the individuation of trait types such as ear bones or jaw bones. While she maintains that such specific types have a functional component, she agrees with Amundson and Lauder that there is a broader, non-functional category that encompasses both ear bones and jaw bones, as well as their ancestral gill arches. What puts this broad category together? Not function, since there is no shared function, but rather the shared developmental pathways. Each animal in this lineage developed its traits because it inherited genes and other developmental factors from its parents. So even if it turned out that

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[4]This kidney belongs to my ancestor $n - a$ times on the maternal side, then a times paternally, then once more maternally.

we cannot define mammalian ear bones without mentioning their function, we do not actually have to define them at all! This is because all we need to explain is the simple fact that my ear bones are on the same lineage as my parents'. To this end, all we need is to point out that my ear bones came from developmental mechanisms inherited from those that produced my parents'. Such inheritance, in turn, can be explained in terms of non-teleofunctional, physico-chemical descriptions of gametes, genes, organelles, intercellular signaling, epigenetic switches etc. Of course, these physico-chemical descriptions may differ over long time periods, but they remain sufficiently consistent between consecutive generations. Once we have thus secured the phylogenetic link between one generation and the next, we can repeat the process for as many generations as needed.

Neander's second argument maintains that certain homological categories must involve functions, because they are abnormality inclusive. For instance, a malformed heart is a heart not because of its structure or morphology, which are, after all, malformed, but because it has the function to pump blood. Griffiths replies in 2006 that a malformed heart is a heart simply because of its origin, namely, because it was produced by the same developmental mechanisms that also make other hearts in that species. In 2009 Rosenberg and Neander reply to Griffiths that these developmental mechanisms only count as *the same* because they have the same functions (pp. 332–33). The two argue that developmental mechanisms themselves can vary and change quite a bit in time, so they cannot be typed solely by their changing structure and morphology; instead, they must be typed by their enduring functions.[5]

It seems, however, that Griffiths was right after all. Recall our main point that we only need lineages to be function-free generation-to-generation, and the rest will take care of itself. It may perhaps turn out that we cannot re-identify certain developmental homologies across different species unless we take into account their functions; and it may turn out that

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[5]To be clear, Rosenberg and Neander are not saying that we must type heart-making developmental mechanisms in terms of their function to make hearts, but rather in terms of some other functions. This, however, is an *a priori* hope that will not necessarily come true in practice. Nothing can promise us that no relevant developmental mechanisms will ever turn out to have functions that can only be specified by reference to what they eventually produce.

this is not only of epistemic, but also of metaphysical significance. Generation-to-generation, however, development does not change so suddenly as to make it impossible to re-identify its mechanisms in physico-chemical terms.

(To be sure, I don't take Griffiths to argue that mere homology can explain why a malformed heart is a *malformed* heart, but merely why it is a heart. To explain the nature of malformation, presumably, we need to avert to a background of selection; to explain the nature of malfunction, we certainly do.[6])

Let us now examine Rosenberg and Neander's 2009 argument. The argument is that when a developmental pathway changes so thoroughly as to involve completely (or almost completely) new genes, we can only re-identify this pathway if we talk about the genes' functions, functions that have stayed – at least at a high enough level – the same. But this argument, once again, can be met if we notice that we only need to re-identify the pathway generation-to-generation; the longer term identification will then take care of itself. Since a pathway doesn't flip over to novel genes in a single generation, the difficulty appears to be solved.[7]

Let us therefore sum up. Nanay has argued that we must abandon the etiological theory of teleological function because this theory explains functions and functional categories in a circular manner. Griffiths had argued earlier that we should retain the etiological theory, but make etiologies independent of functional categories, precisely in order to prevent the circularity. Neander and Rosenberg reply to Nanay on similar lines, and argue that we don't need to analyze functions in terms of natural selection acting on functional categories, but merely in terms of natural selection acting on lineages. Nanay replies to Neander and Rosenberg

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[6]Griffiths 1993; 1994.

[7]Assuming a hypothetical case in which the genes did get replaced all-at-once, the offspring's pathway would not be descended from the parents' pathways in any clear sense, and it would be a mere accident that it still produces a similar – though non-homologous – phenotypic trait. It may seem that a partial exception is provided by canalization, a phenomenon that allows development to 'abstract' from certain genetic variations and produce the same phenotype. If we encountered a canalization case in which the entire genotype is replaced generation–to–generation, then presumably the developmental process would exhibit further inherited physico-chemical features that enabled a non-functional re-identification anyway.

that these lineages cannot be individuated except by reference to functional categories. Worryingly, Neander and Rosenberg themselves have previously given persuasive arguments designed to show that homology often depends on function. This article addresses these arguments, and shows how to escape them: Regardless whether the arguments are correct with respect to long-term homological categories, they do not apply to generation-to-generation homology. The latter, moreover, is sufficient for individuating the lineages needed to explain teleological functions.

References

Amundson, Ron and George V. Lauder (1994). "Function Without Purpose: The Uses of Causal Role Function in Evolutionary Biology". In: *Biology & Philosophy* 9, pp. 443–469.

Griffiths, Paul E. (1993). "Functional Analysis and Proper Functions". In: *British Journal for the Philosophy of Science* 44, pp. 409–422.

— (1994). "Cladistic Classification and Functional Explanation". In: *Philosophy of Science* 61, pp. 206–227.

— (2006). "Function, Homology, and Character Individuation". In: *Philosophy of Science* 73, pp. 1–25.

Leahy, Brian and Maximilian Huber (2017). "Two arguments for the etiological theory over the modal theory of biological function". In: *Synthese* 194, pp. 1169–1187.

Nanay, Bence (2010). "A Modal Theory of Function." In: *Journal of Philosophy* 107, pp. 412–431.

— (2012). "Function attributions depend on the explanatory context: a reply to Neander and Rosenberg's reply to Nanay". In: *Journal of Philosophy* 109, pp. 623–627.

Neander, Karen (2002). "Types of Traits: The Importance of Functional Homologues". In: *Functions: New Essays in the Philosophy of Psychology and Biology*. Ed. by André Ariew, Robert Cummins, and Mark Perlman. Oxford University Press, pp. 390–415.

Neander, Karen and Alex Rosenberg (2012). "Solving the Circularity Problem for Functions: A Response to Nanay". In: *Journal of Philosophy* 109, pp. 613–622.

Rosenberg, Alex and Karen Neander (2009). "Are Homologies (Selected Effect or Causal Role) Function Free?" In: *Philosophy of Science* 76, pp. 307–334.

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