Adaptation and its analogues: Biological categories for biosemantics

Hajo Greif

Warsaw University of Technology, Faculty of Administration and Social Sciences, Plac Politechniki 1, 00-661 Warsaw, Poland

A B S T R A C T

"Teleosemantic" or "biosemantic" theories form a strong naturalistic programme in the philosophy of mind and language. They seek to explain the nature of mind and language by recourse to a natural history of "proper functions" as selected-for effects of language- and thought-producing mechanisms. However, they remain vague with respect to the nature of the proposed analogy between selected-for effects on the biological level and phenomena that are not strictly biological, such as reproducible linguistic and cultural forms. This essay critically explores various interpretations of this analogy. It suggests that these interpretations can be explicated by contrasting adaptationist with pluralist readings of the evolutionary concept of adaptation. Among the possible interpretations of the relations between biological adaptations and their analogues in language and culture, the two most relevant are a linear, hierarchical, signalling-based model that takes its cues from the evolution of co-operation and joint intentionality and a mutualistic, pluralist model that takes its cues from mimesis and symbolism in the evolution of human communication. Arguing for the merits of the mutualistic model, the present analysis indicates a path towards an evolutionary pluralist version of biosemantics that will align with theories of cognition as being environmentally "scaffolded". Language and other cultural forms are partly independent reproducible structures that acquire proper functions of their own while being integrated with organism-based cognitive traits in co-evolutionary fashion.

1. Introduction

Ruth Millikan's aptly titled 1984 book *Language, Thought, and Other Biological Categories* inaugurated a strong naturalistic programme in the philosophy of mind and language that has become known as "teleosemantics" or "biosemantics". Its mission is to explain how linguistic and cognitive forms acquire and carry their meanings by recourse to a natural history of functions as selected-for effects of language- and thought-producing mechanisms. Biosemantics explicitly relies on the Darwinian concept of natural selection of variant hereditary traits, which is extended by analogy to phenomena that are not strictly biological, such as reproducible linguistic and cultural forms. There is no systematic attempt in biosemantics to investigate whether and how these analogues of natural selection might interact with the Darwinian evolution of cognitive traits. Developing a conceptual grasp of such interactions might strengthen biosemantic theory and help to solve some of its problems. The aim of this essay is to explicate various interpretations of these interactions, and to critically explore their bearing on biosemantics. So the meta-question behind this inquiry is:

Q1 To what extent is the analogy between naturally selected traits and intentionally designed forms supported by real relations between these domains?

If biosemantics is indeed a naturalistic programme that at least in part seeks to answer philosophical questions by recourse to scientific concepts and theories, its biological categories will be anchored in biological theory in some way and to some degree. In that case, the domain of the real relations in Q1 is not supposed to be empty. Under this premiss, I will argue that the domain of possible real relations can be meaningfully explored by contrasting adaptationist with pluralist readings of the evolutionary concept of adaptation – a concept that is only marginally considered in the biosemantic literature.

Of the interpretations that emerge, two will be particularly relevant: First, on a linear model that takes its cues from the evolution of co-operation and joint intentionality, linguistic forms and their functions are grounded in the adaptive requirements of information exchange and environment-bound co-ordination tasks. Second, on a mutualistic model that takes its cues from mimesis and symbolism in the evolution of

human communication, language is a reproducible structure with its own proper functions and analogue conditions of heredity, variation and selection. Its functions are coupled with human cognitive traits but do not per se subserve human adaptive requirements in the biological sense. In this essay, I will sketch a path towards an evolutionary pluralist version of biosemantics that will align with theories of cognition as being environmentally "scaffolded". Language and other cultural forms are partly independent structures that acquire proper functions of their own while being integrated with organism-based cognitive traits in co-evolutionary fashion. The key advantage of this image over the linear model is that it might better explain the emergence and use of complex, abstract and fictional types of reference.

I will first briefly describe the core tenets of Millikan's theory of proper functions and its methodological commitments (Section 2). I will then outline and discuss the concept of adaptation in contemporary evolutionary theory, contrasting the claims of the adaptationist programme with the main lines of evolutionary pluralist argument (Section 3). The resulting interpretations of the relations between evolutionary processes and their analogues and their bearing on biosemantic theory will be the respective topics of Sections 4 and 5.

2. Proper functions, biology and analogy

The key biological category in biosemantics is natural selection. Natural selection and analogously characterised processes in culture and learning are mobilised to account for the selected-for or "proper functions" of animal and human abilities of representing world affairs, but also for the capacity of language to do so. The following considerations will focus on this basic idea, and they will mostly follow Millikan's original expression of this idea. However, I will also refer to the main alternative versions of biosemantics developed by Fred Dretske, Karen Neander, David Papineau and Peter Godfrey-Smith.

Before outlining the core tenets of Millikan's original version of biosemantics, two observations on methodology are in place: First, her reference to "biological categories" has been expressly metaphorical in intent from the start (Millikan, 2017, p. 5). Her claim is neither that theoretical concepts from biology can be transferred to the domain of language and thought in literal and wholesale fashion, nor are these concept transfers expected to add to the body of biological theory. Instead, a partial and qualified analogy is introduced in order to identify a set of properties that biological, mental, linguistic and cultural phenomena all have in common. Second, and by implication, Millikan's metaphorical use of biological categories is systematic in the way that Mary Hesse (1966) and Max Black (1962) outlined in their accounts of the role of metaphor and analogy in science. Theoretical concepts are transferred from an established domain of science to a less explored "target" domain in order to develop explanations and theories for the latter. In the present case, Darwinian evolution is the source and language and thought are the target domain.

According to Darwin's original definition (1859), natural selection is the differential reproduction of variant forms of hereditary traits within a population over a number of generations, on the grounds of how the effects of those variant traits respond to conditions in the population's environment. If the principle of natural selection has "analogues in learning and cultural selection" (Millikan, 2017, p. 4), these will account for the differential reproduction of variant reproducible features within a population or, in Millikan's (1984) terms, "reproductively established family" of such features on the grounds of the effects that they produce for members of that population in response to conditions in their environment. The reference to "features" instead of "organisms" and "traits" in my present reconstruction shall highlight the fact that the analogues of natural selection do not necessarily operate on organic traits. Instead, the biosemantic analogues of natural selection affect populations of reproducible artefacts or forms of behaviour. Learning and cultural selection will give rise to histories of reproduction and selection in their own right. However, in specific cases and in specific ways, the mechanisms of natural selection and its analogues might interlock, as will be outlined in Section 4.

In committing her- or himself to an unitary mode of etiological explanation across the board of admissible phenomena, the biosemanticist will recur to the contributions that the effects of the biological traits or other reproducible features or "mechanisms" involved have made to their reproduction within a population of – natural or artifactual – bearers, as compared to the effects of variant forms of those mechanisms in that population. By virtue of conferring a reproductive advantage upon their bearers over the course of generations, the mechanisms that produce those effects will acquire the "proper function" of producing them (Millikan, 1984, p. 28 and Ch. 1–2 in general). Not just any assortment of same-looking effects will be subsumable to the same functional-historical account. They have to be results of the same history of being reproduced in the same way under the same type of conditions in order to have the same proper function.

It is the *direct* proper function of a reproductively established mechanism to generate the kind of effects in question if these effects, qua individually bearing certain relations to the environment, have in sum conferred a reproductive advantage upon bearers relative to non-bearers of that mechanism in a population. In turn, the individual effects have the *derived* proper function of being adapted to some concrete world affair, called "adaptor" (Millikan, 1984, pp. 40–41), if they have been produced by some such mechanism that has been reproductively established throughout a sequence of earlier generations for producing effects of the same general type. Having been produced by such a mechanism is necessary and sufficient for possessing the corresponding derived proper function, whereas successfully performing that function in the individual case is not. Conversely, the mechanisms in question possess their direct proper functions because a sufficient number of them has successfully produced the relevant effects with sufficient frequency over generations of a population to incur a fitness value for their bearers.

Accordingly, proper functions in the first place pertain to the mechanisms or, in Millikan's original wording, "devices" that produce the relevant effects, and only in derived fashion to the individual instantiations of these effects. "Mechanism" and "device" should here be understood in the broadest sense, so as to include material patterns and behavioural routines that produce some environment-directed effect in frequent and regular fashion. This effect will have made a necessary contribution to the reproduction of members of the type of mechanism in question. It will therefore account for the establishment of a *type* of mechanism in the first place. Typically, a mechanism's contributions to the conditions of its reproduction will be relevant on the level of a superordinate system, such as an organism or a population, although this is not required by definition. The functions of sub- and superordinate systems are often "nested" and dependent on each other, but might also compete on various levels. However, in order to meet the adaptive requirements of the members of a population of organisms, the proper functions of various systems and sub-systems will have to be co-ordinated to some degree.

Accordingly, the tokens produced by the mechanisms in question have not been directly selected for their effects. It is the producing mechanisms that are selected for *by proxy of* the effects of the individual tokens that they and their ancestors produced in the past. To ignore this proxy relation is a common and fateful misunderstanding of the central claims of biosemantics. The misunderstanding is common, and perhaps also intuitive, enough to be reproduced even by such accomplished philosophers as Frank Jackson (2006), who assumes it to be a biosemantic claim to say: "x believes that P iff x is in a state that is selected (in the evolutionary sense) to co-vary with P". Instead, the claim should read, to retain Jackson's phrasing as far as possible: "x believes that P if there are mechanisms within x that have been selected (in the evolutionary sense) for producing tokens of P-type beliefs that reliably co-vary with instantiations of P". Note that there is no biconditional in the rephrasing, as other things than the specific mechanisms indicated here may cause items otherwise indistinguishable from P-belief tokens, and as

they may do so without having the proper function of doing so. However, if produced by the selected-for mechanisms, a P-belief token has the derived proper function to thus co-vary with a concrete P-affair. The mechanisms involved have to produce appropriate tokens with sufficient frequency to ensure reproduction of those mechanisms and their bearers. These tokens might even fail to perform their function quite often, as long as a sufficient reproduction rate is ensured for the mechanisms and their bearers.

Millikan's favourite example of such mechanisms in animate nature are bee dances: It is the direct proper function, in terms of having been naturally selected for, of dance-producing and -perceiving mechanisms in bees to guide worker bees to locations of nectar. In turn, it is the derived proper function of any given individual bee dance to make a watching bee fly towards the concrete location of nectar. These relations are best expressed in terms of mathematical functions: transformations in the location of nectar on different occasions are matched by transformations in the direction, angle, and waggle frequency of the dance. A correct mapping between dance patterns and locations of nectar is the "Normal condition", in Millikan's terminology, for fulfilling the function of bee dances to make bees procure nectar. This function may often fail to be fulfilled, but it will have to be fulfilled frequently enough to ensure the reproduction of bee-dance mechanisms in bee populations.

While being applicable to animal signalling and artefact functions alike, the primary target of Millikan's analysis are the proper functions of human language and thought. They are addressed not primarily as evolved, selected-for cognitive traits but in terms of their representational content. Representations work as "internal stand-ins exemplifying structure-preserving mappings of affairs in the environment" (Millikan, 2017, p. 4). They do so because their producer and/or consumer mechanisms have been selected for enabling such relations.

On the "thought" side of the equation, cognitive traits have the proper functions of either producing or using (or "consuming") external behaviours or internal processes that stand in such rule-governed mapping relations to certain types of world affairs. These mapping relations do not have to bear a picture-like similarity relation to their object. Instead, they are understood as point-to-point correspondences of the kind that is found in mathematical functions. The mapping rules are determined in accordance with what the consumer mechanisms involved require the behaviour or process in question to stand for. Any concrete representational content depends on the "Normal" conditions of the fulfilment of consumer functions, that is, the conditions under which the consumer mechanism's proper functions have been selected for with respect to a given type of mapping relation. (The term "Normal" is capitalised by Millikan to highlight its technical meaning in this context.) Human cognitive accomplishments are special within this context, Millikan maintains, primarily for the ability to use, and only secondarily for the ability to produce, mappings that involve subject-predicate structures and negation transformations. These are the necessary prerequisites for articulating and using propositional content, making inferences and performing acts of identification.

On the "language" side of the equation, language adds a particular level of proper functions to the picture, inasmuch as it is not a mere vehicle of content to be transmitted between speakers and hearers. Instead, it is itself composed of reproducible items, namely lexical, grammatical, and syntactic elements that form reproductively established mechanisms with proper functions of their own. Their roles in reference-making not only depend on co-operating producer and consumer mechanisms in speakers and hearers but also on their own reproduction in language use.

This twofold dependence gives rise to a more concrete research question for our inquiry into the relation between the mechanisms involved:

Q2 What dependence relation exists between the naturally selected-for proper functions of human cognitive traits and the proper functions of language as a mechanism established by analogues of natural selection?

On the one hand, the guidance of human activities through language-use might be strongly mediated and indirect, but there is, Millikan (2006) maintains, a bedrock of more immediate biological functions on which it rests. On the other hand, the reproductively established mechanisms of language may become coupled with human producer and consumer mechanisms. These two kinds of mechanism may also compete and mutually shape each other to some extent, as Millikan (2004, Ch. 2) notes.

In what follows, I will demonstrate that the possible answers to the previous question partly depend on the interpretation of the relationship between adaptation, as the conceptual counterpart of natural selection, and its analogues that goes into the biosemanticist's argument. This interpretation might be rather implicit, but has implications for the style and direction of the biosemantic programme.

3. Adaptation, adaptationism, pluralism

In evolutionary terms, if an organic trait has acquired a function qua having been selected for, it is an adaptive trait. The trait is an adaptation to the conditions in the environment to which its effects have differentially responded over a number of generations. Given that the proper functions of language, artefacts and other cultural forms are understood in analogy to the proper functions of hereditary organic traits, the question arises whether and to what extent they can be characterised as adaptations, too.

However, references to the notion of adaptation are conspicuously rare in the biosemantic literature, despite the central conceptual role it assigns to biological functions and natural selection. In *Language, Thought, and Other Biological Categories*, one only finds a few uses of "adapt" and "adapted", which Millikan expressly distinguishes from adaptation in a biological sense (1984, p. 40). She later published one paper that contains an explicit defence of the notion of the human mind as an evolutionary adaptation (Millikan, 1989a), and one chapter that discusses the notion of adaptation and its critiques more broadly and extensively (Millikan, 1993b). Other classic works in biosemantics vary in their reference to adaptation: While the foundational text in etiological functionalism (Wright, 1973) as well as David Papineau's inquiries (1984; 1987; 2001a; 2001b) that ran in parallel with Millikan's do not consider it either, and while even the biologically much more deeply informed defence of "The Teleological Notion of 'Function'" by Karen Neander (1991a,b) omits it, too, a brief discussion of its relevance is provided by Fred Dretske (1988, pp. 45–47). Peter Godfrey-Smith (1994) explicitly employs the notion of adaptation when gauging the appropriate timescale for a history of functions. His work is an exception in the field though, for not merely being biologically informed but profoundly shaped by Richard Lewontin's critical views of adaptationism (see *p.*1, *p.*2 and *p.*4 below).

If one looks for reasons for the relative absence of the notion of adaptation from biosemantics, there is a prima facie straightforward if not obvious answer. It comes in two parts: First, biosemantics as a philosophical approach to mind and language originated from and primarily addressed problems within the tradition of disciplinary philosophy, so one should not expect a wholesale and systematic commitment to biological concepts and theories from its classic works in particular. In fact, while Dretske referred to pertinent biological literature already in 1988, the other members of the founder generation started to do so only after publishing their original theoretical statements (Millikan in 1989a; 1989b; 1991, to a fuller extent in 2004; Papineau in 2001a). Even the limited evolutionary analogies and general naturalistic outlook of early biosemantics were sufficient to solicit stiff resistance from more purely minded philosophers. Second and in line with the programme's original intentions, any commitment to a biologically defined notion of adaptation would conflict with the explicit biosemantic aim of attaining a level of generality that encompasses analogues of selected-for functions outside the domain of biological phenomena proper. Unlike for the much broader concept of functions and its biological and non-biological uses,

referring to the features of artefacts, linguistic structures and cognitive processes as adaptations would be a conceptual overreach in this respect, and is rightfully avoided.

There is a complication though: To the extent that the biological categories and the evolutionary naturalistic approach of biosemantics substantially rely on biological theories and their explanations of the origins and functions of human language and thought, and given that adaptation is the conceptual counterpart to natural selection in Darwinian evolutionary theory, acceptance by the biosemanticist of any established definition of selected-for functions in the biological domain will imply at least implicit acceptance of a corresponding notion of adaptation, even if one carefully avoids applying the term "adaptation" to analogues of naturally selected-for functions. Even if the evolutionary concepts in biosemantics are merely intended to be informal analogies that seek to abstract from the detailed and partly contested definitions within biology, they will still be partial analogies of some specific among the various conceptions of the pertinent phenomena. Otherwise, they will risk ending up inconsistent or vacuous, inept of informing more than a vaguely science-inspired philosophy.

Under an understanding of biosemantics as a genuinely naturalistic project, acceptance of variant notions of natural selection-*cum*-adaptation will give rise to variant pictures of the relations between biological functions and their analogues, which I will discuss under points *i*.1 through *i*.4 in Section 4: Language, artefacts and other reproducible cultural forms that are subject to selection might be explainable by reference to a biological model of selection-for and adaptation but otherwise remain independent phenomena, but they might also be understood either as biological adaptations in a direct sense or as subservient to biological adaptations, or they might be found to be independent but interact with biological adaptations.

In order to assess the scope and depth of the possible relations between natural selection, adaptation and their analogues, a basic understanding of adaptations in the biological sense will be required. Given that the term has received numerous definitions in evolutionary theorising over time that vary in reference to processes, properties of organisms and properties of traits – compare, for example, the classic works of Wright (1931), Fisher (1930), and Williams (1966) respectively – a first step will be to focus on *adaptive traits* as the pertinent meaning of adaptations in the present context. The model for proper functions in biosemantics are the selected-for effects of organic traits. Given that adaptive traits, too, have been variously defined in the literature, I will try to formulate a definition that is as basic, unequivocal and uncontroversial as possible in a contested field:

A. Adaptation: A trait *T* will be adaptive only if all of the following conditions are fulfilled in the aetiology of *T*:

a.1 *Fitness*: *T* responds to a certain set of conditions *C* in a population *P*'s shared environment *E* in such a way that its effects ϑ increase the probability of reproduction of *T*-bearers relative to bearers of variant traits *T′* in *P* whose effects $\vartheta′$ respond differently to the same *C* in *E*.

a.2 *Heredity*: *T* and *T′* replicate through mechanisms whose degree of fidelity is sufficient to ascertain that differential reproduction between *T* and *T′* in *P* under *C* over a number of generations *N* depends on variance in fitness.

a.3 *Selection-for*: Differential reproduction between *T*- and *T′*-bearers over *N* can be directly attributed to the effects ϑ of *T* for *T*-bearers in *P* under *C*, as compared with variant $\vartheta′$ of *T′* for *T′*-bearers in *P* under *C*.

The bottom line of *A* and any like-minded definition is that *there will be no adaptation without selection for the effects of heritable traits of a population of organisms in a given environment*. Conversely, and when applied to biological phenomena, this definition complements the definition of proper functions in biosemantics: *Whenever a trait has a proper function, it is an adaptation to the conditions responsible for its selection*. For example,

the haemoglobin present in most vertebrates' blood has the selected-for function of storing, transporting and releasing oxygen in the organism. It is an adaptation to oxygen-supply requirements in aerobic organisms whose metabolism requires more oxygen than can be dissolved in the blood plasma. Temporary storage and transport of oxygen is the selected-for function of its biochemical properties. Conversely, its spectral properties, which make it appear red when oxygenated, have not been selected for but only selected, as they do not contribute to its relevant biochemical properties. In many arthropods and molluscs, haemocyanin has been selected for the same oxygen-supply task while appearing blue under oxygenation. In evolutionary terms, haemoglobin and haemocyanin did not compete within the same populations but are hereditary traits of differently constituted species that have been selected for the same type of effect under the same type of conditions in different locales (Burmester, 2001; van Holde et al., 2001).

Evolutionists' disagreements on adaptation arise from variant interpretations of the relevant terms in *A*: what overall status adaptations have in an evolutionary framework, what the units and mechanisms of heredity are, what the units and levels of selection are, and what the presumed relations between trait, organism and environment are. There is a wide spectrum of possible positions to be taken on each and all of these interpretations, but evolutionists largely align into two distinct camps, one "adaptationist" and one "pluralist". Basically, where the adaptationist will adhere to a restrictive interpretation of *A* while assigning a central role to adaptation in evolution, the pluralist will allow for various interpretations of adaptation under *A* while assigning it a more circumscribed role in evolution.

To make this difference in approach clear, a first pertinent conceptual distinction is that between natural selection *of* some trait and natural selection *for* that trait, which is addressed in *a*.3. It has been introduced by Elliott Sober (1984) and explored in its bearing on biosemantic arguments by Goode and Griffiths (1995); Artiga (2011); Fulda (2015). Selection-for always occurs with respect to certain effects of a trait, whereas selection-of may include aspects of a trait that are independent of adaptive requirements, or it may involve traits that free-ride on a selected-for trait. In order to demonstrate that a trait has been selected for, its particular contributions to the organism's overall fitness will have to be spelled out. Only selection for the effects of a trait under an array of specific conditions will make it an adaptive trait. The point of dissent between the adaptationist and the pluralist is the extent to which these conditions can be identified for any specific trait, so that, in our above example, haemoglobin and haemocyanin bear unequivocal fitness values.

A second, related conceptual distinction relevant to the interpretation of *A* has been highlighted by Elizabeth Lloyd (2017). Traits might either be characterised as adaptive whenever hereditary variance, selection-for and differential fitness obtain, or only if and when conditions *a*.1 and *a*.3 actually effect modifications of a trait that go beyond the boundaries of ancestral variance in *P*, thereby affecting condition *a*.2. Only in the latter case, accumulated selection processes can be held responsible for actually shaping or "engineering" a trait, such as the presence and function of haemoglobin and haemocyanin in vertebrates and molluscs respectively. On these grounds, the adaptationist argues that natural selection is the main or exclusive creative factor and an "optimising agent" in evolution, whereas the pluralist maintains that other factors are relevant, too.

The archetypical version of what would later be christened the "adaptationist programme" by its critics was formulated in George C. Williams' *Adaptation and Natural Selection* (1966). His way of making adaptation an expressly restrictive, "onerous concept" was, first, to confine it to cases where selection-for actually furnishes evolutionary design. Second, he tied adaptation to a narrow conception of genetic inheritance, which in turn is defined in terms of natural selection: "a gene could be defined as any hereditary information for which there is a favorable or unfavorable selection bias equal to several or many times its rate of endogenous change." (Williams, 1966, p. 25) Genes are understood here not as concrete material entities but as a "cybernetic

abstraction", and natural selection as a "statistical abstraction" (Williams, 1966, p. 33). This argument has been pushed further towards a much more material, DNA-centric view of gene selection by Richard Dawkins (1989), which then became the paradigm of the adaptationist programme instead of Williams' cybernetic view. Even if that programme is not taken as far as postulating "selfish DNA" as the main driver of evolutionary processes, it claims that neither phenotypical traits nor groups or species are ultimately exposed to selection but genes as the units of heredity. The selectively relevant environment of a gene are, first and foremost, its alleles. Organism and environment are only considered at a secondary level that is deemed reducible to processes at the genetic level. The relationships between gene, organism and environment are thereby subsumed under a unitary mechanistic, nomological explanation – "the laws of physical science plus natural selection" (Williams, 1966, pp. 6–7). Accordingly, only those traits will count as adaptive which are genetically inherited within a population and shaped by selective pressures from the environment.

The critical approach taken by the pluralist starts from the observation that, in order for this perspective to work, an organism's traits have to be viewed in isolation from each other and mapped onto a certain genetic unit of heredity in order to find a specific adaptive effect for each of them. In turn, a given set of environmental conditions is determined as being mainly or exclusively in charge of shaping a set of adaptive responses through natural selection. The reductive, nomological approach to explanation that manifests in the adaptationist view might be altogether inadequate to the complexity of evolutionary phenomena, whose nature cannot be inferred from simplified low-level phenomena that are chosen for the sake of model tractability.

A set of interrelated positive pluralist arguments that are relevant to the present argument can be described as follows:

*p.*1 *Traits may become established without being selected for.* Seemingly adaptive, selected-for traits may be "spandrels" instead (Gould and Lewontin, 1979). They might be by-products of adaptive traits that have been selected for different effects, or they might have been shaped by phyletic or developmental constraints, which are as such beyond the regime of natural selection. Conversely, structures of these kinds may be co-opted for some use on grounds other than having been selected for. As "exaptations" (Gould and Vrba, 1982), these co-opted structures do not serve a function and are not adaptive unless they become subject to natural selection for their effects at some later stage.

*p.*2 *There are multiple, partly independent levels of selection.* Natural selection may affect genes as well as individuals, groups, species and various other levels of biological organisation, where each of them might be the lowest level that can be identified in terms of a given set of fitness differences (Lewontin, 1970; Hull, 1980; Lloyd, 2017; Okasha, 2006; Wade, 2016). Selection processes at the various levels might either be hierarchically nested, or they might interact in co-ordinated fashion, but they might also conflict with respect to the effects that are being selected for. There is no necessarily given hierarchy under which selection processes on these various levels would serve a unitary set of adaptive purposes, as can be demonstrated on the example of frequency-dependent selection (Jeler, 2017).

*p.*3 *There are multiple, partly independent units and mechanisms of heredity.* If one takes Williams' original (1966) cybernetic definition of a gene by its word, not only DNA but any entity that is replicable with a degree of fidelity and with a reproductive rate that are jointly sufficient for it to be subject to selection may count as a gene, including cultural artefacts or Dawkinsian "memes" (Dawkins 1989; Wimsatt 1980; Hull 1982; for the relation between genes and selection, see Wright 1980; Sterelny and Kitcher 1988; Beurton et al., 2000; Griesemer 2000). Extending the critiques of a DNA-centric view, Developmental Systems Theory (Oyama, 2000; Oyama et al., 2001) postulates the existence of systems that combine organismic and environmental factors in an account of the transmission of phenotypic traits, from differential expression of identical genotypes (Bateson, 2001; Gordon, 2001) to distinct developmental routes to a similar phenotype ("phenocopying", Goldschmidt, 1949). Either way, environmental and other non-genetic factors are placed on equal explanatory footing with genetic ones.

*p.*4 *Organisms partly shape the ecologically and selectively relevant conditions in their environments.* Such shaping may occur coincidentally or purposefully, but either way, organisms are not passively exposed to selection (Lewontin, 1982, 2000). Purposeful shaping of the environment may involve the creation of material structures and artefacts or systematically seeking out favorable conditions (Godfrey-Smith, 1996). The adaptationist notion of pre-existing environmental conditions as ecological niches into which organisms adapt will be replaced by one of niche construction (Odling-Smee et al., 1996) or environmental scaffolding (Sterelny, 2010; Caporael et al., 2014), where conditions are modified not only for the attainment of proximate goals but ultimately also for further type *A* processes, broadly conceived. Adaptation becomes a moving target once an organism's or population's environment is acknowledged to be partly of their own making.

If there are various mechanisms apart from natural selection by which traits become fixed in a population (*p.*1), and if there are multiple and partly independent levels of selection (*p.*2), and if ontogenetic development is not sufficiently defined by genetic information (*p.*3), and if organisms and populations themselves shape some of the selectively relevant properties of their environments (*p.*4), these conditions will *individually* suffice to make the case that there are key factors in evolution that are not subsumable under an adaptationist explanation. To the extent that these conditions are interrelated by association and family resemblance rather than by necessity, they allow for gradations and selective focus between them. However, to the extent that these conditions coalesce into a unified programme, *p.*1 through *p.*4 will *jointly* suffice to make the positive case that these factors permit reproducible artificial structures with their own mechanisms of heredity whose effects may become subject to forms or analogues of natural selection. This includes the possibility that structures and functions established on the analogue level interact with conditions relevant to natural selection.

4. Interpreting biological categories

The positions identified in previous discussion provide biosemantics with a broad spectrum of possible interpretations of how its various biological categories relate to each other and inform its programme:

*i.*1 There are analogies between naturally selected-for functions and the domain of language and cultural forms, to the extent that similarly structured processes can be detected in either domain, and be described and at least partly explained in the same evolutionary terms. However, forms of cultural evolution, along with their mechanisms of heredity, variance and selection and the resulting fitness conditions remain largely independent from biological evolution. This interpretation puts biosemantics in proximity to theories of cultural evolution as an autonomous domain (Heyes, 2018; Mesoudi, 2011).

*i.*2 Language and cultural forms have naturally selected-for direct proper functions on the level of the organic traits that realise them and on the grounds of the genetic information that enables them, whereas all their individual expressions have proper functions derived from the operations of those hard-wired traits vis-a-vis concrete conditions in their users' environments. This interpretation views language and culture as direct expressions or as effects of the expression of hereditary traits that are designed by natural selection. This interpretation would put biosemantics in proximity to theories

that commit to a strict, gene-centric reading of adaptationism (Barkow et al., 1992; Pinker and Bloom, 1990).

i.3 There is a relation between selected-for functions in the evolutionary domain and the domain of language and cultural forms, where this relation is linear and hierarchical. There are processes of information transmission, variance and selection-for that occur within the domain of language and cultural forms proper, but these subserve and are dependent on naturally selected-for functions in the evolutionary domain. Fitness values for linguistic and cultural forms materialise in biological adaptations. This interpretation puts biosemantics in proximity to theories of the evolution of language and culture that assign priority to biological adaptations (Cavalli-Sforza and Feldman 1981; Lumsden and Wilson 1981; Boyd and Richerson 1985; Durham 1991; for the key sources in the present context, see below). An inverted version of this picture is provided by memetics, according to which biological evolution partly subserves cultural selection processes (Dawkins, 1989).

i.4 There is an interaction between selected-for functions in the evolutionary domain and the domain of language and cultural forms, where this interaction is mutual and non-hierarchical. The products and effects of processes of information transmission, variance and selection-for in the domain of language and cultural forms may furnish some of the conditions relevant to informational, developmental and selection processes in the evolutionary domain, broadly conceived. Analogues of fitness values may pertain to language and cultural artefacts themselves, where these may affect or be integrated with fitness values of their users' biological traits. This interpretation puts biosemantics in proximity to genuinely co-evolutionary and scaffolding theories of language and cognition (which I will more closely consider below).

Of these interpretations, *i*.1 is the most modest and systematically least forceful, whereas *i*.2 is strong but so reductionist that it carries little systematic force and ultimately contradicts the biosemanticist's aims, while *i*.3 appears as the prima facie most straightforward and *i*.4 as the systematically most far-reaching interpretation for the biosemantic programme. In fact, *i*.1 is limited to proposing a modelling relation on the grounds of partial analogies, in which some key characteristics of evolutionary processes provide a template for the explanation of processes in learning and culture. A modelling relation of this kind neither formally implies nor informally involves any further claim concerning factual relationships between the processes in either domain. To the extent that the purpose here is to explore possible *substantial* relations between these domains, *i*.1 can be exempted from further consideration even though, taken by itself, it is a tenable interpretation of the biosemantic project if conceived of as a biologically inspired but not genuinely naturalistic endeavour. Conversely, *i*.2 can be exempted from more detailed consideration for entirely collapsing the domain of language and culture into the domain of biological adaptations. It leaves no space for an investigation of language and culture in their own right. The justification for doing so is offered by a strict and material reading of adaptationism, according to which everything that could potentially be selected for when exposed to a certain set of conditions in the environment can ultimately only be an expression of a certain string of genetic information, and according to which everything that is an adaptation has been designed by a process of natural selection for the effects of the traits thus expressed. Given these limitations of *i*.1 and *i*.2, the following discussion will focus on the two remaining, more substantial interpretations.

One will find support both for *i*.3 and for *i*.4 in the biosemantic literature, but also for the systematically weaker assumption of plain analogy (*i*.1), with gradations between them and without one interpretation clearly prevailing over the others. In the case of Millikan's writings, it is notable that she virtually never cites the classic sources of *i*.3 or *i*.4, apart from Dawkins' adaptationist-minded memetic take on a hierarchical approach (1989), while explicitly, repeatedly and affirmatively referencing Pinker's outright reductionist *i*.2 view, which she never

systematically explores beyond endorsing the generic claim that language must be a biological adaptation (Millikan, 1998, 2000, 2003).

Despite these apparent adaptationist commitments, there is some ambiguous inclusion of spandrels and exaptations as possible sources of proper functions in Millikan (1993b), contrary to the explicit reservations against such a strategy in Gould and Lewontin (1979) and Gould and Vrba (1982). Moreover, Millikan in several places endorses the view that the primary role of natural selection is that of a control function that stabilises existing traits (Millikan 1989a, 1993b; 2004, p. 8–9 n2; 2017, p. 16, 84 n1). This contrasts with the general biosemantic commitment to a definition of proper functions in terms of selected-for effects as a source of design, as exemplified in Millikan's reference to "the engineering [of representations] having been owed to a process of selection on some level or levels" (2017, p. 4). Here, selection is supposed to do at least some of the engineering. If both claims are to be true, natural selection, and arguably its analogues, too, will have to serve both stabilising and design functions – giving the biosemanticist the task of telling apart their respective contributions. This is a task that Godfrey-Smith 1994 contends with in his "modern history" account of proper functions, according to which the causes of the recent maintenance of a trait or other feature in a population takes precedence over teleological and design considerations that address temporally more remote conditions. The design of a trait might partly owe to conditions other than having been selected for (cf. *p*.1).

Not as obviously tied to immediately biological questions, Millikan in some places critically appreciates memetic arguments and analyses how the putative aims of memes as a "second replicator" may either complement or lie at cross purposes with the biological functions of human cognitive traits. She suggests that the former, while being subject to their own regime of heredity, variation and selection, may become adopted for coordinative functions among members of human populations (Millikan, 2004, Ch. 2). The space of possible relations between various evolving systems of either kind raises the question of how their proper functions are in fact integrated with each other. Millikan refers to such integration in terms of "serial" (1984, p. 35) or "nested" proper functions (2017, p. 160) but appears to point towards two distinct shapes that such integration may assume.

Under the presumption of a type *i*.3 hierarchical model, the functions of one system or subsystem subserve the functions of another, superordinate one. It may be maintained, for example, that a visual system's structured output feeds into a detection system, which in turn is used to produce behaviours towards what is detected. All co-ordination between the participating systems will be geared towards the superordinate system's functions, hence towards its adaptive requirements, which presupposes, first, that the superordinate system is in fact the relevant reproducing unit that dictates a hierarchy of subordinate functions, and, second, that the individual unit's adaptive needs are in line with the overall adaptive needs of its population. These assumptions in turn presuppose uniformity of, or coordination between, selectively relevant conditions and adaptive needs on all levels, from organic traits and reproducible artifactual forms to whole populations. As the memetic approach to language and culture expressly does not meet this condition, its inclusion in a natural-historical account of the proper functions of these forms would require specific explanations of how it may be subsumed under a hierarchical approach.

In other places, however, traits are characterised as being co-ordinated across various levels of organisation in more mutualistic and less hierarchical type *i*.4 fashion. Various systems and sub-systems might have proper functions that are reproductively established each in their own right and adapted to conditions in their shared environments. In that process, those systems or sub-systems may become part of the selectively relevant conditions of each other. They may share the same ecological environment, in terms of relevant ambient conditions in a particular locale, while forming part of the specific selective environments for each other, in terms of the conditions for each other's reproduction (for this distinction, see Brandon 1995). The relevant phenomenon is called "co-adaptation". It may affect

relationships between parts of an organism in the formation of complex traits (as in Darwin's original 1859 coinage of the term) as well as the joint selection of genes at different loci (Dobzhansky, 1950) and ecological interactions between species that co-evolve either to mutual symbiotic benefit or into stable predator-prey relationships (Thompson, 1994, 2005). However, co-adaptation may also concern multi-species systems that might themselves become units of natural selection as "holobionts" (Gilbert and Tauber, 2016; Lloyd and Wade, 2019; Roughgarden et al., 2018). The paradigm holobionts are multicellular host organisms and their microbiota, which may become interactors in selection processes, provided that their interactions remain in proper balance. In all of the previous cases, there is selection for a set of effects jointly produced by otherwise distinct systems or sub-systems, with or without co-operative purposes being involved. If this latter, more pluralistic approach to the integration of functions is maintained, the proper functions of various traits or structures on various levels of organisation will interact in open-ended fashion rather than being reducible to one unit or level of selection and a corresponding unitary set of proper functions.

The latter, type *i*.4 interpretation in particular allows for the inclusion of inter-organismic relations and environmental structures into an image of co-evolutionary relations in which "The organismic process has no skin" (Millikan, 1993a, p. 179). Artefacts or other reproducible structures that affect the environment of their creators and users might be co-ordinated with organic traits in such a way that the performance or the establishment of the proper functions of either relies on the establishment and performance of the proper functions of the other, hence on simultaneous selection for their respective effects. In the human case in particular, the reproducible non-organic structure that appears to be closely intertwined with the evolution of cognition is language, without which the human mind could not perform, and possibly would not even possess, some of its core functions.

5. Varieties of Co-adaptation

In view of developing a more detailed understanding of the hierarchical type *i*.3 and the mutualist type *i*.4 interpretation of the co-evolution between biological traits and cultural forms, and on the grounds of the preceding discussion of the role that the concept of adaptation might play for biosemantics, the following set of definitions can be introduced:

C. Co-adaptation: Cognitive traits T on the organic level and reproducible cultural and linguistic forms L are co-adapted if and when all of the following conditions are met:

c.1 *Adaptation:* In accordance with a broad interpretation of A, T and L (ad *a*.2) reproduce on the basis of mechanisms of genetic or non-genetic heredity respectively, (ad *a*.1) produce differential effects ϑ_t and ϑ_l with respect to a set of conditions C_t and C_l in their shared environment E, and (ad *a*.3) are selected for these effects.

c.2 *Proper function:* T and L each have acquired direct proper functions of their own, by virtue of their effects ϑ_t and ϑ_l having made a necessary contribution either to their original establishment or to their continued reproduction within a population P, or to both.

The previous hierarchical *i*.3 and mutualistic *i*.4 interpretations can be accommodated by providing alternate versions of the last condition in the C set:

c.3$_a$ *Hierarchy:* Effects ϑ_l of L belong to the selectively relevant conditions C_t for the establishment or maintenance of T in such a way that the performance of the proper functions of L is a necessary condition for T to be adaptive for a population P of T-bearers and L-users. The converse might hold for ϑ_t of T for L.

c.3$_b$ *Mutualism:* Effects ϑ_l of L belong to the selectively relevant conditions C_t for the establishment or maintenance of T, and vice versa for ϑ_t of T to C_l for L, in such a way that T and L are individually adaptive to C_l and C_t conditions respectively and jointly adaptive for a population P of T-bearers and L-users.

Despite outlining markedly distinct states of affairs, and despite their apparent alignment with distinct views of the evolution of cognition, *c*.3$_a$ and *c*.3$_b$ need not be altogether mutually exclusive. Instead, they might be complementary and can be used to describe different types, levels or temporal stages of system organisation that may be coupled with each other, where mutualistic lower-level T/L couplings support higher-level cognitive traits, or where lower-level hierarchical structures underlie a more mutualistic co-evolution of organic traits and cultural forms.

If this analysis is to the point, *c*.3$_a$ and *c*.3$_b$ might help to explicate the programmatic difference between Dretske's and Neander's causal-informational and Millikan's and Papineau's "consumer" varieties of biosemantics (see Dretske 1988, 2001; Neander 2012; Millikan 2001, 2004; Papineau 1984 respectively; see also; Godfrey-Smith 2020). By the same token, *c*.3$_a$ and *c*.3$_b$ might jointly help to resolve the apparent ambiguity between the hierarchical (*i*.3) and mutualist (*i*.4) interpretations of the biological categories that I diagnosed in Millikan's writings in particular.

According to the causal-informational approach, the content of a representation is the world affair that it has the function to provide information about. The function of a representation is determined by that bundle of properties of an object, process or situation which to detect or communicate is relevant to a concrete organism or to the members of a specific population, as determined by their specific adaptive needs. The informational approach thereby adopts an environment-to-organism perspective: representations are produced in response to the conditions in the organism's environment, and they are shaped by the organism's needs with respect to these conditions. These conditions might include the exchange of information between members of a population, but the paradigmatic unit of analysis are an organism's elementary perceptual detection mechanisms. Higher-order human cognitive abilities and language are analysed from the same perspective of informational requirements as these more basic mechanisms.

According to the consumer approach, the content of a representation is the mapping between the representation and a world affair that is used by a system in such a way as to perform its proper functions under Millikan-"Normal" conditions (see p. 4 above) – those conditions which account for the proliferation and maintenance of the consumer systems in a population. The function of a representation is determined by the conditions for the fulfilment of the proper functions of its user. In a relevant subset of cases, the presence and proper functioning of co-operating representation-producing systems are part of these conditions. The consumer approach adopts an organism-to-environment perspective: representations are used, and partly produced, in accordance with the conditions in the organism or population that make them Normally respond to conditions in their environment. This perspective might include internal representations, but forms of communication between members of a population are its natural paradigm.

Whereas adaptive needs with respect to the environment, and therefore the conditions at the information source, appear paramount to the informational approach, dynamic and more mutualistic processes of co-adaptation between consumer and producer mechanisms that might become partly detached from adaptively relevant conditions in the environment form a key part of the consumer approach to biosemantics. However, despite their explicit commitments to each one side of this simplified image, biosemantic theories sometimes are more multi-faceted or even ambiguous about the relevant conditions on either side. Both the notion of tracking conditions in the environment in perception and communication and the idea of representing absent, distant, possible or

fictional world affairs by semantically productive structures are pervasive in Millikan's work but often run in parallel. An explicit connection between them is formulated in her recent comparative discussion of "infosigns" and "intentional signs" (Millikan, 2017) that is designed to capture some arguments from informational biosemantics. In an attempt to reconcile informational and consumer approaches, Nicholas Shea (2007) suggests that basic forms of representation, whose success is directly cashed out in terms of survival and reproduction, are anchored in environmental information as an "input condition" while that condition might be relaxed for higher-order forms of representation.

In order to anchor the distinction between the informational and the consumer approaches to biosemantics in more systematic evolutionary theorising, so as to better support them and relate them to each other, I will turn to partly matching empirical modelling approaches to the co-evolution of language and cognition. With some risk of over-simplification and dichotomising admitted, there are, on the one hand, hierarchical approaches to the co-evolution of language and cognition that parallel $c.3_a$ above. Broadly subsumable under this set are studies on the co-evolution of language and cognition through co-operation and joint intentionality by Michael Tomasello (2008, 2014) and Morten Christiansen, Kenny Smith and Simon Kirby (Christiansen and Kirby 2003; Christiansen and Chater 2008; Smith and Kirby 2008; but see also Boyd and Richerson 2009; Bowles and Gintis 2011 on the evolution of social cooperation more generally and Skyrms (2003); Godfrey-Smith (2020) on the evolution of signalling games in that context). On the other hand, there are more mutualistic coevolutionary approaches that parallel $c.3_b$. These are exemplified by the works of Merlin Donald (1991) on mimesis and exograms and Terrence Deacon (1997) on language-brain co-evolution. This is also the domain of theories of "cognitive niche construction", according to which cognition is closely intertwined with a number of other abilities that manifest themselves beyond somatic boundaries (Sterelny, 2007, 2012; Clark, 2006; Laland, 2017), and related theories of environmental scaffolding (Caporael et al., 2014; Clark, 1997; Sterelny, 2010) that highlight the role of material or ideational structures in the development of organisms and their traits, abilities and social organisation (see also Gibson and Ingold 1993; Gärdenfors and Lombard 2020; Malafouris and Renfrew 2010; Renfrew 2012; Killin 2017; Greif, 2017).

All of these accounts equally support the claim in *C* that *T* and *L* are co-adapted to the extent that the performance of the proper functions of language depends on the coordination between biologically evolved cognitive traits and culturally evolved artifactual and linguistic structures. They are also likely to agree, against the assumption of an innate, domain-specific "language faculty" in Pinker and Bloom (1990) and Chomsky (2006), that the biologically evolved cognitive traits involved in language use are significantly more domain-general and that key structuring features of human language pertain to reproducible linguistic forms themselves. Likewise, they will agree in their scepticism towards a presumed superiority of memetic cultural replicators.

However, hierarchical and mutualistic views are likely to diverge in several other respects. Most obviously, they will disagree on whether biological or cultural factors take the respective lead, or whether these factors interact in mutual shaping processes that ultimately undermine the very distinction between them. Methodologically, hierarchical and mutualistic views will have to decide whether or not they seek to infer a mechanisms's original conditions of selection from the conditions of its current proper functioning, and what role natural selection plays in explaining the proper functions of language. On this background, the respective approaches can be outlined as follows:

H_a The hierarchical model: The key factor in the evolution of language lies in practical coordination with respect to some world affair between members of a group, facilitating the human-specific abilities of imitation learning and joint intentionality that are required for the relevant tasks. The proper function of language use will be primarily and directly biological, with natural selection providing the core of the explanation of its design. Language will be an adaptation to the conditions in the environment of a specific population of organisms that relies on complex collaborative activities of resource procurement and protection. Cultural and linguistic forms make a key contribution to these adaptive functions but will overall remain subservient to them. They primarily provide the means of exchanging complex information required for the collaborative activities in question. The evolution of language is thereby explained in light of the proper functions of language as they are discernible from a contemporary perspective.

H_b The mutualistic model: The key factor in the evolution of language lies in the development of complex social behaviours among members of a group, which is facilitated by embodied "mimetic" skills that also form the basis of ritual, art, dance and music. The proper function of language use primarily lies in forms of communicative expression between group members that are neither *per se* nor *ab initio* referential. In part, these forms are subsequently exapted (see *p*.1 above) for reference-making. Other factors besides natural selection will have to be included in the explanation of this process. To the extent that language is a biological adaptation, it will be an adaptation to the emerging requirements of symbolic communication between members of a population. Cultural and linguistic forms become part of the conditions of the selection of the biological traits that enable these practices. The evolution of language can therefore only be explained in light of the specific situation of early *homo* populations, which might have been different from contemporary conditions of language use.

Keeping in mind that the approaches subsumed under these two general models were largely formulated independent from and later than the original statements of the biosemantic programme, one will still recognise their respective parallelism to the biosemantic leitmotifs of activity-oriented co-ordination and of representing absent, distant, possible or fictional world affairs. The main disagreement between the two models concerns the route between elementary forms of representation in perception and action and higher-order forms of representation in thought and language.

Remarkably, many examples mobilised by Millikan and other biosemanticists in support of their arguments are borrowed from the domain of animal signalling. Bee dances, mating displays and warning calls are typically tied to immediate practical requirements and display a combined descriptive and directive "pushmi-pullyu" character (Millikan, 1995). These examples and their discussion tend to leave an explanatory gap with respect to how and why, in terms of natural history, the differences between the abilities and kinds of reference-making involved in animal signalling and human language first came to pass. After all, it is not a given that their origins and purposes are of the same kind. Co-operation and practical co-ordination might not even be the norm in animal signalling, given that animal signals often serve deception instead, and hence are more ambivalent in function than an animal signalling-based model of the origins of language suggests (Sterelny, 2003, 2006; Birch, 2019; Martínez, 2019; Skyrms and Barrett, 2019). Even if animal signals provide the model, truthful or pragmatically adequate representation of world affairs might be just one among a variety of functions of linguistic forms, as Millikan highlights in (2018), and hence provides only one among a variety of explanations for their reproduction in populations of language-users. It might not be their primary proper function, and it might not have been the first.

Hence, the main point of contention between H_a and H_b is whether one shall assimilate the functions of language to functions of information exchange and co-operation between individuals that is modelled on certain, information- and co-operation-oriented forms of animal signalling, or whether one will do better assimilating them to ritual and symbolism, whose functions are more self-contained, being geared towards forms and modes of interaction within a group. Only in the former case, the representational content of utterances and their frequency of being

true or pragmatically adequate will unequivocally contribute to an explanation of the selection of their producer and consumer mechanisms. In the latter case, in contrast, the primary selected-for function of linguistic utterances appears to lie not in *what* is communicated but in the fact *that* something is communicated and *how* it is communicated. Moreover, the possibility should be considered that the explanation of the origins of the respective biological traits and linguistic forms is not identical with an explanation of their more recent maintenance in human populations. These explanations might undergo transformations in either direction, from information and practical co-ordination to symbolism and ritual and vice versa.

The relative advantage of H_b over H_a lies in the greater autonomy from the model of animal signalling that it grants to forms human language, and in its promise of overcoming if not closing the explanatory gap between them that has been identified as one of the major problems for biosemantics (see, for example Neander and Schulte, 2021). Where a signalling-based approach faces the difficulty of explaining just how and why higher-order, abstract forms of representation emerged from perceptual detection and animal signals, and where its candidate explanations will be quite directly measured with the yardstick of the potential adaptive value of those higher-order forms, the mutualist model takes higher-order forms of representation as phenomena in their own right, with conditions of selection of their own. Their interplay with the selection for corresponding organic traits will form the mutualist model's domain of the explanandum, for which it has a more diversified, pluralistic repository of explanantia. The mutualist model also leaves more room for the philosopher's intuition that there is something specific if not special about human thought and language that cannot be easily cast in the form of adaptive values. The more detached the properties of language become from direct adaptive needs, the more free they are to become exapted for such uses in more sophisticated ways than offered by signalling-based accounts. Still, this interpretation of the biosemantic project will not only retain but possibly also strengthen its commitment to evolutionary naturalism.

6. Conclusion

If the previous analysis is to the point, the answer to the general question of this inquiry (Q1) is this: The proper functions of linguistic forms are, on the one hand, rooted in the realm of developmental structures whose operations and functions are partly independent of biological adaptation *sensu strictu*, but bear tenable partial analogies to the latter, in being subject to forms of heredity, variation and selection-for. On the other hand, they interact with the evolution and maintenance of cognitive traits in human populations. Only in conjunction will the histories of linguistic forms and organic traits provide the full picture of the foundations of human language and thought.

With respect to answering the more specific question of this inquiry (Q2), the proper functions of language as a reproductively established mechanism are neither *ex hypothesi* necessarily nor *de facto* exclusively based on signal-based reference to and co-ordination of practical affairs that would subordinate them to human adaptive needs on the biological level. If the mutualist H_b model is correct, forms of language might have first been established and maintained for producing other effects that have no direct biological fitness values attached to them but in more indirect ways became a human-made part of the selectively relevant conditions in the evolution of human cognition. Conversely, if the hierarchical H_a model is correct, forms of language might have been exapted from functions of immediate adaptive relevance for more abstractive, symbolic communicative purposes. A comprehensive argument to justify the choice between these positions is beyond the scope of this essay, but I am hopeful to have begun to make the case, on the basis of pluralist evolutionary arguments, that an alignment with a mutualist H_b model would optimally adapt biosemantics to its original purpose of formulating a strong, comprehensive and balanced naturalistic programme in the philosophy of mind and language.

References

Artiga, M. (2011). On several misuses of Sober's selection for/selection of distinction. *Topoi, 30*, 181–193. https://doi.org/10.1007/s11245-011-9113-8

Barkow, J. H., Cosmides, L., & Tooby, J. (Eds.). (1992). *The adapted mind: Evolutionary Psychology and the generation of culture*. Oxford/New York: Oxford University Press.

Bateson, P. (2001). In Oyama, et al. (Eds.), *Behavioral development and Darwinian evolution* (pp. 149–166), 2001.

Birch, J. (2019). Altruistic deception. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences, 74*, 27–33. https://doi.org/10.1016/j.shpsc.2019.01.004

Black, M. (1962). *Models and metaphors*. Ithaca: Cornell University Press.

Bowles, S., & Gintis, H. (2011). *A cooperative species: Human Reciprocity and its evolution*. Princeton: Princeton University Press.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.

Boyd, R., & Richerson, P. J. (2009). Culture and the evolution of human cooperation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 364*, 3281–3288. https://doi.org/10.1098/rstb.2009.0134

Brandon, R. N. (1995). *Adaptation and environment* (2 ed.). Princeton: Princeton University Press.

Burmester, T. (2001). Molecular evolution of the arthropod hemocyanin superfamily. *Molecular Biology and Evolution, 18*, 184–195. https://doi.org/10.1093/oxfordjournals.molbev.a003792

Cavalli-Sforza, L. L., & Feldman, M. W. (1981). *Cultural transmission and evolution: A quantitative approach*. Princeton: Princeton University Press.

Chomsky, N. (2006). *Language and mind* (3 ed.). Cambridge/New York: Cambridge University Press.

Christiansen, M. H., & Chater, N. (2008). Language as shaped by the brain. *Behavioral and Brain Sciences, 32*, 429–448.

Christiansen, M. H., & Kirby, S. (Eds.). (2003). *Language Evolution*. Oxford/New York: Oxford University Press.

Clark, A. (1997). *Being there: Putting brain, body and world together again*. Cambridge: MIT Press.

Clark, A. (2006). Language, embodiment, and the cognitive niche. *Trends in Cognitive Sciences, 10*, 370–374.

Darwin, C. (1859). *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life* (1 ed.). London: John Murray.

Dawkins, R. (1989). *The selfish gene* (Revised edition). Oxford: Oxford University Press. originally published 1976.

Deacon, T. W. (1997). *The symbolic species*. New York/London: The Co-Evolution of Language and the Brain. Norton.

Developing scaffolds in evolution, culture, and cognition. In Caporael, L. R., Griesemer, J. R., & Wimsatt, W. C. (Eds.), *The Vienna Series in Theoretical Biology*, (2014). Cambridge: MIT Press.

Dobzhansky, T. (1950). Genetics of natural populations: Xix. origin of heterosis through natural selection in populations of *drosophila pseudoobscura. Genetics, 35*, 288–302.

Donald, M. (1991). *Origins of the modern mind: Three stages in the evolution of culture and cognition*. Cambridge: Harvard University Press.

Dretske, F. (1988). *Explaining behavior reasons in a world of causes*. Cambridge/London: MIT Press.

Dretske, F. (2001). Norms, history and the mental. In D. M. Walsh (Ed.), *Naturalism, evolution and mind* (pp. 87–104). Cambridge: Cambridge University Press.

Durham, W. H. (1991). *Coevolution: Genes, culture, and human diversity*. Stanford: Stanford University Press.

Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford: Clarendon Press.

Fulda, F. (2015). A mechanistic framework for Darwinism or why Fodor's objection fails. *Synthese, 192*, 163–183. https://doi.org/10.1007/s11229-014-0557-4

Gärdenfors, P., & Lombard, M. (2020). Technology led to more abstract causal reasoning. *Biology and Philosophy, 35*, 40. https://doi.org/10.1007/s10539-020-09757-z

Gibson, K. R., & Ingold, T. (Eds.). (1993). *Tools, language and cognition in human evolution*. Cambridge: Cambridge University Press.

Gilbert, S. F., & Tauber, A. I. (2016). Rethinking individuality: The dialectics of the holobiont. *Biology and Philosophy, 31*, 839–853. https://doi.org/10.1007/s10539-016-9541-3

Godfrey-Smith, P. (1994). A modern history theory of functions. *Noûs, 28*, 344–362.

Godfrey-Smith, P. (1996). *Complexity and the function of mind in nature.* Cambridge: Cambridge University Press.

Godfrey-Smith, P. (2020). *In the beginning there was information? Studies in history and philosophy of science Part C: Studies in history and philosophy of biological and Biomedical sciences, 80* p. 101239. https://doi.org/10.1016/j.shpsc.2019.101239

Goldschmidt, R. B. (1949). Phenocopies. *Scientific American, 181*, 46–49.

Goode, R., & Griffiths, P. E. (1995). The misuse of Sober's selection for/selection of distinction. *Biology and Philosophy, 10*, 99–108. https://doi.org/10.1007/BF00851989

Gordon, D. M. (2001). In Oyama, et al. (Eds.), *The development of ant colony behavior* (pp. 141–148), 2001.

Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society, B, 205*, 581–598.

Gould, S. J., & Vrba, E. S. (1982). Exaptation – a missing term in the science of form. *Paleobiology, 8*, 4–15.

Greif, H. (2017). What is the Extension of the Extended Mind? *Synthese, 194*(11), 4311–4336. https://doi.org/10.1007/s11229-015-0799-9

Griesemer, J. R. (2000). In Beurton, et al. (Eds.), *Reproduction and the reduction of genetics* (pp. 240–285), 2000.

Hesse, M. B. (1966). *Models and analogies in science.* Notre Dame: University of Notre Dame Press.

Heyes, C. (2018). Cognitive Gadgets. In *The cultural evolution of thinking.* Cambridge: Belknap.

Hull, D. L. (1980). Individuality and selection. *Annual Review of Ecology, Evolution, and Systematics, 11*, 311–332.

Hull, D. L. (1982). The naked meme. In H. C. Plotkin (Ed.), *Learning, Development, and Culture* (pp. 273–327). Chichester: Wiley & Sons.

Jackson, F. (2006). The epistemological objection to opaque teleological theories of content. In G. Macdonald, & D. Papineau (Eds.), *Teleosemantics* (pp. 85–99). Oxford: Oxford University Press.

Jeler, C. (2017). Multi-level selection and the issue of environmental homogeneity. *Biology and Philosophy, 32*, 651–681. https://doi.org/10.1007/s10539-017-9578-y

Killin, A. (2017). Where did language come from? Connecting sign, song, and speech in hominin evolution. *Biology and Philosophy, 32*, 759–778. https://doi.org/10.1007/s10539-017-9607-x

Laland, K. N. (2017). Darwin's Unfinished Symphony. In *How culture made the human mind.* Princeton: Princeton University Press.

Lewontin, R. C. (1970). The units of selection. *Annual Review of Ecology and Systematics, 1*, 1–18.

Lewontin, R. C. (1982). Organism and environment. In H. C. Plotkin (Ed.), *Learning, Development, and Culture* (pp. 151–170). Chichester: Wiley & Sons.

Lewontin, R. C. (2000). *The triple helix: Gene, organism, and environment.* Cambridge/London: Harvard University Press.

Lloyd, E. A. (2017). Units and levels of selection. In E. N. Zalta (Ed.), *The Stanford Encyclopedia of philosophy. Summer 2017.* Stanford: The Metaphysics Research Lab. https://plato.stanford.edu/archives/sum2017/entries/selection-units/.

Lloyd, E. A., & Wade, M. J. (2019). Criteria for holobionts from community genetics. *Biological Theory, 14*, 151–170. https://doi.org/10.1007/s13752-019-00322-w

Lumsden, C., & Wilson, E. O. (1981). *Genes, mind and culture: The coevolutionary process.* Cambridge: Harvard University Press.

Malafouris, L., & Renfrew, C. (Eds.). (2010). *The cognitive life of things: Recasting the boundaries of the mind.* Cambridge: McDonald Institute for Archaeological Research.

Martínez, M. (2019). Deception as cooperation. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences, 77*, 101184. https://doi.org/10.1016/j.shpsc.2019.101184

Mesoudi, A. (2011). *Cultural evolution: How Darwinian theory can explain human culture and synthesize the social sciences.* Chicago/London: University of Chicago Press.

Millikan, R. G. (1984). *Language, thought, and other biological categories.* Cambridge/London: MIT Press.

Millikan, R. G. (1989a). Biosemantics. *Journal of Philosophy, 86*, 281–297.

Millikan, R. G. (1989b). In defense of proper functions. *Philosophy of Science, 56*, 288–302.

Millikan, R. G. (1991). Speaking up for Darwin. In G. Rey, & B. Loewer (Eds.), *Meaning in mind: Fodor and his critics* (pp. 151–164). Oxford: Blackwell.

Millikan, R. G. (1993a). Explanation in biopsychology. In J. Heil, & A. Mele (Eds.), *Mental Causation* (pp. 211–232). Oxford: Oxford University Press.

Millikan, R. G. (1993b). Propensities, exaptations, and the brain. In *White Queen Psychology and Other Essays for Alice* (pp. 31–50). Cambridge/London: MIT Press.

Millikan, R. G. (1995). Pushmi-pullyu representations. *Philosophical Perspectives, 9*, 185–200.

Millikan, R. G. (1998). Cognitive luck: Externalism in an evolutionary frame. In P. Machamer, & M. Carrier (Eds.), *Philosophy and the sciences of mind* (pp. 207–219). Pittsburgh University Press and Universitätsverlag Konstanz. Pittsburgh-Konstanz Series in the Philosophy and History of Science.

Millikan, R. G. (2000). *On clear and Confused ideas. An essay about substance concepts.* Cambridge/New York: Cambridge University Press.

Millikan, R. G. (2001). What has natural information to do with intentional representation? In D. M. Walsh (Ed.), *Naturalism, evolution and mind* (pp. 105–125). Cambridge: Cambridge University Press.

Millikan, R. G. (2003). Vom angeblichen Siegeszug der Gene und der Meme. In A. Becker (Ed.), *Gene, Meme und Gehirne. Geist und Gesellschaft als Natur* (pp. 90–111). Frankfurt: Suhrkamp.

Millikan, R. G. (2004). *Varieties of meaning.* Cambridge/London: MIT Press.

Millikan, R. G. (2006). Useless content. In G. Macdonald, & D. Papineau (Eds.), *Teleosemantics* (pp. 100–114). Oxford: Oxford University Press.

Millikan, R. G. (2017). Beyond concepts. In *Unicepts, language and information.* Oxford: Oxford University Press.

Millikan, R. G. (2018). Biosemantics and words that don't represent. *Theoria, 84*, 229–241. https://doi.org/10.1111/theo.12146

Neander, K. (1991a). Functions as selected effecs: The conceptual analyst's defense. *Philosophy of Science, 58*, 168–184.

Neander, K. (1991b). The teleological notion of 'function. *Australasian Journal of Philosophy, 69*, 454–468.

Neander, K. (2012). Toward an informational teleosemantics. In D. Ryder, J. Kingsbury, & K. Williford (Eds.), *Millikan and her critics* (pp. 21–36). Chichester: Wiley-Blackwell.

Neander, K., & Schulte, P. (2021). Teleological theories of mental content. In E. N. Zalta (Ed.), *The Stanford Encyclopedia of philosophy. Spring 2021.* Stanford: The Metaphysics Research Lab. p. html. URL: https://plato.stanford.edu/archives/spr2021/entries/content-teleological/.

Odling-Smee, F. J., Laland, K. N., & Feldman, M. W. (1996). Niche construction. *The American Naturalist, 147*, 641–648.

Okasha, S. (2006). *Evolution and the levels of selection.* Oxford: Oxford University Press.

Oyama, S. (2000). *The ontogeny of information: Developmental systems and evolution* (2 ed.). Durham: Duke University Press.

Oyama, S., Griffiths, P. E., & Gray, R. D. (Eds.). (2001). *Cycles of Contingency. Developmental systems and evolution.* Cambridge/London: MIT Press.

Papineau, D. (1984). Representation and explanation. *Philosophy of Science, 51*, 550–572.

Papineau, D. (1987). *Reality and representation.* Oxford: Blackwell.

Papineau, D. (2001a). The evolution of means-end reasoning. In D. M. Walsh (Ed.), *Naturalism, evolution and mind* (pp. 145–178). Cambridge: Cambridge University Press.

Papineau, D. (2001b). The status of Teleosemantics, or how to stop worrying about Swampman. *Australasian Journal of Philosophy, 79*, 279–289.

Pinker, S., & Bloom, P. (1990). Natural language and natural selection. *Behavioral and Brain Sciences, 13*, 707–784.

Renfrew, C. (2012). Towards a cognitive archeology: Material engagement and the early development of society. In I. Hodder (Ed.), *Archaeological theory Today* (2 ed., pp. 122–140). Cambridge: Polity Press.

Roughgarden, J., Gilbert, S. F., Rosenberg, E., Zilber-Rosenberg, I., & Lloyd, E. A. (2018). Holobionts as units of selection and a model of their population dynamics and evolution. *Biological Theory, 13*, 44–65. https://doi.org/10.1007/s13752-017-0287-1

Shea, N. (2007). Consumers need information: Supplementing teleosemantics with an input condition. *Philosophy and Phenomenological Research, 75*, 404–435. https://doi.org/10.1111/j.1933-1592.2007.00082.x

Skyrms, B. (2003). *The stag hunt and the evolution of social structure.* Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9781139165228

Skyrms, B., & Barrett, J. A. (2019). Propositional content in signals. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences, 74*, 34–39. https://doi.org/10.1016/j.shpsc.2019.01.005

Smith, K., & Kirby, S. (2008). Cultural evolution: Implications for understanding the human language faculty and its evolution. *Philosophical Transactions of the Royal Society, B, 363*, 3591–3603.

Sober, E. (1984). *The nature of selection: Evolutionary theory in philosophical focus.* Cambridge: MIT Press.

Sterelny, K. (2003). *Thought in a hostile world.* Oxford: Blackwell.

Sterelny, K. (2006). Language, modularity, and evolution. In G. Macdonald, & D. Papineau (Eds.), *Teleosemantics* (pp. 23–41). Oxford: Oxford University Press.

Sterelny, K. (2007). Social intelligence, human intelligence and niche construction. *Philosophical Transactions of the Royal Society, B, 362*, 719–730.

Sterelny, K. (2010). Minds: Extended or scaffolded? *Phenomenology and the Cognitive Sciences, 9*, 465–481.

Sterelny, K. (2012). *The evolved apprentice: How evolution made humans unique.* Cambridge: MIT Press.

Sterelny, K., & Kitcher, P. (1988). The return of the gene. *The Journal of Philosophy, 85*, 339–361.

The concept of the gene in development and evolution. In Beurton, P. J., Falk, R., & Rheinberger, H. J. (Eds.), *Historical and Epistemological Perspectives,* (2000). Cambridge: Cambridge University Press.

Thompson, J. N. (1994). *The coevolutionary process.* Chicago: Chicago University Press.

Thompson, J. N. (2005). *The geographic mosaic of coevolution.* Chicago: Chicago University Press.

Tomasello, M. (2008). *The origins of human communication.* Cambridge/London: MIT Press.

Tomasello, M. (2014). *A natural history of human thinking.* Cambridge: Harvard University Press.

van Holde, K. E., Miller, K. I., & Decker, H. (2001). Hemocyanins and invertebrate evolution. *Journal of Biological Chemistry, 276*, 15563–15566. https://doi.org/10.1074/jbc.R100010200

Wade, M. J. (2016). *Adaptation in metapopulations.* Chicago: University of Chicago Press.

Williams, G. C. (1966). *Adaptation and natural selection. A critique of some current evolutionary thought.* Princeton: Princeton University Press. Reissue with new preface, 1996.

Wimsatt, W. C. (1980). The units of selection and the structure of the multi-level genome. *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association*, 122–183. https://doi.org/10.1086/psaprocbienmeetp.1980.2.192589

Wright, S. (1931). Evolution in mendelian populations. *Genetics, 16*, 97–159. https://www.genetics.org/content/16/2/97, arXiv:https://www.genetics.org/content/16/2/97.full.pdf.

Wright, L. (1973). Functions. *Philosophical Review, 82*, 139–168.

Wright, S. (1980). Genic and organismic selection. *Evolution, 34*, 825–843. https://doi.org/10.1111/j.1558-5646.1980.tb04022.x