Living and Experiencing: Response to Commentaries

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Abstract

In our target article, "Learning and the evolution of conscious agents" we outlined an evolutionary approach to consciousness, arguing that the evolution of a form of open-ended, representational, and generative learning (unlimited associative learning, UAL) drove the evolution of consciousness. Our view highlights the dynamics and functions of consciousness, delineates its taxonomic distribution and suggests a framework for exploring its developmental and evolutionary modifications. The approach we offer resonates with biosemioticians' views, but as the responses to our target article show, our proposal also faces challenges and has led to suggestions that extend, develop and qualify it. Our response to the 14 varied and rich commentaries starts with the recurring and deep question raised by many of them – the relation between life and sentience. We explore this question by introducing and expanding on "vivaciousness", a term we coined to describe the turbulent, flexible exploration-stabilization processes inherent in the living condition, as well as addressing the related concepts of Umwelt and selfhood. We then consider the question of the adequacy of unlimited associative learning (UAL) as an evolutionary transition marker (ETM) of *minimal* consciousness (rather than as a marker of a complex form of sentience), and the possible precursors of sentience. The engagement with these broad themes is entangled with a discussion of evolutionary transitions, constitutive emergence and the function/s of consciousness. The suggestions of our commentators, urging us to explore new concepts and new avenues of research within the framework of a richer view of evolution are then discussed. We end by briefly considering what we regard as a conceptual lacuna, which is leading to the indiscriminate use of the term "sentience" and which awaits further investigation.

1. Introduction

We are very grateful to all commentators on our target article, “Learning and the evolution of conscious agents” (Jablonka & Ginsburg 2022) and thankful for the opportunity to engage with views that often challenge ours yet share enough common ground to allow fruitful discussion. As Sharov (2022) has shown, our evolutionary transition approach mostly matches the semiotic competence levels of organisms discussed by biosemioticians. Olteanu too (2022) points to the resonance between our theory and the biosemiotic approach to learning and consciousness, while other biosemioticians [Campbell (2022), Hendlin (2023), Tønnesson (2022)] emphasize both the common ground and the need to incorporate terms such as Umwelt into our framework and to expand on the continuity between life and mind. Trestman (2023) discusses the correspondence between our approach and the phenomenological perspective, emphasizing the notion of duration, temporal flow and goal-directed behavior that were seen as fundamental to conscious experiencing. He notes that within the phenomenological school of thought, learning is regarded as intrinsic to consciousness, since “the dynamics of consciousness can be seen as a learning process as a whole.” Irwin (2023) too sees value in the methodological road map we provided, but like several other commentators, points to open questions, presents important challenges and emphasizes new research directions. Nevertheless, he believes that there is enough common ground between his approach and ours to open a productive dialogue.

We cannot do justice and discuss all the topics raised by our commentators, but in the following sections we address concerns that were central to most of them, many of which overlap in spite of their different emphases. The suggestions and critiques of the commentators open up new avenues of philosophical and evolutionary investigation and are an opportunity to further clarify our position, extending and qualifying our approach to the evolution of sentience. The dominant themes we address here are: The relation between life, cognition and sentience and the notion of vivaciousness (section 2); The Umwelt of living and living-sentient organisms (section 3); The status of UAL as a marker of minimal consciousness (section 4) and the transitions in the evolution of consciousness that we have suggested (section 5); Constitutive emergence and the functions and goals of consciousness (section 6); Evolutionary trends in the evolution of consciousness (section 7), and the incorporation of conscious choices in the Extended Evolutionary Synthesis (section 8). All these topics are brought together in the conclusion (section 9), which also points to a conceptual lacuna in current discussions of subjectivity and subjecthood.

2. Life and Sentience

The assumption that there is no life without sentience is reflected in the biopsychic stance of some of our commentators, who regard all living beings, from bacteria to humans, as sentient. This biopsychic assumption is clearly stated by Reber, Baluška & Miller (2022) and by Meincke (2023), but a biopsychic stance is also implied in the commentaries of Hendlin (2023), Tønnessen (2022), and Riskin (2023). Interestingly, the Buddhist Abhidharma school makes a similar assumption with regard to the necessary relation between life and sentience but reaches a diametrically different conclusion. According to the view expressed by this influential school of Buddhism, only sentient beings are alive; since plants are not regarded as sentient/conscious beings, plants are not regarded as living organisms (Lama, 2005).

Like other modern biologists, we reject both the biopsychists' approach and the untenable Buddhist Abhidharma position. The view held by us and some of our commentators [most explicitly, Irwin (2023), Moreno (2023), Noble (2022) and Trestman, (2023)] is that living beings include all organic autonomously reproducing organisms, but that not all living beings are sentient/conscious. Our research project is based on the assumption of an *evolved* qualitative distinction between conscious and non-conscious modes of being, although we recognize the evolutionary continuity between them and are aware of grey areas that defy categorization. On our view, the question of how consciousness evolved from a non-conscious, living, mode of being is crucial. For biopsychists, who regard consciousness as a primitive of life, this question is identical to the origins of life question, although, interestingly, biopsychists do not seem to engage with the origin of life research project.

Before we go on to address the life-sentience relation and some of the biopsychists' concerns and intuitions, we would like to note that, as stressed by Campbell (2022), the topics of consciousness (and the evolution of consciousness) were avoided by most biosemioticians, so the necessity of making distinctions between conscious and non-conscious beings was not a central question within this theoretical framework. The reluctance to make qualitative distinctions between forms of life was seen as the necessary consequence of an adherence to the evolutionary continuity between living organisms, although evolutionary continuity does not preclude major, qualitative evolutionary transitions (Maynard Smith & Szathmáry, 1995), a point which is acknowledged and discussed by Sharov (2022) and developed by other biosemioticians (e.g., Hoffmeyer & Stjernfelt, 2016) and to which we return in a subsequent section.

2.1 Sentience and Vivaciousness, Subjectivity and Subjecthood

Reber, Baluška & Miller (2022) suggest that biological systems are cognitive systems and that all cognitive systems are sentient, equating biological cognition with sentience. As we indicated in our target article and in previous publications, we do not regard cognition and sentience as synonyms. We defined a cognitive system as a system that can learn and argued that learning is an ancient capacity of living organisms, which preceded sentience. We wrote: "Learning encompasses or enables all the features that have been listed as capacities or mechanisms of cognition [i.e., mechanisms and processes that underlie information acquisition, storage, processing, and use, at any level of organization] so any system with the capacity to learn can be described as a cognitive system." (Ginsburg & Jablonka, 2021a, p. 2). Indeed, based on their mechanisms of acquiring storing and using information, all living systems are cognitive systems: Lyon (2015) attributed cognition to bacteria on the basis of their sophisticated information processing capacities; protists like ciliates and amoeba are cognitive systems since they can learn by sensitization and/or habituation, and so can some plants and fungi, and as simple models have suggested, very limited associative learning can occur in single cells based on cellular networks (Fernando et al., 2009; Ginsburg & Jablonka, 2009). Sentience on the other hand, is, we suggested, much more evolutionarily recent and depends on a particular type of complex cognition, operationalized by UAL. As we argued, sentience requires complex dynamic architecture (it is no surprise to us that learning machines are relatively easy to construct but sentient machines do not exist). Just as life requires complex interactions among different systems (metabolic networks, membranes, heredity-memory mechanisms that together allow regulated self-production), so, we argued, does sentience depend on the dynamics of complex cognition.

The claim that not all living and cognizing organisms are sentient has been challenged by several of our commentators. Meincke (2023), following Hans Jonas' view of life and mind, claims that a more inclusive notion of consciousness than the one we suggest, a notion that includes all living organisms, is required to do justice to the intricacy of living processes. She attributes the capacities "choice", "self-transcendence", and "taking a stand on life" to all living agents. However, this metaphorical language is, in our view, tautological – it is part of the definition of living rather than an argued for and justified attribute. An attempt to justify the need for sentience in all life forms is offered by Reber, Baluška & Miller (2022) who state that something they call "self-referencing" (which is assumed to require sentience) is necessary for living processes. Self-referencing is not clearly defined, but we assume that it requires regulatory mechanisms that sense deviations from homeostasis and recruit systems that lead to repair and re-equilibration. Reber, Baluška & Miller attribute to us a position which we have never held: they claim that we assume that each of the regulatory control mechanisms in living organisms evolved independently and state that "There is no model of evolutionary biology that we are aware of that allows for such a wide variety of mechanisms to emerge independent of a self-referencing, internal instantiation". To the best of our knowledge, all origin of life theories are based on both the coming together and the co-evolution of complex chemical systems, rather than on the autonomous evolution of each singular mechanism. As Gánti's model of minimal life suggests, minimal living organisms are complex entities, having the partially overlapping capacities for metabolism, individuality, dynamic regulation-based stability, informational control, growth, hereditary continuity, and irreversible dissolution. Open-ended plasticity is afforded by the material organic constitution of such beings and is operationalized by the *coupling* of the processes that enable the above capacities (modeled by Gánti's chemoton) through processes that harness stochasticity, which as Noble (2021, 2022) states, is recruited through natural and intentional selection to enable adaptive responses to changing external and internal conditions. This stochastic and semi-stochastic exploration underlies the precarious life-cycles of individuals and is the basis for the evolutionary continuity of lineages of living organisms. However, the recognition of co-evolution and co-dependence among the chemical mechanisms that enable ontogenetic self-preservation and evolutionary continuity does not require the attribution of mentality – of feeling or of perception. None of the current origin of life theories (with which, as we noted, the biopsychists seem reluctant to engage), suggest mentality.

The dynamics of life as we know it, are, as we suggested in the target article, very different from the dynamics of inanimate matter. Vivaciousness was the term we introduced to characterize the intrinsic dynamics of living beings. We defined vivaciousness as "the inner, plastic, default dynamic state of a living system which is necessary for sustained active living" and suggested that this dynamic state defines the inwardness of individual living entities with a certain type of material (water-based) plasticity that are distinct from their milieu though always interacting with it. We fail to understand why Meincke (2023) considers the notion of a non-sentient inwardness as an oxymoron. It seems to us that Meincke is equating inwardness with mental subjectivity.

Interestingly, Aristotle's discussion of the concept of food (*On the Soul,* 1984) is a de facto recognition of the process we now call metabolism, which Meincke regards as an indicator of mentality. The processes that render a substance food, were, for Aristotle, the hallmark of the *nutritive soul* not necessitating a *sensitive soul*, although he recognized that the nutritive soul is the dynamic scaffold on which sensitive living souls are built. Meincke adopts Jonas' position linking life and sentience, assuming that intrinsic value has to be mental (rather than inherent in the non-mental dynamics of the mechanisms of self-preservation). Jonas' and Meincke's position is an a-priori claim that cannot therefore provide an answer to Thompson's challenge to Jonas: "Why can't there be intrinsically purposive, autopoietic agents that respond to values as norms of flourishing but without feeling hedonic value or affective valence?" (Thompson, 2022). A self/world registration coupled with minimal metabolic control are indeed necessary, as Campbell (2022) notes, for the construction of a mental self, but on our theory, this is not sufficient. All organisms have minimal metabolic control, and all have some distinction between self-generated and world-generated (sensorially identical) stimuli. However, this does not mean that the intrinsic valence underlying these capacities are mentally experienced.

Maybe the a priori assumption that intrinsic value must be mentally experienced is related to a different understanding of the terms "subject" and "subjective experiencing". Subjective experiencing, as Tønnessen (2022) defines it, is "the experiencing of the subject". However, a "subject", as we understand the term, does not necessarily have mental states. A subject does have closure (and hence also a necessary inwardness and individuality) and is an agent that interacts with object/s external to it, reacting differently to world-generated and self-generated identical stimuli. Such reafferent reactions, were, we suggested, the non mental precursors of the mental sense of self, and such reactions may be thought of as constituting "subjecthood". But such subjecthood is as yet not *mental subjecthood*. Olteanu (2022) may have interpreted our usage of the term "subjective" in biosemiotic terms (as belonging to a subject, as subjecthood) and not in the common sense of equating "subjective experiencing" with "mental experiencing", implying private, mental states such as perceiving the taste of banana ice cream and feeling fear.

We lack a concept that captures non-mental subjecthood, and we believe that biopsychists use the notion of sentience to cover this conceptual gap. If their notion of sentience is indeed used to refer to subjecthood, then the notion of phenomenal consciousness or sentience that they employ is radically different from our notion, which is defined in terms of perception (mental experiencing of sensory stimuli) and feeling (mental evaluations). It is never concretely stated by biopsychists what the sentience of non-neural organisms entails. Do single-celled organisms, plants and fungi feel pleasure? Pain? Fear? Do bacteria and plants have mental experiences of smells and sights? What does the notion of *unconsciousness* mean with regard to these organisms? For example, what is the state of an unconscious living bacterium? How do living cells interact to generate both an anesthetized, unconscious animal states, and conscious states? What is the difference? We are *not* assuming, as Meincke claims, that the interactions between such sentient cells in an unconscious or a conscious animal are additive rather than emergent. Most complex biological interactions are non-linear and in this sense the outcomes of the interactions are emergent. However, the onus is on the biopsychists to address and explain the distinction between conscious and unconscious living organisms at both the level of the organism as a whole, (e.g., a mammal) versus the level of the parts, (e.g., the cells comprising the animal). Such an analysis may lead to the conclusion that the sentience of cells and the sentience of multicellular organisms has very different meanings, and necessitates new conceptual distinctions (Ginsburg & Jablonka, 2021b).

Although we introduced the term vivaciousness to distinguish between living and non-living matter and to point to the hiatus between living organisms and inanimate matter, we did not attempt to compare vivaciousness in different kingdoms. We did note that the vivaciousness characteristic of nervous systems has a neural aspect that is not found in nerveless plants, but we did not compare intensities of vivaciousness and nowhere have we attributed, as Riskin (2023) claims, less vivaciousness to plants than to animals. As Lamarck emphasized, the way that plants interact with the a-biotic environment is very different from that of animals, and their survival strategies are, as a result, profoundly different, so the way their vivaciousness is expressed is likely to be different too. Fecundity, however, is not a very good measure of overall vivaciousness, although like other living processes (e.g., thinking) it does require energy and a level of arousal which Trestman (2023) calls vivacity. We did not try to construct a scale of vivaciousness, although we believe that the energetic considerations that Trestman discusses are important and that access to energy sources, which as Lamarck noted, is different for plants and animals, is crucial for any response, of any living organism, to changing conditions.

3. The Umwelt of Living and Living-Sentient Organisms

Riskin (2023) wants us to emphasize the interactions between different living beings and products of living beings. In the target article we discussed the effect of sentient animals on the physiology and morphology of non-sentient organisms such as plants. As we proposed, during the Cambrian era, conscious animals, mainly arthropods, exerted enormous pressure on all living organisms through their interactions with them and led to the evolution of camouflage, of poisons, new cooperative and parasitic interactions as well as to learning arms-races. There were reciprocal interactions and on-going co-evolution between sentient and non-sentient living organisms, and, as Lamarck noted and Riskin emphasizes, within the large ecological picture of our planet, these interactions included the products of living beings, of metabolism-derived minerals, which were both products and facilitators of evolving life forms. Lamarck indeed stressed, as Riskin reminds us, the multi-directional interactions within the planet's ecology, but he also repeatedly emphasized the special mode of living of animals, whose hallmark structure, which underwent many transformations during the evolutionary history of animals, was the nervous system, a system he regarded as crucial for mental life. In chapter 6-9 of our book (Ginsburg & Jablonka, 2019), we described the geological, geo-chemical, ecological and developmental conditions that enabled the evolutionary emergence of the sentient mode of being; the whole of chapter 9 is devoted to the ecological context in which sentience emerged and evolved. Maybe we should have widened, as Riskin suggests, our discussion of the interacting web of which we are all part and engaged more with the effects of sentience on niche construction and the evolution of ecological, developmental and social systems. There is no doubt that a more in-depth discussion of the interactions of animals, plants, fungi, unicellular organisms and minerals, would enrich our understanding of evolution including the special case of the evolution of sentience. Still, we are not clear what fundamental difference this richer picture would make for our view of the distribution of sentience.

A similar point to that raised by Riskin arises within the context of our commentators' discussion of Umwelt, the self-centered world of a living being, which involves the generation of species-specific models of the environment. As Uexküll & Kriszat [(1934), cited by Kull & Favareau, 2022] explained: “All that a subject perceives becomes his perceptual world and all that he does, his effector world. Perceptual and effector worlds together form a closed unit, the Umwelt”. In current ecological terminology, “Umwelt” is closely related to the notion of niche, since organisms living in the same environment (“same” as measured by an external observer) can have different *relevant* environments, depending on their sensory, motor and cognitive capacities. The notion of Umwelt implies niche construction and active and reciprocal environmental, developmental, cognitive and social scaffolding, since there are mutually constructing and on-going relations between the organism and the relevant milieu which it senses and in which it acts. The significance of such reciprocal interactions has been accommodated and stressed by early evolutionists like Lamarck and Darwin, but it was downplayed by the standard neo-Darwinian evolutionary theory that has dominated evolutionary theorizing for much of the 20th century. It has become again of central importance to the current rethinking of evolutionary theory (the Extended Evolutionary Synthesis, the EES), a 21st century version of evolutionary theory which stresses agency, niche construction, plasticity and the multiple ways of information transmission within and between generations (Laland et al., 2015). The role of consciousness and intentional selection within this framework is one of the topics that are only now beginning to receive attention (Noble, 2021; Jablonka, 2021).

As Tønnessen (2022) rightly points out, the origin of the Umwelt is very ancient. We believe, as we think he does, that the co-construction of organisms and their relevant environment is as ancient as life itself. We also agree with him that a “sense saturated” Umwelten emerged during the Cambrian (with UAL), but we do not understand the basis of his claim that a primitive, *mental* sense of self preceded the Umwelten of sentient, Cambrian animals, and that the notion of Umwelt presupposes sentience. The latter assumption is also apparent in Kull & Favareau's commentary (2022). They claim that “umwelt per se, as sentience, appears long before consciousness in the world of living organisms”. They therefore seem to equate Umwelt and sentience and assume that consciousness is different from sentience. Their view is that the appearance of perceptual space and a specious present mark sentience, and that the latter is the outcome of the interactions of the organism-environment. The first mental expressions of “togetherness with the world”, they suggest, may have already been in place in organisms that could only learn in a limited way, but could nevertheless perceive composite wholes. As we suggest in the next sections, these assumptions need re-packing.

4. Is UAL a Marker of *Minimal* Consciousness?

Most commentators including Irwin (2023), Meincke (2023), Campbell (2022), Kull & Favareau (2022) and Belardinelli and Pievani (2023) question our specific criteria for minimal consciousness, as operationalized by UAL, because, they claim, these criteria are too demanding. Meincke concedes that “… the evolution of the nervous system has facilitated subjective experience or ‘consciousness’ in a more robust sense, while insisting that there were precursors. Indeed, this is what we ought to expect given how evolution works”. We have no doubt that there were indeed precursors, and in our 2019 book we devoted two chapters (chapters 6 and 7) to the evolution of the precursors of UAL, but we argued that we have no *positive arguments* suggesting that the animals displaying limited forms of associative learning (precursors of UAL) were sentient. Criteria for defining sentience in a more minimal manner than that suggested by us and listed in the target article, are needed, and this is the route taken by Irwin’s commentary.

Irwin’s main point, like that of the other commentators who take issue with UAL as a transition marker of minimal consciousness is that “the list of criteria proposed by Jablonka & Ginsburg (2022) is too expansive for truly minimal consciousness”, proceeding to ask: “Does “minimal consciousness” equate to the simplest form of consciousness, of which no simpler form of consciousness can be experienced, or does it mean the minimal mode of being in which some form of consciousness is fully emergent?” As we stated in previous publications (Birch, Ginsburg & Jablonka 2020,

2021) as well as in the target article, we can only *positively* identify which animals are conscious, but we cannot decisively say which animals are not conscious, because the UAL dynamics that satisfy all the consciousness criteria we have listed are only clearly evident when the transition to UAL has gone to completion, in other words, when consciousness is fully emergent. However, when living organisms show no UAL-like dynamic architecture, these organisms are unlikely to be sentient in the sense employed in discussions of phenomenal consciousness (which is the notion of consciousness we are interested in). These include unicellular organisms, fungi, plants, as well as some animals (e.g., cnidarians). All these organisms show remarkable adaptive plasticity and all display limited learning, but, on our view, they are unlikely to have mental experiences (perceive and feel; although we are, as we repeatedly stressed, aware of the alarming gaps in our knowledge, so our position with regard to the distribution question is open to qualified changes).

Irwin suggests that our minimal consciousness is not minimal, but rather a fairly late stage in the evolution of consciousness, preceded by a much simpler form of consciousness that does not require the demanding list of capacities that we suggest. He proposes that three capacities: (i) *unification and differentiation*, (ii) *selective attention and vigilance* (which require exploration-stabilization mechanisms) and (iii) *a sense of self*, are sufficient for minimal consciousness. The additional capacities we list – global accessibility, working memory/specious present, flexible value system, mapping of world, body and their relations, and goal-directed behavior – have, he argues, evolved later and contributed to a more advanced form of consciousness, which is operationalized by UAL.

We believe that the minimal list suggested by Irwin, includes, implicitly, all the eight capacities that we listed. Consciousness is a system property and the capacities that we listed are partially overlapping and form a coupled, integrated, dynamic system. For example, there can be no unification and differentiation of composite sensory stimuli without global accessibility and interaction between different modalities, memory traces and evaluations. All these interactions require world and body mapping and are based on back-and-forth feedbacks and reentrant interactions that require time, so some form of working memory to sustain the ongoing past and future oriented integrations and evaluations is necessary for this kind of associations to form. As Trestman (2023) notes, duration (which includes retention and protention) is central to the phenomenological view of consciousness as well as to ours – when stimuli are presented for a very short time they are not consciously processed. Since discrimination between composite sensory stimuli and selection among composite actions is context-dependent, a value system that requires the flexible ability to prioritize evaluations is needed, and this requires some enduring reference point which enables a stable perspective. Indeed, some of the testable predictions of the UAL theory are that there will be ontogenetic, medical and phylogenetic correlations among the different aspects of UAL (discrimination, working memory, flexible value system and second order conditioning). Trestman points, in addition, to the dynamics of surprisal (the mismatch between expectation and actuality), a process that we discussed at length in our 2019 book but did not give it enough space in the target article. These dynamics are intimately related to the dynamics of learning and highlight the importance of attention.

Although we believe that our list of capacities characterizes consciousness as we defined it in the target article, we are aware that the scope and richness of consciousness may vary, and as Hendlin (2023) rightly point out, there are tradeoffs among different cognitive and sensory capacities (language, for example, led to emotional and perceptual costs; see Jablonka, Ginsburg & Dor, 2012). Consciousness, we suggested, evolved several times and was probably lost in some lineages during evolution (for example, when in some lineages animals lost their brains). We recognize the different sensory and motor aspects of consciousness in different animals, as well as dimensions and degrees of conscious experience which may be more or less rich and unified (Birch, Schnell, & Clayton, 2020). Nevertheless, these many variations, which Hendlin emphasizes, do not mean that a distinction between conscious and non-conscious organisms is impossible – the recognition of gradations does not preclude qualitative distinctions between sentient and non-sentient living states. Just as the project of minimal life focuses on the most basic features of life, which underlie the endless diversity of living forms, so too, we have focused on the transition between non-conscious and minimally conscious animals, from which all the many diverse varieties of consciousness subsequently evolved.

But even if one accepts these caveats one can legitimately ask how rich UAL needs to be, for example how multidimensional the integration between modalities needs to be, how unified the sense of self needs to be, or how extended working-memory must be (Birch, Schnell, & Clayton, 2020). Meta-analysis of fear conditioning when the predictive stimuli are subliminal (e.g., under masking or distracting conditions) suggests that such conditioning may require consciousness (Mertens & Engelhard 2020). Furthermore, a recent study by Skora & Scott (2023) suggests that in humans all instrumental learning, even when not requiring composite action-representation, requires consciousness and cannot be performed under making conditions. One interpretation is that in humans, who have a fully operational consciousness and very strong top-down cognitive control, even simple learning often involves consciousness (just as reflex reactions, such as the blink reflex are mentally experienced). However, the alternative interpretation is that even simple forms of instrumental learning are indicative of consciousness, because, as Skora & Scott (2023) suggest, instrumental learning requires highly complex cognitive dynamics.

5. Transitions in the Evolution of Consciousness

If there was a transition to a new, sentient mode of being, does this suggest that a saltational, punctuated, evolutionary change has occurred? How gradual was the evolutionary transition to sentience?

Synechism, the philosophical approach advocated by Peirce, which focuses on continuities instead of assumed discontinuities, is, as Campbell (2022) notes, part of the basic conceptual toolkit of biosemioticians. However, the recognition of fundamental continuities between all stages of evolution and development does not imply that qualitative distinctions between different evolutionary or developmental stages cannot or should not be made. There is a qualitative distinction between black and white even if there are all shades of grey in between. Similarly, there is a qualitative difference between non-linguistic and linguistic-symbolic communication even though there is evolutionary continuity between them. There is also a qualitative difference between the blastula stage and the organogenesis stage in the embryogenesis of mammals, although some of the intermediate points along the trajectories between these developmental stages may be impossible to classify. As noted by Sharov (2022), some biosemioticians, though committed to the continuity thesis, recognize qualitative stages in the evolution of semiosis and even subscribe to a great chain of semiosis (although a bush would have been a better frame of thinking than a chain), investigating the steps in the evolution of semiotic competence (e.g., Hoffmeyer & Stjernfelt, 2016) and suggesting distinctions and evolutionary transitions between different semiotic systems. To repeat: gradations do not imply that qualitative distinction cannot be made. The whole evolutionary transitions research project (Maynard Smith & Szathmáry, 1995) is based on the assumption that qualitative changes did occur during evolutionary history and that the study of these qualitative changes, the rates and patterns of their evolution, can illuminate important questions such as the evolution of the genetic code, multicellularity and human language. There is no a-priori commitment to particular evolutionary rates or particular evolutionary patterns. Hence, our answer to Belardinelli and Pievani's question about the nature of the evolutionary transition to consciousness – whether UAL is the result of gradual or saltational evolution – is that we are not committed to either, especially since the time scale implied by the term “saltational” or “punctuated change” needs to be specified. The Cambrian explosion took millions of years, but was very rapid at the geological time scale, given the immense changes that occurred during this era.

As we have noted, in the animal kingdom, limited associative learning (LAL) is much more wide-spread than UAL, and had first emerged, probably, in the late Ediacaran or very early Cambrian. LAL was enormously advantageous and enabled, as Kull & Favareau (2022) noted, the formation of on-line distinctions between images (including images made up of many parts). However, it *did not* enable context sensitive discrimination learning, which requires, we argued, global accessibility, mapping, a flexible value system, working memory, a sense of self and selective attention – the whole list of overlapping capacities that we describe when describing minimal consciousness.

6. Constitutive Emergence and the Functions and Goals of Consciousness

The question of the relation between UAL and consciousness and the related question of the function/s of consciousness when it first emerged, is another important question raised by Belardinelli & Pievani (2023). Can we conceive of consciousness, they ask, as an emergent property, “a side effect of new learning abilities [and was] later coopted for new functions, and to enhance learning abilities”? In our opinion the notion of a side-effect or a by-product is inappropriate in this context. As we stress throughout the paper (and in our 2019 book), we see consciousness as a system property that is *constituted* by the processes and structures that underlie the capacity for UAL.

This is an opportunity to clarify what we mean by constitutive or componential emergence, and how we distinguish it from what we shall call spin-off emergence. With spin-off emergence there is a causal outcome of the target process that need not contribute to the functioning of this target process. An example is the sound of heart beats, which is caused by the operations of the heart and the circulatory system but does not itself contribute to the function of the heart. With constitutive/componential emergence on the other hand, the outcome is constituted by the parts and causal outcome processes themselves – the operations of the heart are constituted by heart-muscle cells and their systemic interactions; these are the kind of emergent causal interactions that explains whole-part relations. If consciousness was a spin-off causal emergent property it could be an exaptation as Belardinelli and Pievani suggest, but if consciousness is *constituted* by UAL dynamics, the notion that it is a by-product makes no sense (it is like saying that the heart’s pumping activity is a by-product of heart cells’ organization and activity). In other words, if sentience is constituted by the cognitive processes operationalized by UAL, there cannot be UAL dynamics without consciousness, and consciousness cannot be an originally functionless exaptation that only at later evolutionary stages was coopted for its current function. This means that the functions of the cognitive dynamics that constitute the capacity for UAL are also the functions of consciousness. As we write in the target article “We see subjective experiencing as constituted by cognitive-neurological functional operations such as integration within and between modalities, sensory-motor mappings, memory and evaluation processes, and regard the functions of these constitutive processes as some of the specific functions of subjective experiencing”.

We argued that thinking about the goals of consciousness may illuminate the functions of consciousness in a more general way. We suggested that the goal of symbolic-rational consciousness is to define and satisfy abstract symbolic values like freedom and justice, while the goal of sentience is to define and satisfy felt needs. There are whole realms of new functions that sentience and symbolic-rational consciousness open-up because consciousness and reflectiveness define new spaces of exploration and selection and define new goals. We used Kant’s term “purposefulness without purpose” to define these new exploration spaces, which are open-ended and cannot be described in terms of specific goals. Kant used this term to explain the notion of aesthetic judgment, which allows what he called the “free play of imagination”, the exploratory freedom that art allows. This freedom is, however, bound by the “common sense”, the shared sensory, cognitive and cultural-aesthetic biases of the judging individuals, who are thus able to meaningfully communicate about their judgments. Our discussion of the teleological transitions to living, sentient and rational-symbolic modes of being emphasizes the evolution of open-endedness and distinguishes these transitions from other types of evolutionary transitions (we discuss this topic in more detail in Ginsburg & Jablonka, 2020).

7. Evolutionary Trends in the Evolution of Consciousness

Although our main goal was to uncover principles of sentience that can be applied to animals with very different nervous systems, the study of the patterns of consciousness-evolution, and especially the study of the progressive trend in the evolution of consciousness in vertebrates that Moreno highlights, can reveal important constraints and affordances in the evolution of consciousness. There are, as Moreno (2023) pointed out, important differences between arthropods, cephalopods and vertebrates in the extent and scope of both cognition and conscious awareness. This, as he admits, does not exclude the existence of some form of minimal consciousness in some arthropods and cephalopods, but it tells us something important about the evolutionary history of consciousness. He argues that the embodiment of vertebrates, the multiple degrees of freedom of their movement and the necessary coordination between neural and muscle systems, which their body plan allows, enabled this progressive evolution. Although the importance of embodiment in the evolution of consciousness in all three phyla was explored by Trestman (2013) and we discussed this topic in our book (2019, pp. 395-398), Moreno points to additional important and specific aspects of *vertebrate* development and physiological-morphological organization, which enabled the progressive evolution of consciousness in this clade. These include internal skeleton and fine-tuned controlled cardio-circulatory system facilitating rapid motility, and an autonomic nervous system (ANS) that controls fundamental homeostatic functions, which enabled vertebrates to cope with newly met and often stressful conditions. These affordances do not exist in arthropods and cephalopods, so the complexification and diversification of consciousness in invertebrates, was, Moreno, argued, constrained.

We are grateful to Moreno for the evolutionary perspective he has offered and agree with him that the evolution of consciousness in vertebrates has taken more open-ended routes than those taken in arthropods and cephalopods (although we must caution that the huge diversity of forms in the many species of arthropods is as yet poorly studied). His suggestions call for a comparative study of different groups within and between phyla focusing on *differences* rather than similarities between their embodied cognitive systems. Our concentration on the similarities of consciousness-supporting structures and processes in vertebrates and invertebrates was necessary to establish some general principles of conscious-supporting organization, but we agree that in order to go forward we need analyses of the differences among the co-evolved brains and bodies in different animal groups. We recently focused on basal vertebrates – fish – and analyzed the neural structures of UAL, which correspond to the structures of a global neural workspace (GNW) in basal fish (Zacks & Jablonka 2023). We found that in fish, the

GNW is instantiated by the event-memory system in the hippocampal homologue, a finding that suggests a strong connection between the evolution of declarative-like memory and the evolution of consciousness and may require some modification of the original UAL model that we offered. It will be very informative to study the differences between the three UAL-displaying lineages in view of our current knowledge of their cognitive embodiment and the evolutionary history of their nervous systems and extend this study to animals that show limited associative learning.

The vertebrate trend towards progressive sophistication of cognition and sentience is dramatically manifest in the idiosyncratic consciousness of humans. The evolution of human symbolic consciousness is a big topic which we hardly touched in our target article (but see Dor & Jablonka, 2010; Jablonka, Ginsburg & Dor, 2012; Shilton et al., 2020, and Shilton, 2022 for discussions of different aspects of symbolic language evolution and musicking), but since the topic was addressed by some of our commentators, especially Campbell (2022) and Olteanu (2022), we shall briefly comment on it here.

In our target article we did not define symbols, but since we realize that the term "symbol" is open to several interpretations, we would like to clarify how we use it. Our notion of symbols follows Cassirer (1953-1957) and Deacon (1997) and we define symbols as (i) learned conventional signs that refer to objects, processes, and their attributes and relations, as well as (ii) to other symbols within the symbolic system, forming a self-referential system that (iii) obeys rules linking symbols into symbol-combinations that are likely to be meaningful (Jablonka & Lamb, 2014). The evolution of a symbolic system of representation and communication is most obviously instantiated in human language, and we indeed believe, as Olteanu rightly pointed out, that the evolution of the symbolic-linguistic world created a qualitative difference between human and non-human consciousness. As we indicated in our target article, we follow Dor's (2015) functional characterization of language as a technology for the instruction of imagination, which enables communication about virtual realities. Dor's view emphasizes analogical reasoning, which was central to James' view of the evolution of language (James, 1890) and points to relevant precursors in the evolution of this capacity (Dor, 2023) as well as to the role of social, within-group interactions in the process (Jablonka, 2017). Although the transition to the symbolic realm is very different from the transition to sentience, we believe that all teleological transitions (to life, to sentience, to the symbolic-rational) show communalities (discussed in chapter 10 of our 2019 book and in a Ginsburg & Jablonka, 2020). Both differences and communalities can be illuminated by biosemiotic analyses.

In the age of AI, the ways in which technology may extend human (and non-human) cognition and consciousness is becoming, as Olteanu notes, an urgent and practical issue. In our recent book (Ginsburg & Jablonka, 2022) we discussed the human manufacturing and use of tools “that become, literally, neurologically, part of the definition of what we call our “self”, extending and altering not only our cognitive reach but the very representation and feel of our bodies”. This cyborg facet of human nature has been discussed by Clark (2004), but current 21st century AI-based technologies are dissolving boundaries between human and non-human biological individuals and between biological individuals and machines in ever accelerating and deepening manner. Learning to incorporate these technologies is scaffolding the construction of new forms of human cognition and consciousness. The possibility of sentient robots raises additional fundamental questions about the significance of material embodiment, the necessity for physiological and morphological ontogenetic sequences, and the need for a nested hierarchy of value (or valence) systems (Bronfman, Ginsburg & Jablonka, 2021). If sentient robots can be built from non-biological materials, this will problematize, in a new way, the relation between life (as we currently know it) and sentience.

8. **Conscious Choices and the Extended Evolutionary Synthesis**

All the commentators of our target article emphasized the importance of agency, niche construction (i.e., Umwelt dynamics) and plasticity, which entails exploration and the harnessing of stochasticity. These processes are central to the evolutionary re-thinking that the extended evolutionary synthesis (EES) is promoting, and all are indeed discussed and studied within the EES framework (for a current review see Chiu, 2022).

The same processes and the general view of evolution as driven by the actions of proactive agents has also been, as our commentators have illustrated, central to the biosemiotic perspective.

In line with the EES view, we argue, as Olteanu (2022) notes, that some biological processes are both evolutionary and ontogenetic: how we define them may depend on the level of biological organization we focus on. For example, neural selection in the nervous system is an evolutionary process when we focus on the changes within the nervous system during embryogenesis and learning, but it is, at the same time, an ontogenetic (maturation and learning) process at the level of the whole life-cycle of the organism. We also highlighted the interactions of ontogeny and phylogeny through the processes of genetic accommodation, which, we believe, were central to the evolution of learning strategies, including UAL, as well as to the evolution of behavior-related morphological and physiological traits.

We would like to highlight here one aspect that was discussed in Noble's (2022) commentary and is tied up with the EES' emphasis on agency and active niche construction: selection that depends on mentally felt desires, aversions and other feelings. This type of "selection by mental choice", which we briefly discussed in the target article, is part of what Noble calls intentional selection and is related to Darwin's notion of sexual selection by mate choice. As Noble observed, while Darwin's distinction between natural selection and human, rational, design-driven (artificial) selection has been widely accepted (although here too there are interesting and ambiguous cases that are hard to classify), sexual selection by mate choice as distinct from natural selection was often challenged. Moreover, although Darwin did assume that sexual selection through mate choice is based on mental faculties (Darwin, 1871) very little attention has been given, even by Darwin himself, to the difference between the evolutionary outcomes of selection driven by feelings and mentally perceived percepts and goals and selection that is not based on mentally experienced choices. It has been widely assumed that Monod's famous 1954 aphorism "What is true of *E. coli* must also be true of elephants", which points to the basic molecular communality between all forms of life, implies that what is true of elephants must also be true of *E. coli*. This reciprocal claim is obviously wrong, and Monod never made such a claim (and not just because elephants, unlike bacteria are conscious being). However, the significance of the fact that elephants and other animals make choices based on their mental evaluations while organisms such as bacteria and plants do not, makes, we argued, a big difference to evolutionary dynamics. If the capacities we listed as characterizing consciousness are seen as sufficient, and if these capacities are operationalized by UAL dynamics, then selection by mental choice enormously expands the cognitive, social-selection-relevant Umwelt of animals. We discussed the intricate and subtle perceptual and behavioral patterns in the living world that would never have evolved if animals were not able to perceive and evaluate them, but the effects of mental choice go beyond that. "The sense for the beautiful" that Darwin discussed in the context of sexual selection through mate choice, as well as the sense of social self-identity and social care that we share with other conscious social animals are cognitive-affective constructions resulting from social selection that would not exist but for the evolution of mental experiencing. We believe that the similarities and differences between mentally-blind, mental-choice driven, and rationally-driven types of selection and their many consequences need to be a central research project of the EES.

9. Conclusions: A Missing Concept?

One of the problems that was emphasized both by us and by most of our commentators is that the concepts of consciousness and sentience are vague umbrella terms covering not only the many varieties and facets of consciousness about which there is some general consensus but also cases about which there is much less consensus. The fact that notions such as "choice" and "meaning" are liberally and metaphorically used aggravates this problem. We may have added to the confusion, by using the mentally-laden term "value" instead of valence (a complaint made by Belardinelli & Pievani2023), although we did carefully define "value" in Table 1 of the target article.

One way of dealing with this terminological muddle is to avoid the use of the term consciousness/sentience or even mentality altogether (as many biosemioticians of the

20th century chose to do) and apply different types of distinctions when discussing different living organisms. This is not acceptable from our point of view because we assume that consciousness can be characterized in a way that acknowledges the obvious and important fact that we and some other organisms go through mental states such as joy, pain, and fear and that the emergence of this states and of the conscious mode of being are the outcomes of biological evolution. A second possibility is to define mentality broadly enough so that it can cover all living beings. We found no broad definition of mentality or sentience that does not identify it with an active, adaptively plastic living state. The adoption of this broad notion means that the distinction between living and mentally-experiencing neural organisms disappears, and with it the notion of unconscious living states.

The third possibility is to apply mentality on the basis of an acceptable characterization of phenomenal consciousness (not necessarily the one we suggested), and at the same time to acknowledge that we lack a concept that does justice to the internal, self-preserving, plastic state of living organisms that distinguishes them from nonliving, and that can bridge the gap between non-sentient and sentient organisms. We realize that this third option will be regarded with derision by most bio-psychists, but we believe that distinctions that acknowledges the subjecthood, the vivacious inwardness of some living organisms without identifying or endowing then with subjectivity (which presupposes mentality) can be useful. Such a concept (or a group of concepts) can help us understand how organisms with a mental kind of subjecthood had evolved, what kind of subjecthood can be attributed to non-neural organisms, and whether parts of organisms such as isolated brains or brain organoids may have “islands of consciousness” as some cognitive scientists suggested (Bayne, Seth & Massimini, 2020). Our suggested term “vivaciousness” is a step towards the development of a concept of subjecthood that can be applied to the autopoietic exploratory-turbulent inwardness of all living beings without implying mentality (i.e., phenomenal consciousness).

Vivaciousness cannot, however, do all the conceptual bridging work. Already in our earliest publications we suggested that something we called “overall sensation” may have been the precursor of mental inwardness. In our 2019 book we wrote: “Animals with a ceaselessly active, interconnected nervous system and multiple sensors have what we call “overall sensation” – the kind of overall sensory buzz that was first alluded to by Lamarck when he described the internal activity underlying the “inner feeling”, the feeling of existence. The overall sensation is made up of spontaneous neural activities, neural activities resulting from homeostatic maintenance like those of pacemakers, and neural activities occurring as the animal responds to contingent conditions. As a metaphor, the overall sensation can be regarded as white-noise. We see it as a functionless, as-yet feelingless by-product of a sensory-motor system that dynamically processes electrical and chemical signals. Overall sensation is constantly changing. Different sensations may become distinguishable from each other when persistent stimuli activate a particular local circuit. Other overall sensations may be generated when there is transient selective stabilization of altered neural states, and when simple forms of learning add their temporary signatures to the overall buzz of neural activity. Although the overall sensation with its various signatures is not subjective experiencing, it is, we suggest, the evolutionary raw material from which it emerged, and the specific patterns and “signatures” it manifests are therefore of special interest to us.” (Ginsburg & Jablonka, 2019, p. 279). Whether this notion is useful and in what ways it can be applied to non-neural multicellular organisms is open to discussion and further study.

Another notion that was important for us, was Damasio’s notion of proto-self (Damasio, 2010). When discussing the notion of the self we followed the ideas of Merker (2007) and Metzinger (2007) who, from different starting points, came to a similar notion of minimal self, based on the ability of organisms to represent their world and their body as interacting with the world yet distinct from it. We suggested (in chapter 4 of our 2019 book) that the precursor of these complex representations was an evolutionary elaboration, in the context of learning composite associations among sensory stimuli and actions, of the ability of animals to distinguish between the effects of sensory stimuli that are the outcomes of their own activity from identical sensory inputs received from the external world. An example is the difference in our response to the darkness caused by our eye blinks (which is not experienced as darkness) and the brief episodes of darkness that we do experience when identical “blinks” are externally imposed. The ability to respond differently to self- and world-imposed stimuli does not require mental states, but it may be an important precursor, a proto-self, that was necessary for the emergence of a feeling of self, of ownership of one’s actions.

These are as yet insufficiently developed suggestions, but we hope that thinking along these lines may yield interesting results. We believe that the urging of our commentators to look more closely at what we called the “gray areas”, is very important. We are grateful to them for this and for all the other important and enlightening comments on our target article.

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