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## *Could All Life Be Sentient?*

**Abstract:** *This paper concerns biopsychism, the position that feeling is a vital activity of all organisms or living beings. It evaluates biopsychism specifically from the perspective of the enactive conception of life and life–mind continuity. Does the enactive conception of life as fundamentally a value-constituting and value-driven process imply a conception of life as sentient of value? Although a plausible case can be made, there remains a conceptual and inferential gap between differential responsiveness to value and hedonic value or affective valence. Nevertheless, the case for zoopsychism — that animals are the only sentient living beings — over biopsychism is also inconclusive.*

**Keywords:** affect; autopoiesis; biopsychism; consciousness; enactivism; feeling of being alive; hedonic value; life; life–mind continuity; panpsychism; sense-making; sentience; valence; value; zoopsychism.

### 1. Introduction

I wish to consider the proposition that all life is sentient, that all living beings are sentient beings. ‘Sentience’ means the capacity to feel (from the Latin verb, *sentire*). So the proposition I wish to consider is that all organisms have the capacity to feel. Are there any plausible, if not decisive, reasons to advance in support of this proposition? If there are, how should we weigh them against the reasons for restricting sentience to animals or human beings?

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It is important to be clear at the outset about the minimal conceptual requirements for ‘sentience’ as I am using the term. In the nineteenth century, ‘sentience’ was sometimes used in physiology to mean ‘responsiveness to sensory stimuli’. For example, Michael Foster, in *A Textbook of Physiology*, wrote of ‘a stimulus being brought to bear on some sentient surface’ (Foster, 1883, p. 485). This meaning of sentience is not suitable for my purposes. I am using ‘sentient’ in its meaning of ‘able to feel’ (see also Pereira Jr., 2021). Part of what it is to be a feeling is to have a hedonic value or affective valence, a quality of pleasantness or unpleasantness, or perhaps neutrality. Mere responsiveness to stimulation, or irritability in the physiological sense (the ability to receive and respond to a stimulus), is a different concept from that of being able to feel. Unless such responsiveness is taken to entail responsiveness to hedonic value or affective valence, irritability is different from sentience.

I will approach the question of whether all life is sentient from the perspective of the enactive conception of life (Thompson, 2007; Di Paolo, 2018). Central to this conception is the continuity between life and mind. According to the enactive life–mind continuity thesis, the same concepts of individuality, agency, sense-making, and value that are required for explaining the phenomena of life are required for explaining mental phenomena. This thesis has been argued for extensively elsewhere, so I will not repeat those arguments here (see Thompson, 2007; Di Paolo, Buhrmann and Barandiaran, 2017; Di Paolo, Cuffari and De Jaegher, 2018). Instead, I will focus on the following question: does the enactive conception of life as fundamentally and intrinsically a *value-constituting* and *value-driven* process require or imply a conception of life as *sentient of value*, where this means being sentient of *hedonic value* or *affective valence*?

## 2. Biopsychism

Ernst Haeckel, writing at the end of the nineteenth century, called the position that all organisms are sentient beings ‘biopsychism’ (Haeckel, 1892). Feeling, he stated, can be conceived ‘now as a universal world-principle, now simply as a vital activity of all organisms, now simply as the particular mental activity of man’ (*ibid.*, p. 3). The first position is panpsychism, the position that all matter is ‘ensouled, that is to say... endowed with *feeling* (pleasure and pain)’ (*ibid.*, p. 6). Haeckel favoured panpsychism. He called the third position ‘zoo-psychism’, which he understood as the viewpoint that ‘real soul-life’,

by which he meant the separation of feeling and will, is the attribute only of the higher animals, and reaches its fullest development in the human being. Biopsychism, the position that feeling is proper to all organisms but not to all matter, is an intermediate position between panpsychism and zoopsychism, according to Haeckel's classification.

Given Haeckel's contrast between panpsychism and biopsychism, it is natural to take biopsychism to mean that all *and only* organisms are sentient. I am going to set aside this stronger claim. Evaluating it would require evaluating the possibility of non-organismic and artificial sentient entities, such as robots that are not organizationally or functionally equivalent, at a sufficiently fine-grained level, to organisms (Thompson, 2011a; see also Godfrey-Smith, 2016). This issue about artificial sentience is not my concern here. Instead, I wish to focus just on the proposition that if something is an organism, then it is sentient.

Since I will be approaching this proposition from the perspective of the enactive conception of life, this paper can also be understood as addressing the question of how we should understand the relationship between the enactive conception of life and biopsychism.

### 3. Life

The enactive approach draws on theories of how a system must be organized to be a living system. These are theories of 'minimal life', defined as the minimal organization required for a system to be an individual living system. The main theories are Humberto Maturana and Francisco Varela's theory of autopoiesis (Maturana and Varela, 1973/1980; 1980), Robert Rosen's metabolism-repair (*M,R*) systems (Rosen, 1991), and Tibor Gánti's chemoton theory (Gánti, 1975). Central to these theories is an emphasis on bounded self-production, metabolic closure, and adaptive self-regulation as the prototypical characteristics of life.

The relationship between individual self-production and transgenerational reproduction in the organization of living systems is a complicated issue (see Moreno, 2019). Logically and conceptually, the capacity to reproduce presupposes an individual reproducer; therefore, reproduction presupposes self-production of the individual (Maturana and Varela, 1980, pp. 96–111; Thompson, 2007, p. 96). So there can be no adequate theory of transgenerational reproduction without an account of individual self-production. Nevertheless, if the system that is self-producing is a reproducing system, then

reproduction is also constitutive of its organization. The three theories of minimal life just mentioned differ in their approaches to the relation between self-production and reproduction. Maturana and Varela's theory of autopoiesis, and Rosen's theory of metabolism-repair systems, focus on the necessary and sufficient conditions for the self-production of an individual living system apart from whether the system has any capacity for reproduction (the generation of new individuals linked transgenerationally). These theorists' paradigm is a minimal cell, a cell with an organization minimally sufficient for it to be a distinct, self-producing entity, minus any capacity for reproduction. Thus, in the theory of autopoiesis, reproduction is regarded as a complexification of the autopoietic organization instead of a defining feature. In contrast, Gánti's chemoton theory focuses on sustainable life, life that is able to continue transgenerationally. He reasons that only forms of life that persisted for long enough could have become the ancestors of life-as-we-know it. Hence he includes reproduction, and information storage and transmission, in his list of capacities jointly sufficient for life. The second capacity takes the form of an 'informational subsystem' that carries information about the whole system and makes possible 'unlimited heredity', the capacity to form reproductive lineages of open-ended length (see Ginsburg and Jablonka, 2019, pp. 20–23). Thus, for Gánti, an open-ended heredity system belongs to the minimal organization of life-as-we-know-it.

Since the enactive conception of individual living systems as value-constituting and value-driven originated historically from the theory of autopoiesis, I will focus on autopoietic theory here.<sup>2</sup> The question I wish to address is whether the enactive conception of life as autopoietic implies a conception of life as in some sense sentient.

#### 4. Autopoiesis

The theory of autopoiesis makes two fundamental claims. First, the defining property of life is its *organization*; and second, the defining property of life's organization is that it is *autopoietic*. 'Organization' means the set of relations that define a system as belonging to a given class, in contrast to 'structure', which means the system's actual

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<sup>2</sup> It must be emphasized that the enactive viewpoint goes well beyond autopoietic theory to the point that some of its core ideas about agency and value conflict with aspects of classical autopoietic theory (see Di Paolo, 2009; 2018).

realization, the concrete components and relations that physically constitute a system of a given class (Maturana and Varela, 1980). ‘Autopoietic’ means ‘self-producing’. It refers to a self-producing organization that dynamically maintains itself through time and constant material turnover. Concrete autopoietic systems may be instantiated in a wide variety of physicochemical structures, and a given structure may belong to more than one class of organization (Bessie is a living organism, an animal, a mammal, and a cow). Structures also change over time at many different timescales (metabolic and developmental), even if the organization remains invariant (Bessie was a calf and is now a milk cow).

The paradigm system having an autopoietic organization is the living cell. The structural realization of its autopoietic organization consists of (1) a semipermeable boundary, (2) chemical reaction networks taking place within the boundary, and (3) an interdependency between the boundary and the reaction networks, such that the reaction networks produce the boundary while the boundary supplies necessary conditions for the regeneration of the reaction networks.

Maturana and Varela’s original definition of autopoiesis reads as follows:

An autopoietic system is organized (defined as a unity) as a network of processes of production (transformation and destruction) of components which:

- (i) through their interactions and transformations continuously regenerate and realize the network of processes and relations that produces them; and
- (ii) constitute the system as a concrete unity in the space in which the processes exist by specifying the topological domain of its realization as a network. (Maturana and Varela, 1980, pp. 78–9)

This definition states that living systems are organized as networks of biochemical processes that satisfy two conditions. Following Ezequiel Di Paolo (2018), we can call them ‘self-production’ and ‘self-distinction’. Condition (i), self-production, means that the operation of processes in the network regenerates the set of relations between processes in the network. Condition (ii), self-distinction, means that the network emerges as a distinct topological unity in the domain of biochemical interactions. Thus an autopoietic system is materially self-producing and self-distinguishing. Due to the circularity (recursive self-production) inherent in these conditions, Maturana and Varela (1980; 1987; Varela, 1979) described an autopoietic system as having ‘organizational closure’ or ‘operational closure’, where

‘closure’ means that every process constitutive of the network’s organization both enables and is enabled by another such process (see Di Paolo and Thompson, 2014).

Although Maturana and Varela proposed that structurally realizing the autopoietic organization is necessary and sufficient for a system to be living, subsequent researchers have argued that being autopoietic is only necessary but not sufficient for a system to be living (Bourguine and Stewart, 2004; Bitbol and Luisi, 2005; Di Paolo, 2005). It turns out to be possible to instantiate the autopoietic organization in artificial life (AL) systems or synthetic chemical systems that are self-producing and self-distinguishing (that meet conditions (i) and (ii)) simply by virtue of having an autocatalytic membrane with operational closure, but without having any internal chemical reaction network, and hence that have nothing like a metabolism and active self-regulation in relation to the environment (the immediate chemical milieu) (see Thompson, 2007, pp. 122–7, for examples and discussion). Such systems self-individuate and regenerate themselves as topological unities, but do not exhibit directed behaviours in relation to their environments. From an origins-of-life perspective, they can be thought of as autocatalytic vesicles or proto-cells, but not as metabolic systems.

Recent work emphasizes that a further condition for the living organization must be explicitly included, a condition Di Paolo calls ‘adaptivity’ (2005; 2018). This is the ability of the network to modulate its states in relation to its viability boundary, beyond which the network cannot maintain its integrity and disintegrates. This kind of self-modulation in relation to the environment requires that the network be able to distinguish between conditions that move it closer to or further away from its viability boundary, and that the system behaves accordingly by moving away from deleterious conditions or transforming them into advantageous ones. Adaptivity implies path-dependent, directed behaviours (Di Paolo, Thompson and Beer, 2021). Bacterial chemotaxis — the directed movement of bacteria towards nutrients and away from toxins — is a case of autopoiesis plus adaptivity (Egbert, Barandiaran and Di Paolo, 2010).

In summary, according to recent elaborations of the theory of autopoiesis, physically instantiating an adaptive, autopoietic organization is necessary and sufficient for being an individual living system. My question is whether instantiating autopoietic adaptivity also implies some kind of sentience.

## 5. Sense-making

Maturana and Varela do not mention sentience in their original, canonical writings on autopoiesis. They do mention cognition, however, advancing their now well-known position that autopoiesis entails cognition, and hence that cognition belongs to the nature of living systems.<sup>3</sup> As Maturana writes in an early paper: ‘Living systems are cognitive systems, and living as a process is a process of cognition’ (Maturana, 1970/1980; Maturana and Varela, 1980, p. 13).

Maturana (1970/1980) reasons in a way that anticipates current theories of ‘active inference’ and ‘predictive processing’ (Friston, 2013; Clark, 2015; Ramstead, Kirchhoff and Friston, 2019). Living systems can enter into interactions only that are specified by their organization. Each internal state requires that certain conditions and interactions with the environment occur for the system to move to the next state, and the circularity (autopoietic closure) of the system’s organization is taken to imply that the system will return to the same (or very similar) internal states in a cyclic process. Maturana continues:

Thus, the circular organization implies the prediction that an interaction that took place once will take place again. If this does not happen the system disintegrates; if the predicted interaction does take place, the system maintains its integrity (identity with respect to the observer) and enters into a new prediction. In a continuously changing environment these predictions can only be successful if the environment does not change in that which is predicted. Accordingly, the predictions implied in the organization of the living system are not predictions of particular events, but of classes of interactions. Every interaction is a particular interaction, but every prediction is a prediction of a class of interactions that is defined by those features of its elements that will allow the living system to retain its circular organization after the interaction, and thus, to interact again. This makes living systems inferential systems, and their domain or interactions a cognitive domain. (Maturana and Varela, 1980, p. 10)

Given this perspective, Maturana defines a ‘cognitive system’ as ‘a system whose organization defines a domain of interactions in which it can act with relevance to the maintenance of itself’, and he defines ‘cognition’ as ‘the actual (inductive) acting or behaving in this domain’ (*ibid.*, p. 13). Thus a ‘cognitive domain’ is ‘the domain of all

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<sup>3</sup> For this entailment to hold, autopoiesis must be understood to include adaptivity. See Di Paolo (2005; 2018; Thompson, 2007).

the interactions in which an autopoietic system can enter without loss of identity' (*ibid.*, p. 136). It follows that the nervous system does not create cognition but rather expands the cognitive domain of life by expanding the organism's domain of interactions (*ibid.*, p. 13).

From the perspective of subsequent enactive developments, particularly the enactive view of life as constituted by both autopoiesis and adaptivity, Maturana's assumption that the living system will return to the same (or very similar) states of its circular organization is problematic. Enactive theorists argue instead that living systems and their environments are non-stationary (the probability distributions of their states and states of their environments do not or need not remain constant), and they do not have to converge to non-equilibrium steady states (Di Paolo, 2018; see also Di Paolo, Thompson and Beer, 2021, for extended discussion of this issue).

Varela's later formulation that 'living is sense-making' embraces these points (Varela, 1991; 1997).<sup>4</sup> The adaptively self-individuating organization of life, in its ongoing structural realization, dynamically brings forth *sense*. 'Sense' has the double meaning of 'significance' and 'directedness' (path-dependent directionality). 'Bringing forth' means not just being causally generative but also constituting in the sense of being a condition of possibility for how something shows up or is present under a certain aspect (Thompson, 2007, p. 15). Bringing forth sense is tied to the system's purposiveness. Adaptive autopoiesis (autopoiesis plus adaptivity) implies purposiveness: each constituent process both produces and is produced by another one, such that the system is a self-producing and self-distinguishing whole (autopoiesis); and the system regulates itself as a whole in relation to conditions registered as deleterious or advantageous (adaptivity). Sense-making is tied to the purposive character of adaptivity. The conditions or surroundings of such a system have sense given its purposiveness. The system constitutes its conditions and surroundings as having sense relative to its purposes, the overarching purpose being to regulate itself in relation to its viability boundary. Adaptive autopoiesis thus brings forth (generates and constitutes) a value-laden world for the organism, a place of attractions and repulsions, affording approach and avoidance (Thompson, 2004; 2007, p. 157; 2011b).

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<sup>4</sup> To the best of my recollection, Varela never explicitly stated the exact words 'living is sense-making' in his writings, though he did use this expression frequently in conversation.



Varela's statement that living is sense-making can be extended by saying that living is sense-making in precarious conditions (Thompson, 2011b). Precarious conditions are ones in which the self-producing and self-individuating processes of autopoiesis cannot sustain themselves in the absence of the autopoietic network in otherwise equivalent physical situations. Remove such processes from their enabling networks and they will tend to run down or atrophy. Precarious conditions imply the constant need for adaptivity, for regulating activity and behaviour in conditions registered as advantageous or deleterious with respect to the system's viability in a non-stationary environment (Di Paolo, 2018). Sense-making in precarious conditions is part of the deep continuity of life and mind.

Living as sense-making in precarious conditions is one of the core ideas of the enactive approach to cognition. It bridges from the theory of autopoiesis to enactive cognitive science (see Thompson, 2007; Di Paolo, 2018; Di Paolo, Buhrmann and Barandiaran, 2017; Di Paolo, Cuffari and De Jaegher, 2018; Di Paolo, Thompson and Beer, 2021). The bridge goes roughly as follows. Autopoiesis serves as a paradigm for the more general concept of an *autonomous system*. The core idea of the enactive approach is that autonomous sense-making is necessary and sufficient for cognition. An autonomous system is defined as an *operationally closed* and *precarious system* (Di Paolo and Thompson, 2014).<sup>5</sup> Precarious conditions imply the constant need for adaptivity, for regulating activity and behaviour in conditions registered as advantageous or deleterious with respect to the system's viability in a non-stationary environment (Di Paolo, 2018). Adaptivity implies sense-making, which is behaviour or conduct in relation to norms of interaction that the system itself brings forth on the basis of its adaptive autonomy. An adaptive autonomous system produces and sustains its own identity in precarious conditions, registered as better or worse, and thereby establishes a perspective from which interactions with the world acquire a normative status. Certain interactions facilitate autonomy and other interactions degrade it. In Merleau-Ponty's words: 'each organism, in the presence of a given milieu, has its optimal conditions of activity and its proper manner of realizing

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<sup>5</sup> 'Operational closure' means that every process proper to the system's organization both enables and is enabled by another such process; and 'precarious' means that such processes cannot sustain themselves in the absence of the system in otherwise equivalent physical conditions (Di Paolo and Thompson, 2014).

equilibrium', and each organism 'modifies its milieu according to the internal norms of its activity' (Merleau-Ponty, 1963, pp. 148, 154). For the enactive approach, a system is cognitive when its behaviour is governed by the norm of the system's own continued existence and flourishing. Basic cognition, on this view, is not a matter of representing independent states of affairs but rather of establishing agent-centred relevance through the need to maintain an identity that is constantly facing the possibility of disintegration.

## 6. Sentience

If autopoietic adaptivity suffices for sense-making, does it also suffice for some kind of sentience? Although sentience seems to be sufficient for sense-making — things can have sense or significance to the extent that they feel a certain way — is sentience necessary for sense-making? To put the question another way, does being value-constituting and value-driven, in the enactive sense just discussed, require or imply sentience of value?

Varela's viewpoint seems to have shifted over the years. In 1987, in the *Mind and Life Dialogues with the Dalai Lama*, he made the following remarks, speaking from his perspective as a neurobiologist:

The behavior of the bacterium or amoeba is one of avoiding some things and seeking others, much like the behavior of clearly sentient beings like cats and humans. Hence I have no basis for saying the behavior is not of the same kind, although I would say there is no *consciousness* of pain or pleasure. The amoeba intrinsically manifests a differentiation between what it likes and what it doesn't like. In that sense, there is sentience. (Hayward and Varela, 1992, p. 67)

Here it is behaviour (understood as the ongoing coupling of an autopoietic unity with its environment), and the similarity of the behaviours of unicellular organisms to those of animals, that is taken to indicate sentience. Varela uses 'sentience' here to mean the sensitivities and preferences exhibited in approach and avoidance behaviours, in being drawn to and actively seeking something versus being repulsed and actively avoiding something. Bacteria exhibit a complex range of such behaviours, which comprise sensory discrimination, sensorimotor coordination, learning, and memory (Lyon, 2015). Such behaviours constitute sense-making; they involve both differential responses to stimuli as having significance and value, and following advantageous directions and avoiding deleterious ones (as in chemotaxis). At the same time, Varela doubts that there is any

‘consciousness of pain or pleasure’. From the context of the larger discussion, he appears to be using ‘consciousness’ to mean not simply feeling but also the ability to be aware of a feeling as a state of oneself (though not necessarily in a metacognitive sense).<sup>6</sup> So the question of whether bacteria are sentient in the sense of having a capacity to feel — whether they experience stimuli to which they respond favourably or aversively as having positive or negative hedonic values or affective valences — remains unclear (see Thompson, 2015a, p. 341).

In later writings, however, Varela comes close to linking sense-making, value, and sentience. This takes the form of connecting the theory of autopoiesis to Hans Jonas’s philosophical biology (Weber and Varela, 2002).

Jonas (1966; 1968) describes unicellular metabolism as the minimally sufficient requirement for individuality, agency, value, and a subjective point of view. His position is that unicellular metabolic self-production in precarious conditions implies self-concern, an active directedness towards self-preservation. As Di Paolo writes, although Jonas ‘does not specify the need for an adaptive regulation through which the organism evaluates its coupling to specific environmental flows... the need for active regulation is implied in his recognition of the primordial tension of life: materials are essential to the living organism but its identity is dynamic, not tied to the individuation of material constituents but emerging instead as the (risky) ongoing adventure of “riding” material changes “like a crest of a wave” and “as its own [the organism’s] feat” (Jonas 1966)’ (Di Paolo, 2018). Jonas maintains that the same process of self-organization (metabolic self-production) that creates this dynamic form of existence (self-individuation) also creates purposiveness and a subjective point of view in the form of a self-actuating ‘concern’ for being. He argues that self-production entails not simply persistence in the form of self-maintenance, but also self-affirmation, a motivation for self-maintenance, an ‘absolute interest of the organism in its own being and continuation’ (Jonas, 1966, p. 69). Such ‘interest’ or ‘concern’ is not a distinct psychological state; instead, it belongs to the whole existential structure of self-production. In summary, self-

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<sup>6</sup> Another remark about context is important here. In his dialogues with the Dalai Lama, Varela would often try to speak from an ‘orthodox’ or ‘standard’ scientific perspective, so as not to misrepresent the majority scientific viewpoint. He would usually explicitly say when he was speaking from his own perspective, which he considered heterodox.

production generates ‘concern’, an endogenous interest in or motivation for self-preservation and self-enhancement; such ‘concern’ is a form of existence or mode of being, not a mental state; and it instantiates a locus of subjective value in an otherwise valueless and subjectless world.

Described in terms of the enactive conception of life, Jonas’s position is that autopoiesis and sense-making bring forth value and subjectivity in the world. Although Jonas does not analyse the exact relation between value and sentience, he clearly links the two, suggesting that they are co-extensive (see *ibid.*, pp. 63, 66).

Nevertheless, it remains unclear exactly what the link is supposed to be. Why should being directed towards values entail sentience of value? Why should being self-producing, self-individuating, and adaptively self-regulating entail subjectivity in the sense of being sentient? 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? Jonas does not answer these questions.

Varela, writing with Andreas Weber, uses Jonas to link autopoiesis and value, thereby departing from his earlier view with Maturana that value resides solely in the domain of the observer (Weber and Varela, 2002).<sup>7</sup> Varela and Weber draw out the implications for the inter-relation between life, value, and subjectivity: ‘The primordial structure of value... manifests in what can now be called the subjective dimension even for the simplest organisms... A world without organisms would be a world without meaning; and it is in life’s incessant need, that a subjective perspective is established’ (Weber and Varela, 2002, pp. 118–19). Weber and Varela do not explicitly mention sentience. But they apparently accept Jonas’s viewpoint that subjectivity in the form of animate striving and feeling is present in the simplest unicellular organisms. So it is but a short step to the thought that autopoietic sense-making suffices for sentience.

Nevertheless, like Jonas, Weber and Varela do not answer the question of what the exact relation between being responsive to self-constituted values and being a sentient subject is supposed to be. If ‘subjective’ means experiential, why should autopoietic sense-making

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<sup>7</sup> This so-called normative turn in enactive theory raises important but complicated questions about the concepts of value and normativity in the enactive conception of life (Barrett, 2017), but addressing these questions lies beyond the scope of this paper.

entail experience? Given that autopoietic sense-making establishes an agential or purposive dimension, why should it establish a ‘subjective dimension’ in the form of sentience of value (hedonic value or affective valence)? These questions remain unanswered.

It is worth mentioning that biologist Lynn Margulis, known for her work on symbiosis and cell evolution, thought that autopoiesis does suffice for sentience. She had no hesitation in writing about ‘microbial consciousness’ and ‘the conscious cell’ (Margulis, 2001). In her book *What is Life?*, with Dorion Sagan, she wrote:

Not just animals are conscious, but every organic being, every autopoietic cell is conscious. In the simplest sense, consciousness is an awareness of the outside world. And this world need not be the world outside one’s mammalian fur. It may also be a world outside one’s cell membrane. Certainly some level of awareness, of responsiveness owing to that awareness, is implied in all autopoietic systems. (Margulis and Sagan, 1995, p. 122)

In the case of bacteria, ‘awareness of the outside world’ would include differential sensitivity and responsiveness to chemical gradients in chemotaxis, and to chemical signal molecules in quorum sensing. For Margulis and Sagan, this kind of sensing constitutes the simplest form of consciousness.

Margulis and Sagan’s use of the word ‘consciousness’, however, conceals the questions I am trying to bring into clear view. If ‘consciousness’ just means differential responsiveness to the environment and to norms of viability or flourishing, then we still face the question of why such responsiveness should entail or require sentience of value (hedonic value or affective valence). But if ‘consciousness’ means feeling or sentience of value, then the above passage expresses an intuition or conviction, not an argument. For example, if the thoughts are supposed to result from an inference to the best explanation based on biological evidence about the sophisticated cognitive abilities of bacteria as autonomous agents (see Lyon, 2015; Fulda, 2017), we need to know why invoking sentience of value (hedonic value or affective valence) constitutes a better explanation of the evidence than simply invoking responsiveness to value (norms of viability).

## 7. Additional Considerations

Maxine Sheets-Johnstone (1998; 2011) and František Baluška and Arthur Reber (Reber, 2019; 2020; Baluška and Reber, 2019; Reber and Baluška, 2021) have also recently argued that life entails

sentience. Their arguments are independent of theories of the organization of life such as the theory of autopoiesis.

Sheets-Johnstone argues that ‘consciousness is a dimension of living forms that move themselves, that are *animate*’ (Sheets-Johnstone, 1998, pp. 275–6). She regards the bacterium’s ability to discriminate molecular shapes outside of its membrane as ‘a consciousness of something beyond itself’ (*ibid.*, p. 276); and she regards the bacterium’s capacity of self-movement as indicating that it is aware of itself as distinct from its also being aware of its immediate environment (Sheets-Johnstone, 2011, p. 461). In general, according to her viewpoint, the property of being animated (having the capacity to self-generate movement), understood as a general property of life, entails consciousness.<sup>8</sup>

Like Jonas, and Weber and Varela, however, Sheets-Johnstone does not fill in the steps of the argument. All the evidence for molecular discrimination — for example, for distinguishing between intracellular versus extracellular concentrations of signalling molecules (auto-inducers) in quorum sensing — is behavioural and structural. Why should this kind of evidence indicate the presence of consciousness in the sense of subjective feeling or sentience of value, instead of indicating just cognition and autonomous agency minus consciousness? Although bacterial motility is certainly self-generated (Wadhwa and Berg, 2021), and could possibly involve some kind of reafferent sensing whereby the organism senses the consequences of its own actions as such (Jekely, Godfrey-Smith and Keijzer, 2021), thereby instantiating a sensorimotor self (Thompson, 2007; Christoff *et al.*, 2011), why should self-movement and reafference indicate consciousness in the sense of a subjective feeling of selfhood or a sentience of molecular shapes as having hedonic values or affective valences, rather than indicating animate autonomous agency without consciousness? Again, if the argument is supposed to be an inference to the best explanation from empirical evidence, we need to know why the

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<sup>8</sup> Sheets-Johnstone (2011) criticizes my earlier hesitancy about attributing consciousness to all living systems, particularly bacteria (Thompson, 2007, p. 162). My viewpoint, however, is not as fixed as she makes it out to be (see Thompson, 2015a, pp. 335–44). She also criticizes other ideas from my work on phenomenology and cognitive science. Although I sympathize with some aspects of her criticisms, her discussion of my work is unfortunately marred by uncharitable readings, narrow-minded interpretations of terms, and misinterpretations of positions and arguments. Detailing them lies beyond the scope of this essay.

presence of consciousness (sentience) is more probable than its absence.

Reber and Baluška propose a theoretical framework called the ‘Cellular Basis of Consciousness’ (Reber, 2019). According to this framework, life and sentience are ‘coterminous’ (Reber and Baluška, 2021, p. 150), and the explanatory task is to determine the biochemical structures and processes responsible for cellular sentience. Reber and Baluška maintain that prokaryotic cells, the simplest life forms, exhibit flexible and adaptive cognitive behaviours (see also Lyon, 2015; Fulda, 2017), and that such behaviours cannot occur in the absence of sentience. Without sentience, they argue, behaviours can be only fixed and reflex-like, not plastic and flexible. Inflexible behaviours, however, would not have enabled the earliest organisms to respond to their dynamic environment and to evolve (generate adaptive, reproductive lineages) (Reber and Baluška, 2021, p. 151; Reber, 2021, p. 123). Already in prokaryotic organisms, sensory discrimination, learning, memory, and chemical signalling and communication are taken to indicate that stimuli and events have hedonic values or affective valences (Reber, 2019). The ability to sense something as attractive and affording approach, or as deleterious and requiring withdrawal, is taken to be evidence of feeling (affective valence). So biological sensing at the microbial level is supposed to be equivalent to feeling.

Baluška and Reber’s approach is to work forward from prokaryotic life and postulate that life and sentience arose together, rather than to work backward from consciousness as we know it in the human case. Although this approach is certainly reasonable, it does not obviate the need to address the question about how differential responsiveness to values (norms of viability) is supposed to indicate or entail sentience of value (hedonic value or affective valence). Why can’t exhibiting flexible and adaptive cognitive behaviours occur in prokaryotes in the absence of sentience? Why is sentience required for the flexible behaviours of prokaryotes rather than just autopoietic adaptivity without sentience?

Baluška and Reber (2019) identify three candidate biochemical structures for the causal biological basis of sentience: excitable membranes, the dynamic cytoskeleton (microtubules and actin filaments), and special proteins having fivefold symmetries and quasi-crystal properties. The general idea is that these structures are crucial for signal transduction and differential sensing of the intracellular and extracellular milieux. Given the postulate that cellular sensing is

feeling — the principal assumption of the Cellular Basis of Consciousness — these structures are thought to be plausible candidates for the physical causation and realization of sentience.

Again, the question is whether this assumption amounts to more than a brute postulate. What we need is a strong abductive argument: without assuming that unicellular agency is sentient, we cannot explain unicellular behaviour. But if we can explain such behaviour without assuming sentience, there appears to be no explanatory benefit to invoking sentience.

Baluška and Reber (2019) suggest that one kind of behaviour that may require an abductive inference to sentience is the sensitivity of some unicellular organisms (such as paramecia) to anaesthetics (see also Reber and Baluška, 2021). Anaesthetics that cause loss of consciousness in humans cause loss of sensory responsiveness in animals and plants as well as unicellular eukaryotes. If anaesthetics also cause loss of responsiveness in prokaryotes, and it can be established that the mode of action of anaesthetics is always specifically to target sentience, then responsiveness to anaesthetics would provide the basis for an abductive argument for sentience. The counterargument, however, is that anaesthetics have ubiquitous and diverse effects on sensory responsiveness and behaviour, and therefore responsiveness to them should not be taken as definitive evidence of sentience (Draguhn, Mallatt and Robinson, 2020).

Baluška and Reber (2019) think that sentience is ‘encoded’ in the DNA of the earliest cells. Reber (personal correspondence) explains that they mean that genes code for the properties of membranes that are the causal elements for creating sentience. From the enactive perspective, however, this idea is misguided, because the idea that genes ‘code for’ phenotypic traits is problematic (Thompson, 2007, chapter 7), and sense-making (being value-constituting and value-driven) and sentience (hedonic value or affective valence) are systemic properties based on the organizational properties of autopoiesis (or autonomy) and adaptivity. As a general point, the structural properties of DNA do not determine systemic properties at either structural or organizational levels (*ibid.*). Simona Ginsburg and Eva Jablonka, in their review of Reber’s *The First Minds: Caterpillars, Karyotes, and Consciousness* (Reber, 2019), make a similar point: ‘like life, sentience is a system property. Just as there are no genes for life, there can be no genes and codes for sentience, and just as it makes no sense to talk about the metabolic cost of life, there is no sense of discussing the metabolic cost of sentience. Identifying genes



and codes for sentience and discussing its metabolic cost are, as we see it, a category mistake' (Ginsburg and Jablonka, 2020, p. 119). Finally, the hypothesis that structural elements of the cell membrane are causally responsible for creating sentience does not bridge the explanatory gap: exactly how are physical structures crucial for the differential sensing of the external environment and internal milieu supposed to be generative of consciousness in the sense of subjective experience (specifically, sentience of value)?

### **8. Biopsychism and the Enactive Conception of Life**

I would now like to examine how the enactive conception of life might be used to support biopsychism.

If one is going to use the enactive conception of life to argue that all living beings are sentient, the argument would likely proceed along something like the following lines, with the crucial but problematic step occurring at Premise 3:

1. Autonomy (being operationally closed and subject to precarious conditions) plus adaptivity (being able to regulate one's states in relation to one's viability boundary) suffices for purposive sense-making (being differentially responsive to events as having positive and negative values).
2. Autopoiesis (metabolic self-production and self-distinction) plus adaptivity suffices for being an individual living system, and is the minimal molecular instance of adaptive autonomy and sense-making.
3. Sense-making implies both motivation — end-directedness arising from feeling pulled and pushed, attracted and repulsed — and affect, positive and negative valences correlated with such motivation.
4. So motivation and affect are required for sense-making.
5. So adaptive autopoiesis, and adaptive autonomy in general, suffice for motivation and affect, and hence sentience.

The argument begins from the premises that being an adaptive autonomous system suffices for being a purposive and sense-making agent responsive to value, and that adaptive autopoiesis is the minimal molecular instantiation of an adaptive autonomous system. These premises are the foundational, working principles of the enactive approach to life and mind, as reviewed above (see Thompson, 2007;

Barandiaran, Rohde and Di Paolo, 2009; Di Paolo, Buhrmann and Barandiaran, 2017; Di Paolo and Thompson, 2014; Di Paolo, 2018). We can illustrate them concretely with the case of bacteria, while using this case to test the above argument.

Bacteria are the simplest known case of a physical system that instantiates both autopoiesis and adaptivity, and thus are the simplest known biological case of adaptively autonomous agents. A bacterial cell is an autopoietic individual and is adaptively coupled to its environment. Its identity (organization) persists through constant material turnover, and is produced and maintained by that material turnover. A bacterial cell has directed agency and a range of sense-making capacities (Thompson, 2011b; Lyon, 2015; Fulda, 2017). Consider chemotaxis, which, as a metabolically-dependent behaviour, exemplifies autopoiesis and adaptivity (Egbert, Barandiaran and Di Paolo, 2010). Motile bacteria sample the concentration of chemical compounds in their environment and swim towards ones that are nutrients or attractants, and away from ones that are toxins or repellents. The bacteria alternate between swimming in a straight line and tumbling at random. They maintain their direction as long as they detect an increase in the nutrient level over time. If the nutrient decreases, or if they sense that they are moving towards a repellent, they will tumble until they hit on a direction where they again detect an increase in the nutrient. Thus, chemotaxis is a behaviour the organism actively does, rather than passively undergoes, and the exercised agency is ecological — it depends directly on how the organism is dynamically embedded in its environment (Fulda, 2017).

But are bacteria (or prokaryotes in general) sentient? Do their sense-making capacities imply that they are sentient of value, that they are motivated and respond to hedonic values or affective valences? More generally, what is the basis for Premise 3 in the above argument? Granted that sense-making implies purposive agency, and we experience purposive agency as motivated, affective, and conative, what is the reason for thinking that sense-making or purposive agency requires motivation and affect?

We are back to the problem already discussed. On the one hand, there does not seem to be a conceptual entailment from sense-making (being differentially responsive to positive and negative values related to viability) to sentience of value (hedonic value or affective valence). On the other hand, as long as it seems possible to explain sense-making without appealing to sentience, we lack a compelling abductive inference from one to the other.

There is another problem with the above argument. It concerns the relationship between autonomy and autopoiesis. Although autopoiesis plus adaptivity suffices for life, the claim that an adaptive autopoietic system is a sense-making system is based on its being an adaptive autonomous system. In other words, although autopoiesis is the paradigm of autonomy, it is the generic character of autonomy — operational closure in precarious conditions — that implies sense-making (differential responsiveness to values). But there are many candidate autonomous systems, such as the immune system and insect colonies, that we do not think of as sentient individuals. So if all life is sentient, this would have to be in virtue of principles that go beyond those of autonomy (self-individuating identity constitution) and sense-making (being value-constituting and value-driven).

In *Mind in Life*, I also appealed to transcendental principles (Thompson, 2007; see also Thompson, 2011b).<sup>9</sup> Specifically, I appealed to Hans Jonas's principle that 'life can be known only by life' (Jonas, 1966). Jonas's argument is that life, from the perspective of mathematical physics and chemistry, is unrecognizable. Knowing only the laws of mathematical physics and chemistry, not even God would be able to recognize the self-individuating form and purposive directedness of a living being, even in the minimal case of the unicellular organism. It takes life (being a living being) to recognize life. More precisely stated, a necessary condition of the possibility of something's coming into focus for us as an individual living being requires our viewing it as a self-producing (autopoietic) and sense-making unity, and such a viewpoint cannot be derived from physics and chemistry, but instead depends on our own experience of being such a unity. Moreover, that experience fundamentally includes a sentience of value and a 'feeling of being alive': we not only feel the world as having hedonic values or as being affectively valenced, but such feelings involve modulations of a feeling of being alive occasioned by interactions with the environment.<sup>10</sup> So sentience as a feeling of being alive and sentience of value are constitutively interlinked. From this transcendental perspective, we cannot avoid relying

<sup>9</sup> 'Transcendental' is used here to mean a necessary condition of the possibility of something's appearing or being disclosed to our cognition as being a given way or having a given sense or meaning, here the sense or meaning 'life' or 'living being'.

<sup>10</sup> For further discussion of sentience as a 'feeling of being alive', see Thompson and Varela (2001); Thompson (2007, pp. 161–2, 229–30, 354–5; 2015a, pp. 234–6; 335–44; 2015b).

on our own experience of life to comprehend life, and this necessary reliance warrants extending sentience of value and a feeling of being alive to all life.

Of course, this kind of transcendental argument goes beyond the methodological framework of scientific naturalism. I cannot review here the reasons why transcendental philosophers reject scientific naturalism (see Thompson, 2014). Instead, I will simply observe that if one accepts the transcendental phenomenological critique of scientific naturalism, then this form of argument becomes available.<sup>11</sup> Nevertheless, this form of argument is not a first-order scientific argument (it is not abductive), but rather is a kind of meta-argument (an argument about the intelligibility of life as such in advance of science), so it does not address, let alone answer, first-order scientific questions (for example, whether motile prokaryotes sense their own being in movement as such, whether their sensing is affectively valenced, and so on).

In summary, the argument for biopsychism on strictly first-order enactive grounds hits a limit at the point where the question of the exact relationship between sense-making and sentience arises. So the empirical argument is inconclusive. I turn now to panpsychism and zoopsychism.

## 9. Panpsychism

Panpsychism is the position that the mind is a fundamental and ubiquitous feature of reality. One way to formulate panpsychism is that all matter is sentient or that every physical particular has some quality of feeling (Theise and Kafatos, 2013). Panpsychism is an ancient idea that is said to be currently undergoing a revival (Brüntrup and Jaskolla, 2017; Goff, 2017).

Panpsychism faces the well-known ‘combination problem’, which is the problem of how micro-level sentient particulars (such as elementary particles) combine to form macro-level sentient beings or functionally coherent subjects of experience. Panpsychists generally maintain that mental properties belong only to genuine individuals, but not to mere aggregates or collections, or to conglomerates like a rock formation. This raises the question, what is a genuine individual?

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<sup>11</sup> Classical autopoietic theory does not take this step. The step belongs instead to certain versions or developments of the enactive conception of life and mind (Weber and Varela, 2002; Thompson, 2007; 2011b).

Greg Rosenberg (2017) has this question in sight when he suggests that we change the panpsychist framework to address what he calls the ‘boundary problem’ instead of the combination problem. In his words:

The hard nut of the Boundary Problem is that animal experiencers possess a kind of inherent individuality at a physical midlevel of reality, which is hard to explain. If panpsychism is true, why do the boundaries exist *just so*?... Boundaries are harder to explain than combination. We are faced with the need to understand what it is to be an inherent individual in the natural world. (Rosenberg, 2017, pp. 156–7)

The enactive conception of life addresses this question. To be an individual it is not enough simply to be a particular (Jonas, 1968). To be an individual in the biological sense is to be self-individuating, to be a self-producing and self-distinguishing system. It is to have an identity that is produced and maintained by a network of processes that meet the criteria for constituting an autonomous system, the paradigm of which is an autopoietic system (see Di Paolo and Thompson, 2014). So, even if panpsychism is true, the relevant boundaries for individual sentience — for something’s being a sentient individual — may be the ones proper to autopoietic systems or to higher-order ‘meta-cellular’ systems based on autopoietic ones. In other words, even if panpsychism is true, it gives us only elementary sentience, not individual sentience, the sentience of beings as unities rather than mere particulars.

From this perspective, it is logically consistent to maintain both panpsychism, as a general metaphysical thesis about the place of mind in nature, and biopsychism, as a restricted thesis about individual sentience. I make this point not to argue for panpsychism, but simply to observe that panpsychism can avail itself of the enactive conception of life to address Rosenberg’s boundary question, and that by doing so panpsychism can be made consistent with biopsychism about individual sentience.

Nevertheless, biopsychism faces an analogous problem to the panpsychist combination problem and boundary problem. If life suffices for sentience, such that an individual organism, such as a prokaryote, is a sentient being, then what happens to individual cellular sentience in the case of multicellular organisms, cell colonies, or quorum sensing in bacterial populations? This question is one of the big challenges facing biopsychism (see Ginsburg and Jablonka, 2021, p. 21).

In the case of multicellular organisms, the question is whether the constituent individual cells are themselves sentient individuals or

whether they lack individual sentience because of their subsumption and integration into the multicellular individual.

Reber and Baluška (2021) address this issue. They propose that individual cells in a multicellular organism retain their own sentience while contributing to the larger integrated sentience of the organism. Reber's (2019) model is implicit learning. Implicit learning and memory contribute to, but take place independently of, reportable conscious awareness, and they depend on evolutionarily older, sub-cortical systems and pathways. Similarly, individual cell-sentience takes place independently of, but contributes to, the sentience of the larger organism. The organism does not experience the sentient states of its individual cells, but its sentience results from integrating them into a 'larger Gestalt' (Reber and Baluška, 2021, p. 152).

This model is reminiscent of Leibniz's (1703–05/1989) idea that when we hear the roar of the sea, the motion of every single wave affects the body, so that the body perceives every wave, but the sounds are so confused that all we consciously recognize is the roar of the sea. To hear the roar we have to hear the noise of each wave, but we would not notice the noise of the wave if it were all by itself; it is known only in its confused combination with the other sounds. Similarly, the sentience of every cell affects the whole organism, but the organism notices only the 'roar' of their integration into a larger collective pattern.

In summary, panpsychism need not be opposed to biopsychism. In addition, biopsychism about individual sentience appears to have an explanatory advantage over pure panpsychism in being able to propose a way to address the boundary problem by drawing from the enactive conception of life. Although biopsychism has its own 'combination problem' analogous to that of panpsychism, biopsychism arguably provides a better answer to the problem than does panpsychism on its own.<sup>12</sup>

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<sup>12</sup> In addition, although we do not seem to gain any further understanding about the behaviour of electrons by treating them as sentient, the biopsychist argues that we do gain further understanding (empirically or transcendently) about the behaviour of living beings (including prokaryotes) by treating them as sentient.

## 10. Zoopsychism

Zoopsychism restricts sentience to animals.<sup>13</sup> In my arguments for life–mind continuity in *Mind in Life*, I back off from biopsychism and tentatively argue for restricting sentience to animals with nervous systems (Thompson, 2007, p. 162).<sup>14</sup> I give three reasons, none of which seems compelling to me now.

First, following Susan Hurley (1998, pp. 149–50), I suggest that being phenomenally conscious of something (having a felt awareness of it) entails being able to form intentions in relation to it. In other words, the possibility of intentional access to something is proposed as being required for being able to be phenomenally conscious of it. This proposal ties phenomenal consciousness to possession of a cognitive capacity for intentional access to the contents of awareness.<sup>15</sup> But this proposal now seems to me to conflate consciousness in the sense of being able to cognize a sentient state (a feeling) as a state of oneself with consciousness in the sense of sentience (feeling). If the claim is that the two senses of consciousness are inseparable, or that sentience requires or is constituted by such a cognitive consciousness, then we need an independent argument to establish the claim.

Second, I express doubts about whether autopoietic individuality and adaptivity suffice for ‘prereflective self-awareness’, the non-metacognitive and non-conceptual reflexive awareness that is held to belong to the nature of consciousness, according to phenomenological philosophers (Zahavi, 2005) and a variety of philosophers from other traditions (see Strawson, 2013). The reason I give is that reflexive awareness would seem to require the reflexive (recursive and self-referential) elaboration of life processes provided by the nervous system. But this reasoning skirts the question of whether prokaryotic

<sup>13</sup> I am using ‘zoopsychism’ in a somewhat different sense from Haeckel’s. In my usage it refers to the position that animals are the only sentient organisms.

<sup>14</sup> I do not, however, use the terms ‘biopsychism’ and ‘zoopsychism’ in *Mind in Life*.

<sup>15</sup> Sheets-Johnstone, in criticizing this proposal, writes: ‘why would self-moving forms of life, i.e. non-sessile creatures, *not* have “intentional access” to their “sense-makings”?’ (2011, p. 461). This question seems misplaced. I see no reason to suppose that motile prokaryotes have a cognitive capacity for intentional access to their sense-making. To my knowledge, they do not exhibit any behaviour that exemplifies this kind of capacity, and they have no known physical apparatus to support this kind of cognitive capacity (see also Thompson, 2015a, p. 341). Sheets-Johnstone’s defence of cellular consciousness would be better expressed by objecting to the proposed linkage of consciousness and intentional access.

motility involves any sensing of self-movement. If self-movement, sensorimotor coordination, and chemical sensing and signalling already implement a minimal self-versus-other dynamic structure, such that the prokaryotic cell senses its environment, including other cell signals (e.g. in quorum sensing), as distinct from itself, then the prokaryote, in sensing its environment, may also sense its own being in movement (as Sheets-Johnstone, 1998; 2011, argues). If it does, then we can ask whether such sensing involves a ‘feeling of being alive’ (Thompson and Varela, 2001; Thompson, 2007, pp. 161–2, 229–30, 354–5; 2015a, pp. 234–6, 335–44; 2015b). Here the idea is that sentience of value — feeling the environment as hedonically valued or affectively valenced — is constituted by modulations of a feeling of being alive occasioned by interactions with the environment. Notice that this kind of sentience is inherently reflexive: feeling alive inherently involves self-feeling occurring in and through feeling the environment.

Third, I state that it becomes difficult to relate consciousness to unconscious life-regulation processes if one projects consciousness down to the cellular level. This statement, however, does not distinguish between consciousness in the sense of a cognitive capacity for intentional access to the contents of awareness, and consciousness in the sense of sentience, and it does not distinguish between considerations about cells as individual living systems and cells as constituents of multicellular organisms with regard to sentience.

Ginsburg and Jablonka (2020) have recently expressed doubts about extending sentience beyond animals, particularly to unicellular organisms. They question whether biological individuality, agency, and the ability to attribute positive and negative value to environmental stimuli imply sentience. They assert that many of the sense-making capacities of bacteria, such as evaluation of stimuli and sensorimotor coordination, are known to be possible without consciousness in human and non-human animals.

We need to be cautious, however, with this kind of argument. As Ginsburg and Jablonka (2019) rightly maintain, consciousness, like life, is a ‘mode of being’. Many unconscious behaviours in humans (such as fine postural and motor adjustments in action) depend on our conscious mode of being, and in that sense cannot occur in the absence of consciousness. Furthermore, it is not legitimate to infer that bacterial chemotaxis is non-conscious from the fact that certain motor activities in conscious beings can occur unconsciously. The forms of life are different and should be evaluated holistically. Should



prokaryotes, considered as autopoietic unities and ecological agents, be regarded as sentient? That question is not properly addressed by observing that some motile behaviours can occur unconsciously in conscious animals.

Whereas Reber (2019) argues that prokaryotes evaluate stimuli in terms of valence, Ginsburg and Jablonka write: ‘We do not see why the structure and activity of these valence systems, which signal departures from homeostasis and trigger responses that often lead to the relief from stress, require sentience. Of course, one can *assume* that the effects of stress responses entail something like feelings, but this is then an axiom, not an argument’ (2020, p. 118).

The distinction between axiom and argument, however, is not straightforward in the case at hand. It is perfectly legitimate to assume that autopoietic sense-making implies sentience, if making that assumption provides a framework for generating new conceptual models and experimental investigations that increase our understanding of the phenomena of life and sentience. If such progress ensues on the basis of making the assumption, then the new models and experimental investigations constitute an argument in favour of the assumption. So the issue comes down to how generative of scientific and philosophical progress the assumption turns out to be.

Zoopsychists generally appeal to the nervous system, or the brain and the cognitive capacities and behaviours it makes possible, as the crucial requirement for sentience.

One line of thought appeals to the functional characteristics of the nervous system, specifically to the way that it integrates the multicellular body and makes possible sensorimotor agency. For example, Barandiaran (2017) argues that cognition and intentionality depend constitutively on sensorimotor agency achieved through the neurodynamical organization of sensorimotor coordination. He does not mention sentience, but it would appear he thinks that biological sentience also requires neurodynamically organized sensorimotor coordination. Similarly, whereas Fulda (2017) argues that bacteria are adaptive ecological agents, he denies that they are full-fledged cognitive agents and remains agnostic about whether they are sentient.

A different line of thought appeals to the physicochemical properties of neurons, specifically that they are electrically excitable cells. It has been proposed that sentience is an inherent feature of excitable cells, because they undergo an internal electrostatic shock during the sudden reversal of the membrane potential (Cook, Carvalho and Damasio, 2014). Cook (2008) describes this cellular event as the

way that the cell ‘senses’ the charge state of its immediate outside environment. He calls this kind of sensing ‘neuron-level sentience’. When many neurons synchronize their action potentials, they produce the coherent and large-scale electrodynamical states of the brain that are known to correlate with various states of consciousness across the sleep–wake cycle.

Being electrically excitable, however, is hardly exclusive to neurons; indeed, electrical signalling is ubiquitous in living cells. Motile prokaryotes and protists (such as paramecia and amoebae) are excitable cells, cells that create electrical currents when they are stimulated and that form bioelectrical fields. Plant cells also have complex electrical properties and form excitable networks (Wayne, 1993; Masi *et al.*, 2009; Dreyer *et al.*, 2021). What seems special about neuronal excitability is that, when many neurons are interconnected to form neuronal networks or brains, the sum or superposition of their electrical fields generates macroscopic neuroelectrical fields at a higher level of system complexity. These large-scale neuroelectrical fields, measured using EEG, shift in characteristic ways across the sleep–wake cycle and changing states of consciousness.

These observations enable us to sharpen some of the biological questions arising between biopsychism and zoopsychism. Is neurodynamically organized sensorimotor coordination causally required for biological sentience, or is the kind of chemotaxic sensorimotor coordination seen in prokaryotes and protists causally sufficient for sentience? Is neuronal electrical excitability causally required for sentience, or is the electrical excitability found in motile, single-cell organisms such as bacteria, paramecia, and amoebae causally sufficient for sentience? Is large-scale neuronal synchronization causally required for sentience? Or is the excitable network that transmits action potentials along phloem conduits in plants causally sufficient for sentience (Calvo, 2017; Calvo, Sahi and Trewavas, 2017)?<sup>16</sup>

In their recent rich book, *The Evolution of the Sensitive Soul*, Ginsburg and Jablonka (2019) present a detailed evolutionary

<sup>16</sup> Mention of plants raises the related issue of plant sentience, a topic of current debate that deserves consideration in its own right. Unfortunately, space limitations prevent me from a separate and thorough consideration of this issue. See Calvo (2017); Calvo, Sahi and Trewavas (2017); Taiz *et al.* (2019); Mallatt *et al.* (2020); Draguhn, Mallatt and Robinson (2020); Ginsburg and Jablonka (2021); and Linson, Ponskshe and Calvo (2021).

framework that casts light on these questions and supports a zoopsychist perspective. They regard consciousness, like life, as a ‘mode of being’: being alive (being a living system) and being conscious (being a conscious system) are systemic modes of being. The issue between biopsychism and zoopsychism concerns how these modes of being are related: are they coextensive or only partially overlapping?

Ginsburg and Jablonka’s starting point is to list the capacities that they think scientists would generally regard as jointly sufficient (if not individually necessary) for a system being a conscious system. These capacities include global cognitive accessibility of cognitive contents (accessibility of contents from and to perception, memory, and thought, especially to mental attention and working memory), perceptual and cognitive binding (unification and differentiation of perceived and cognized features), selective attention, intentionality (the ability to be directed towards the world and one’s own body in perception and cognition), integration of information over time, evaluation, embodied agency, and making a self/other distinction (see Birch, Ginsburg and Jablonka, 2020, pp. 56–7). The next step is to find the simplest property that requires the presence of systems with these capacities. From an evolutionary perspective, such a property would serve as a ‘transition marker’: its emergence would mark the presence of consciousness, as a mode of being, by virtue of requiring those capacities that suffice for that mode of being.

The method here is analogous to research on the origins of life. In the case of life, Ginsburg and Jablonka draw on Maturana and Varela’s theory of autopoiesis and Gánti’s chemoton theory to propose that the following capacities are jointly sufficient for being a living system: individuation, metabolism, stability, information storage, self-regulation of the internal milieu, growth, reproduction, and death. Following Gánti, and Maynard Smith and Szathmáry (1995), Ginsburg and Jablonka suggest that ‘unlimited heredity’ — the capacity to form varying reproductive lineages of open-ended length — is the single and simplest property that requires a system with these constitutive capacities of life. If we accept that there could be no unlimited heredity without living systems, that unlimited heredity is a ‘transition marker’ indicative of the presence of life, then unlimited heredity becomes a useful explanatory focus for origins of life research.

In the case of consciousness, the question is whether there is an analogous transition marker for the capacities generally regarded as jointly sufficient for being a conscious system. Ginsburg and Jablonka

argue that ‘unlimited associative learning’ is this transition marker. Associative learning is the ability to learn and remember a relation between items, such as a person’s name and their phone number, and thereby associate the items with each other. Unlimited associative learning additionally involves compound stimuli (patterns involving features in more than one sense modality), novel stimuli, second-order conditioning (linking novel, compound stimuli in open-ended chains), trace conditioning (time gaps with no overlap between associatively linked stimuli or events), and flexible and revisable associations with positive and negative values. Since unlimited associative learning likely requires the functional integration of the previously listed capacities that are jointly sufficient for consciousness, it becomes a useful explanatory target for consciousness research.

Although associative learning is traditionally thought to be limited to animals with nervous systems, it may be possible in single-celled organisms (Fernando *et al.*, 2009), and there is one report of associative learning in plants (Gagliano *et al.*, 2016), though a recent study was unable to replicate this finding (Markel, 2020). Unlimited associative learning, however, requires capacities that are known to depend on the brain, particularly on large-scale neural integration. Based on reviewing the animal-learning literature, Jablonka and Ginsburg suggest that unlimited associative learning is present in most vertebrates, some cephalopod molluscs (octopods, squid, and cuttlefish), and some arthropods (fruit flies, honey bees). They also suggest that it is absent in other invertebrate taxa (*Aplysia*, nematodes, annelids).

It is important to note that Ginsburg and Jablonka do not argue that consciousness entails the manifestation of unlimited associative learning; rather, they argue that such learning can occur only in conscious animals and that consciousness depends on the evolved neural architecture for it. Unlimited associative learning can only be a positive marker of the presence of consciousness; it cannot indicate which organisms are not conscious. The cognitive capacities that constitute unlimited associative learning and that are taken to be jointly sufficient for consciousness have not been shown to be necessary for consciousness, particularly for sentience of value.

Direct evidence that unlimited associative learning requires consciousness is currently lacking (Birch, 2020; Browning and Veit, 2021). Although no experiment (to my knowledge) has shown that unlimited associative learning is possible for unconscious or subliminal stimuli, whether unconscious unlimited associative learning is

possible needs to be directly tested. Furthermore, if it were to turn out that unlimited associative learning can occur in non-conscious organisms, then it could not serve as a transition marker for consciousness.

But here we encounter a methodological problem. As Heather Browning and Walter Veit write:

[H]ere we run into the problem of validation — we need first to determine whether or not an animal is conscious before we can tell whether or not UAL [unlimited associative learning] is linked to consciousness, and we have no independent way to do this. Although we can also test for the unconscious performance of UAL, through seeing whether animals (such as humans) we know to be conscious can perform UAL without consciousness (such as through masking experiments), this will not get us far in refuting the account. Even if UAL was performed unconsciously by these subjects, it could be insufficient to reject its link to consciousness... [E]ven if it is performed without active consciousness, it does not follow that it can be performed in the absence of the necessary architecture for consciousness. In this case, it would still be true that only conscious animals could perform UAL, even if they can do so unconsciously at times. (Browning and Veit, 2021, pp. 4–5)

The problem of validation, however, goes deeper. Ginsburg and Jablonka's approach depends on assuming that there is a general consensus about the properties that are sufficient for consciousness and that are not human-specific. But this assumption is questionable. As Christopher Masciari and Peter Carruthers (2021) observe, although most theorists would accept that the properties Ginsburg and Jablonka list *accompany* consciousness, there is no consensus that these properties *constitute* consciousness. For example, it is generally agreed that global cognitive accessibility of cognitive contents accompanies reportable conscious states in humans, but there is no agreement that such global accessibility constitutes consciousness in the sense of subjective experience, let alone sentience (the capacity to feel). But if sentience (hedonic value or affective valence) is our explanatory target, then we find ourselves in an epistemological circle with respect to the problem of validation (Schwitzgebel, 2020): to determine the extent of sentience in the natural world, we need a validated theory of consciousness, but to arrive at such a theory we need to rely on assumptions about how widespread sentience is. Ginsburg and Jablonka have hardly escaped this circle; on the contrary, their way of inhabiting it is to work on the basis of the (controversial) assumption that certain cognitive properties (e.g. global cognitive accessibility) are constitutive of sentience.

The biopsychist, however, denies precisely this kind of assumption by sharply distinguishing between the activity of feeling (sentience) and the activity of cognition, and by choosing instead to inhabit the circle by working on the basis of the assumption that feeling is far more widespread than cognition.

From this perspective, biopsychism and zoopsychism can be seen as making different starting assumptions about the nature of sentience and how to relate phenomenological properties and biological properties, and by developing distinct research programmes based on these assumptions. To settle the issue between biopsychism and zoopsychism, we would need a theoretical argument, informed by empirical evidence, that would be compelling to theorists on both sides of the issue. Given the epistemological circle just mentioned, however, and the divergent assumptions of biopsychism and zoopsychism (to say nothing of panpsychism), it is hard to see how there could be such an argument.<sup>17</sup>

One last argument in favour of zoopsychism, from Peter Godfrey-Smith (2020), is worth considering in this light. Like Ginsburg and Jablonka (2019, p. 456) and Eric Schwitzgebel (2020), but unlike most philosophers of consciousness, Godfrey-Smith believes that sentience is not all-or-none, either present or absent, but instead is a matter of degree, and so can be partly there and partly not (Godfrey-Smith, 2020, p. 263). The question ‘Is it conscious?’ need not have a yes-or-no answer; ‘instead, the goings-on inside an animal can be *more or less experiential*’ (*ibid.*, his emphasis, p. 264). He calls this idea ‘gradualism’, on analogy with phyletic gradualism, the idea that speciation is slow and uniform. Nevertheless, he argues that sentience is not present in all life, even though minimal cognition is. He poses the crucial question and recognizes its force:

Before you stretches a gradual slope that leads into plants, fungi, non-neural animals, protists, and bacteria. If sentience has to come into being gradually, why isn’t *this* the road on which it appears? Why

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<sup>17</sup> It might be thought that the integrated information theory of consciousness (IIT) provides this kind of independent theoretical framework. Indeed, IIT has been used to argue in favour of plant sentience (Calva, Baluška and Trewavas, 2021; Trewavas, 2021). But unless one is already attracted to the idea that consciousness is extremely widespread, including in highly counter-intuitive inorganic cases that we have no reason to believe are conscious apart from IIT, one is not likely to find this theory attractive. IIT also depends on problematic axioms (despite their being presented as self-evident) (see Bayne, 2018). So IIT hardly escapes the epistemological circle in theorizing about consciousness.

doesn't minimal cognition imply minimal sentence? If subjectivity is an important idea in making sense of the evolution of mind, doesn't everything with minimal cognition have a kind of subjectivity, a way things *seem* to it, and so on? (*ibid.*, p. 277)

Although he admits that this question became 'the biggest recurring uncertainty' (p. 278) as he wrote his book, he finally decides that biopsychism is a mistake. I call attention to the reason he gives: 'Minimal cognition is, after all, present in bacteria, and when you look at what they do and how they do it, feeling just seems to not be part of the picture' (*ibid.*, p. 278).

In the end, what decides the matter is a kind of seeing-as, or rather the absence of a kind of seeing-as. Looking at bacteria, Godfrey-Smith says he does not see them as sentient. The decisive reason turns out to be a kind of interpretive perception, the perception of bacteria as not conforming to a certain mode of being, the sentient mode. Coupled to this perception are background convictions about the importance of the nervous system (the book is about animals) and about how widespread we should take consciousness to be. So we are very much within the epistemological circle mentioned above.

Speaking for myself, when I look at videos of what bacteria do and hear biologists talk about how they do it, I have no difficulty seeing feeling as part of the picture. I will never forget Lynn Margulis showing me her films of bacteria and protists while arguing that these organisms should be regarded as sentient. My perception of life was completely changed.<sup>18</sup>

In summary, given the discussion of this section, I do not see compelling reasons to favour zoopsychism over biopsychism. Given the present state of our knowledge, and the apparently unavoidable epistemological circle in theorizing about consciousness in the sense of subjective experience, I see no decisive way to resolve their differences at a first-order naturalistic level (in contrast to the transcendental level mentioned earlier).

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<sup>18</sup> Yes, I can back off from viewing them this way when forced to adopt an abductive stance, but I can do the same for animals when forced into this kind of stance. And certain philosophers — who believe in the conceivability of zombies — say they can do the same for human beings.

## 11. Conclusion

The main purpose of this paper has been to see whether the enactive conception of life as fundamentally and intrinsically a value-constituting and value-driven process requires or implies a conception of life as sentient. As we have seen, the case is inconclusive. There remains a conceptual and inferential gap between differential responsiveness to value (sense-making) and hedonic value or affective valence. Nevertheless, the case for zoopsychism over biopsychism is also inconclusive.

It also emerged that we occupy an apparently unavoidable epistemological circle in theorizing about consciousness. From the enactive perspective, this circularity is to be expected and signals the need for a transcendental perspective on the activity of trying to explain life and sentience (Thompson, 2007). Although I have chosen not to press these points here, I believe the circularity also signals the contradictions involved in trying to understand consciousness using scientific methods and criteria that were designed to exclude it or minimize its role. Maybe a science of consciousness entails a different kind of participatory epistemology, where circularities in criteria of validation are resolved using phenomenological methods for a non-detached engagement with sentience.<sup>19</sup>

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## References

- Barandiaran, X.E. (2017) Autonomy and enactivism: Towards a theory of sensorimotor autonomous agency, *Topoi*, **36**, pp. 409–430.
- Barandiaran, X.E., Rohde, M. & Di Paolo, E.A. (2009) Defining agency: Individuality, normativity, asymmetry, and spatio-temporality in action, *Adaptive Behavior*, **17**, pp. 367–386.
- Baluška, F. & Reber, A. (2019) Sentience and consciousness in single cells: How the first minds emerged in unicellular species, *BioEssays*, **41**, 1800229. doi: [10.1002/bies.201800229](https://doi.org/10.1002/bies.201800229)

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<sup>19</sup> I am grateful to Ezequiel Di Paolo for discussion of this point.



- Barrett, N. (2017) The normative turn in enactive theory: An examination of its roots and implications, *Topoi*, **36**, pp. 431–443.
- Bayne, T. (2018) On the axiomatic foundations of the integrated information theory of consciousness, *Neuroscience of Consciousness*, **2018** (1), niy007. doi: 10.1002/bies.201800229
- Birch, J. (2020) In search of the origins of consciousness, *Acta Biotheoretica*, **68**, pp. 287–294.
- Birch, J., Ginsburg, S. & Jablonka, E. (2020) Unlimited associative learning and the origins of consciousness: A primer and some predictions, *Biology & Philosophy*, **35**. doi: 10.1007/s10539-020-09772-0
- Bitbol, M. & Luisi, L. (2005) Autopoiesis with or without cognition: Defining life at the edge, *Journal of the Royal Society Interface*, **1**, pp. 99–107.
- Bourgine, P. & Stewart, J. (2004) Autopoiesis and cognition, *Artificial Life*, **20**, pp. 327–345.
- Browning, H. & Veit, W. (2021) Evolutionary biology meets consciousness: Essay review of Simona Ginsburg and Eva Jablonka's The Evolution of the Sensitive Soul, *Biology & Philosophy*, **36**. doi: 10.1007/s10539-021-09781-7
- Brüntrup, G. & Jaskolla, L. (eds.) (2017) *Panpsychism: Contemporary Perspectives*, Oxford: Oxford University Press.
- Calvo, P. (2017) What is it like to be a plant?, *Journal of Consciousness Studies*, **24** (9–10), pp. 205–227.
- Calvo, P., Sahi, V.P. & Trewavas, A. (2017) Are plants sentient?, *Plant, Cell & Environment*, **40**, pp. 285–2869. doi: 10.1111/pce.13065
- Calvo, P., Baluška, F. & Trewavas, A. (2021) Integrated information as a possible basis for plant consciousness, *Biochemical and Biophysical Research Communications*, **564**, pp. 158–165.
- Christoff, K., Cosmelli, D., Legrand, D. & Thompson, E. (2011) Specifying the self for cognitive neuroscience, *Trends in Cognitive Sciences*, **15** (3), pp. 104–112.
- Clark, A. (2015) *Surfing Uncertainty: Prediction, Action, and the Embodied Mind*, New York: Oxford University Press.
- Cook, N. (2008) The neuron-level phenomena underlying cognition and consciousness: Synaptic activity and the action potential, *Neuroscience*, **153**, pp. 556–570.
- Cook, N.D., Carvalho G.B. & Damasio, A. (2014) From membrane excitability to metazoan psychology, *Trends in Neuroscience*, **12**, pp. 698–705. doi: 10.1016/j.tins.2014.07.011
- Di Paolo, E.A. (2005) Autopoiesis, adaptivity, teleology, agency, *Phenomenology and the Cognitive Sciences*, **4**, pp. 429–452.
- Di Paolo, E.A. (2009) Overcoming autopoiesis: An enactive detour on the way from life to society, in Magalhaes, R. & Sanchez, R. (eds.) *Autopoiesis in Organizations and Information Systems*, pp. 43–68, New York: Elsevier.
- Di Paolo, E.A. (2018) The enactive conception of life, in Newen, A., De Bruin, L. & Gallagher, S. (eds.) *The Oxford Handbook of 4E Cognition*, pp. 71–94, Oxford: Oxford University Press.
- Di Paolo, E.A. & Thompson, E. (2014) The enactive approach, in Shapiro, L. (ed.) *The Routledge Handbook of Embodied Cognition*, pp. 68–78, London: Routledge Press.
- Di Paolo, E.A., Buhmann, T. & Barandiaran, X. (2017) *Sensorimotor Life: An Enactive Proposal*, Cambridge, MA: MIT Press.

- Di Paolo, E.A., Cuffari, E. & De Jaegher, H. (2018) *Linguistic Bodies: The Continuity Between Life and Language*, Cambridge, MA: MIT Press.
- Di Paolo, E.A., Thompson, E. & Beer, R.D. (2021) Laying down a forking path: Incompatibilities between enaction and the free energy principle, *PsyArXiv*, 19 April. doi: [10.31234/osf.io/d9v8f](https://doi.org/10.31234/osf.io/d9v8f). Forthcoming in *Philosophy and the Mind Sciences*.
- Draguhn, A., Mallatt, J.M. & Robinson, D.G. (2020) Anesthetics and plants: No pain, no brain, and therefore no consciousness, *Protoplasma*, **258**, pp. 239–248. doi: [10.1007/s00709-020-01550-9](https://doi.org/10.1007/s00709-020-01550-9)
- Dreyer, I., Sussmilch, F.C., Fukushima, K., Riadi, G., Becker, D., Schultz, J. & Hedrich, R. (2021) How to grow a tree: Plant voltage-dependent cation channels in the spotlight of evolution, *Trends in Plant Science*, **26** (1), pp. 41–52.
- Egbert, M.D., Barandiaran, X.E. & Di Paolo, E.A. (2010) A minimal model of metabolism-based chemotaxis, *PLoS Computational Biology*, **6** (12), e1001004. doi: [10.1371/journal.pcbi.1001004](https://doi.org/10.1371/journal.pcbi.1001004)
- Fernando, C.T., Liekens, A.M.L., Bingle, L.E.H., Beck, C., Lenser, T., Stekel, D.J. & Rowe, J.E. (2009) Molecular circuits for associative learning in single-celled organisms, *Journal of the Royal Society Interface*, **6**, pp. 463–469.
- Foster, M. (1883) *A Textbook of Physiology*, 4th ed., revised, London: Macmillan.
- Friston, K.J. (2013) Life as know it, *Journal of the Royal Society Interface*, **10**, 20130475. doi: [10.1098/rsif.2013.0475](https://doi.org/10.1098/rsif.2013.0475)
- Fulda, F.C. (2017) Natural agency: The case of bacterial cognition, *Journal of the American Philosophical Association*, **3**, pp. 69–80. doi: [10.1017/apa.2017.5](https://doi.org/10.1017/apa.2017.5)
- Gagliano, M., Vyazovskiy, V.V., Borbély, A.A., Grimonprez, M. & Deczyski, M. (2016) Learning by association in plants, *Scientific Reports*, **6**, 38427. doi: [10.1038/srep38427](https://doi.org/10.1038/srep38427)
- Gánti, T. (1975) Organizations of chemical reactions into dividing and metabolizing units: The chemotons, *BioSystems*, **7**, pp. 15–21.
- Ginsburg, S. & Jablonka, E. (2019) *The Evolution of the Sensitive Soul: Learning and the Origins of Consciousness*, Cambridge, MA: MIT Press.
- Ginsburg, S. & Jablonka, E. (2020) Are your cells conscious?, *American Journal of Psychology*, **133** (1), pp. 117–121.
- Ginsburg, S. & Jablonka, E. (2021) Sentience in plants? A green red herring?, *Journal of Consciousness Studies*, **28** (1–2), pp. 17–33.
- Godfrey-Smith, P. (2016) Mind, matter, and metabolism, *Journal of Philosophy*, **113**, pp. 481–506.
- Godfrey-Smith, P. (2020) *Metazoa: Animal Life and the Birth of the Mind*, New York: Farrar, Straus, and Giroux.
- Goff, P. (2017) *Consciousness and Fundamental Reality*, Oxford: Oxford University Press.
- Haeckel, E. (1892) Our monism: The principles of a consistent, unitary world-view, *The Monist*, **2**, pp. 481–486.
- Hayward, J. & Varela, F.J. (eds.) (1992) *Gentle Bridges: Conversations with the Dalai Lama on the Sciences of Mind*, Boston, MA: Shambhala Press.
- Hurley, S. (1998) *Consciousness in Action*, Cambridge, MA: Harvard University Press.
- Jekely, G., Godfrey-Smith, P. & Keijzer, F. (2021) Reafference and the origin of self in early nervous system evolution, *Philosophical Transactions of the Royal Society B*, **376**, 20190764. doi: [10.1098/rstb.2019.0764](https://doi.org/10.1098/rstb.2019.0764)

- Jonas, H. (1966) *The Phenomenon of Life: Toward a Philosophical Biology*, Chicago, IL: University of Chicago Press.
- Jonas, H. (1968) Biological foundations of individuality, *International Philosophical Quarterly*, **8**, pp. 231–251.
- Leibniz, G. (1703–05/1989) Preface to the *New Essays*, in Leibniz, G.W., *Philosophical Essays*, Ariew, R. & Garber, D. (trans.), Indianapolis, IN: Hackett Publishing Company.
- Linson, A., Pongshe, A. & Calvo, P. (2021) On plants and principles, *Biology & Philosophy*, **39**, art. 19. doi: [10.1007/s10539-021-09793-3](https://doi.org/10.1007/s10539-021-09793-3)
- Lyon, P. (2015) The cognitive cell: Bacterial behavior reconsidered, *Frontiers in Microbiology*, **6**, art. 264. doi: [10.3389/fmicb.2015.00264](https://doi.org/10.3389/fmicb.2015.00264)
- Mallatt, J., Blatt, M.R., Draguhn, A., Robinson, D.G. & Taiz, L. (2020) Debunking a myth: Plant consciousness, *Protoplasma*, **258**, pp. 459–476. doi: [10.1007/s00709-020-01579-w](https://doi.org/10.1007/s00709-020-01579-w)
- Margulis, L. (2001) The conscious cell, in Marijūan, P.C. (ed.) *Cajal and Consciousness: Scientific Approaches to Consciousness on the Centennial of Ramon y Cajal's Textura*, pp. 55–70, *Annals of the New York Academy of Sciences*, **929**, New York: New York Academy of Sciences.
- Margulis, L. & Sagan, D. (1995) *What is Life?*, New York: Simon and Schuster.
- Markel, K. (2020) Lack of evidence for associative learning in plants, *eLife*, **2020**, 9e57614. doi: [10.1007/s00709-020-01579-w](https://doi.org/10.1007/s00709-020-01579-w)
- Masciari, C.F. & Carruthers, P. (2021) Perceptual awareness or phenomenal consciousness? A dilemma, *Biology and Philosophy*, **36**, art. 18. doi: [10.1007/s10539-021-09795-1](https://doi.org/10.1007/s10539-021-09795-1)
- Masi, E., Ciszak, G., Stefano, L., Azzarello, R.E., Pandolfi, C., Mugnai, S., Baluška, F., Arecchi, F.T. & Macuso, S. (2009) Spatiotemporal dynamics of the electrical network activity in the root apex, *Proceedings of the National Academy of Sciences*, **106** (10), pp. 4048–4053.
- Maturana, H.R. (1970/1980) Biology of cognition, in Maturana, H.R. & Varela, F.J., *Autopoiesis and Cognition: The Realization of the Living*, pp. 1–58, Dordrecht: D. Reidel.
- Maturana, H.R. & Varela, F. J. (1973/1980) Autopoiesis: The organization of the living, in Maturana, H.R. & Varela, F.J. *Autopoiesis and Cognition: The Realization of the Living*, pp. 59–140, Dordrecht: D. Reidel.
- Maturana, H.R. & Varela, F.J. (1980) *Autopoiesis and Cognition: The Realization of the Living*, Dordrecht: D. Reidel.
- Maturana, H.R. & Varela, F.J. (1987) *The Tree of Knowledge: The Biological Roots of Human Understanding*, Boston, MA: Shambhala Press.
- Maynard Smith, J. & Szathmáry, E. (1995) *The Major Transitions in Evolution*, Oxford: Oxford University Press.
- Merleau-Ponty, M. (1963) *The Structure of Behavior*, Fischer, A. (trans.), Pittsburgh, PA: Duquesne University Press.
- Moreno, A. (2019) The origins of a trans-generational organization in the phenomenon of biogenesis, *Frontiers in Physiology*, **10**, art. 1222. doi: [10.3389/fphys.2019.01222](https://doi.org/10.3389/fphys.2019.01222)
- Pereira Jr., A. (2021) The role of sentience in the theory of consciousness and medical practice, *Journal of Consciousness Studies*, **28** (7–8), pp. 22–50.
- Ramstead, M.J.D., Kirchhoff, M.D. & Friston, K.J. (2019) A tale of two densities: Active inference is enactive inference, *Adaptive Behavior*, **28** (4), pp. 225–239.

- Reber, A.S. (2019) *The First Minds: Caterpillars, 'Karyotes, and Consciousness*, New York: Oxford University Press.
- Reber, A.S. (2020) The origins of mind: A novel theory based on, of all things, learning, *American Journal of Psychology*, **133** (1), pp. 121–126.
- Reber, A.S. & Baluška, F. (2021) Cognition in some surprising places, *Biochemical and Biophysical Research Communications*, **564**, pp. 150–157.
- Rosen, R. (1991) *Life Itself: A Comprehensive Inquiry into the Nature, Origin, and Fabrication of Life*, New York: Columbia University Press.
- Rosenberg, G. (2017) Land ho? We are close to a synoptic understanding of consciousness, in Brüntrup, G. & Jaskolla, L. (eds.) *Panpsychism: Contemporary Perspectives*, pp. 153–175, Oxford: Oxford University Press.
- Schwitzgebel, E. (2020) Is there something it's like to be a garden snail?, [Online], <http://www.faculty.ucr.edu/~eschwitz/SchwitzPapers/Snails-201223.pdf>
- Sheets-Johnstone, M. (1998) Consciousness: A natural history, *Journal of Consciousness Studies*, **5** (3), pp. 260–294.
- Sheets-Johnstone, M. (2011) *The Primacy of Movement*, revised ed., Philadelphia, PA: John Benjamins.
- Strawson, G. (2013) Self-intimation, *Phenomenology and the Cognitive Sciences*, **14** (1), pp. 1–31.
- Taiz, L., Alkon, D., Draguhn, A., Murphy, A., Blatt, M., Hawes, C., Thiel, G. & Robinson, D.G. (2019) Plants neither possess nor require consciousness, *Trends in Plant Science*, **24** (8), pp. 677–687.
- Theise, N.D. & Kafatos, M.C. (2013) Sentience everywhere: Complexity theory, panpsychism and the role of sentience in self-organization of the universe, *Journal of Consciousness Exploration & Research*, **4** (4), pp. 378–390.
- Thompson, E. (2004) Life and mind: From autopoiesis to neurophenomenology. A tribute to Francisco Varela, *Phenomenology and the Cognitive Sciences*, **3**, pp. 381–398.
- Thompson, E. (2007) *Mind in Life: Biology, Phenomenology, and the Sciences of Mind*, Cambridge, MA: Harvard University Press.
- Thompson, E. (2011a) Replies to commentators, *Journal of Consciousness Studies*, **18** (5–6), pp. 176–223.
- Thompson, E. (2011b) Living ways of sense-making, *Philosophy Today*, SPEP Supplement, pp. 114–123. doi: 10.5840/philtoday201155Supplement14
- Thompson, E. (2014) Review of *Phenomenology and Naturalism: Examining the Relationship between Human Experience and Nature*, eds. Havi Carel and Darian Meacham, *Notre Dame Philosophical Reviews*, [Online], <https://ndpr.nd.edu/reviews/phenomenology-and-naturalism-examining-the-relationship-between-human-experience-and-nature/>
- Thompson, E. (2015a) *Waking, Dreaming, Being: Self and Consciousness in Neuroscience, Meditation, and Philosophy*, New York: Columbia University Press.
- Thompson, E. (2015b) Dreamless sleep, the embodied mind, and consciousness: The relevance of a classical Indian debate to cognitive science, in Metzinger, T. & Windt, J. (eds.) *Open MIND*, Frankfurt am Main: Mind Group, [Online], <https://open-mind.net/papers/dreamless-sleep-the-embodied-mind-and-consciousness-the-relevance-of-a-classical-indian-debate-to-cognitive-science>
- Thompson, E. & Varela, F.J. (2001) Radical embodiment: Neural dynamics and consciousness, *Trends in Cognitive Sciences*, **5** (10), pp. 418–425.

- Trewavas, A. (2021) Awareness and integrated information theory identify plant meristems as sites of conscious activity, *Protoplasma*, **258**, pp. 673–679. doi: [10.1007/s00709-021-01633-1](https://doi.org/10.1007/s00709-021-01633-1)
- Varela, F.J. (1979) *Principles of Biology Autonomy*, New York: Elsevier North Holland.
- Varela, F.J. (1991) Organism: A meshwork of selfless cells, in Tauber, A. (ed.) *Organism and the Origins of Self*, pp. 79–107, Dordrecht: Kluwer Academic Publishers.
- Varela, F.J. (1997) Patterns of life: Intertwining identity and cognition, *Brain and Cognition*, **34**, pp. 72–87.
- Wadhwa, N. & Berg, H.C. (2021) Bacterial motility: Machinery and mechanisms, *Nature Reviews Microbiology*, ahead of print. doi: [10.1038/s41579-021-00626-4](https://doi.org/10.1038/s41579-021-00626-4)
- Wayne, R. (1993) Excitability in plant cells, *American Scientist*, **81** (2), pp. 140–151.
- Weber, A. & Varela, F.J. (2002) Life after Kant: Natural purposes and the auto-poietic foundations of biological individuality, *Phenomenology and the Cognitive Sciences*, **1**, pp. 97–125.
- Zahavi, D. (2005) *Subjectivity and Selfhood: Investigating the First-Person Perspective*, Cambridge, MA: MIT Press.