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Review

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Biological agency: a concept without a research program

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Abstract

This paper evaluates recent work purporting to show that the "agency" of organisms is an important phenomenon for evolutionary biology to study. Biological agency is understood as the capacity for goal-directed, self-determining activity—a capacity that is present in all organisms irrespective of their complexity and whether or not they have a nervous system. Proponents of the "agency perspective" on biological systems have claimed that agency is not explainable by physiological or developmental mechanisms, or by adaptation via natural selection. We show that this idea is theoretically unsound and unsupported by current biology. There is no empirical evidence that the agency perspective has the potential to advance experimental research in the life sciences. Instead, the phenomena that the agency perspective purports to make sense of are better explained using the well-established idea that complex multiscale feedback mechanisms evolve through natural selection.

Keywords: agency, goal-directedness, mechanism, adaptation, self-determination, natural selection

Introduction

Agency has been the subject of increasing attention in biology and allied disciplines, as indicated by the number of special issues, edited volumes, books, and papers devoted to it (e.g., Corning et al., 2023; Fábregas-Tejada et al., 2024; Levin, 2022; Mitchell, 2023; Moczek & Sultan, 2023; Moss, 2024; Newman et al., 2024; Sultan et al., 2022; Švorcová, 2024; Vane-Wright & Corning, 2023). In colloquial contexts, "agency" is a cognitive or psychological term with connotations of freedom, self-determination, and rational control. It is commonly used in human social settings that presuppose a high level of neurobiological complexity among actors. Biological agency, however, has been treated as something that is displayed by all organisms—even those without nervous systems or advanced cognition. Proponents claim that biological agency captures an important phenomenon that has been neglected by the gene-centric research programs in evolutionary biology that originated during the Modern Synthesis. Proponents also suggest that a focus on agency promises to fill in crucial explanatory gaps purportedly left by these traditions, while also supporting an empirical research program capable of revealing previously unknown facts about the biological world.

There are several versions of the agency concept in the recent literature (see Okasha, 2018, 2024), which present orthogonal or even incompatible proposals of its meaning and role in biological research (see Box 2 below). Here, we focus on one prominent understanding of agency, exemplified especially in Sultan et al. (2022), papers in Moczek & Sultan (2023), in Corning et al. (2023), and Newman et al. (2024). In this understanding, agency is an organism's capacity for goal-directed activity and self-determination that is not explained by underlying mechanisms or by natural selection. We refer to this as simply as "biological agency." Biological agency is supposed to be manifested in a diverse set of more specific features, including niche construction, robustness, plasticity, open-ended evolvability, downward causation, internal causal control, and even the origin of evolutionary novelties. Many of these phenomena are those foregrounded by advocates of the Extended Evolutionary Synthesis (EES) (Lala et al., 2024; Laland et al., 2015), and much of the literature on biological agency can be understood as an extension of that controversial framework (Dickins & Dickins, 2023; Futuyma, 2017; Houle, 2024; Noble et al., 2017; Svensson, 2018). In addition, much of the recent work on agency aims to resuscitate the Aristotelian view of biological purpose and teleology as real rather than merely apparent, and as rooted in individual organisms rather than being explained in terms of Darwinian natural selection in populations (Corning et al., 2023; Oderberg, 2018; Turner, 2017; Vane-Wright & Corning, 2023; Walsh, 2015; Woodford, 2016).

The flurry of recent work promoting this "biological agency perspective" has not been subjected to careful scrutiny. We show that the central claims of the agency perspective are misguided, and their acceptance would be detrimental to the progress of the biological sciences (see Box 1 for a summary). The following sections critically examine what we take to be the core aspects of biological agency: goal-directedness,

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Box 1: The central claims of this paper

1. An organism's capacity for goal-directed behaviour does not itself explain any biological phenomena. Apparently goal-directed behaviours are, instead, something to be explained as an evolved characteristic of biological systems.
2. The capacity for goal-directed behaviour (outside of human cognition, which can set arbitrary, novel goals) is explained by Darwinian natural selection acting in populations of individuals.
3. Notions such as self-determination, or the idea that the whole organism is a cause of its own developmental or physiological processes, are either empirically untestable, or restatements of ordinary questions about which causal mechanisms at which scales influence events.
4. Downward causation and context-dependence are "mechanistic" in the sense relevant to experimental biology. They are not mysterious processes that require adopting the teleological form of investigation provided by an agency perspective.
5. Rejection of molecular reductionism or determinism does not necessitate a commitment to the idea of biological agency. Researchers need not embrace the agency perspective in order to acknowledge the importance of multi-level complexity, emergence, and downward causation.
6. The idea that biological goal-directedness is a product of natural selection rather than the inherent agency of organisms does not require a commitment to the idea that all traits are adaptations. It is compatible with genetic drift, mutation, and developmental constraints playing an important role in evolution.
7. Agency is a psychological concept originating in heuristic ascriptions of intentionality. Accordingly, it is applicable only where psychological explanations are useful—i.e., when explaining the behaviour of humans and possibly other neurologically complex organisms such as primates.
8. Agency is not an empirically meaningful property, and incorporating the agency concept into experimental practices will not contribute to progress in biology.

non-mechanistic explanation, and self-determination. Each aspect is problematic in light of current biology. We show that the central claims of the agency perspective are uninterpretable except as promoting a cryptically cognitive or psychological perspective on biological systems, despite assurances to the contrary. In effect, this perspective represents an effort to reinstitute the use of untenable psychological or folk-biological ideas in experimental research on non-human organisms. Because this perspective does not generate testable predictions, it is empirically unproductive. We conclude that biological agency is an empty concept without a research program.

Agency and goal-directedness

Organisms from bacteria to ants to sequoias are generally well-adapted to their environments, and display physiological and/or behavioural tendencies toward certain outcomes and against others. Supposing that all organisms display "goal-directedness" in some form, there are two possible explanations for this. One is to pursue an analogy with the goal-directedness that pervades human psychology by invoking a special property inherent to all living organisms—their agency. While cognitive agency in human beings involves things like intentionality, self-awareness, symbolic reasoning, and complex inference in pursuit of goals (Dennett, 1987), simpler organisms like bacteria lack these mental capacities. It then becomes pressing to clarify what this form of non-cognitive, biological agency is. What is clear is that single-celled organisms have morphological, physiological, and behavioural traits that tend to promote the individual's survival and reproduction. This provides the basis for the other explanation for goal-directedness—namely, that it is adaptation due to natural selection. We argue that this is a sound basis for understanding biological goal-directedness, whereas agency is not.

There is an extensive historical precedent for explaining the goal-directedness or purposiveness of organisms as adaptation arising from the process of natural selection (Boomsma, 2022; Dennett, 1995; Dobzhansky, 1937; Huxley, 1942; Mayr, 1961, 1982; Simpson, 1950; Weismann, 1889, 1893; Williams, 1966). Darwinian explanations of adaptation can be formulated along the following general lines: when individuals in a population have heritable trait variations that cause differential survival and/or reproduction, variants that cause greater survival and/or reproduction will come to predominate. Organisms descending from such populations will display traits and behaviours conducive to survival and reproduction—i.e., adaptations (Lewontin, 1978; Williams, 1966).

Of course, there are many factors that can prevent adaptations from evolving, such as mutational pressure, weak selection, small population size, trade-offs, developmental constraints, and changing environments (Arnold, 1992; Cheverud, 1984; Futuyma, 2010; Lynch, 2007; Orzack, 2024; Pérez-Escudero et al., 2009; Pierce & Ollasen, 1987; Stearns, 1992). But where adaptation does occur, standard Darwinian thinking suggests that it can be explained by natural selection. An organism's "goals," according to this way of thinking, can be understood as outcomes that enhance Hamiltonian inclusive fitness (Hamilton, 1964; Williams, 1966), such as finding a mate or immune defense against infection. Being in the state of seeking these outcomes—"goal-directedness"—is due to positive selection in the past, and is thus equivalent to adaptation. Those who embrace this Darwinian interpretation of the phenomena generally seek to avoid misleading associations with cognitive or represented goals by only referring to technical evolutionary concepts (e.g., adaptation, fitness, selection, and unit of selection) known to have applicability in non-human contexts. These concepts are connected with a body of evolutionary theory that is demonstrably useful for conducting empirical research and advancing biological science by allowing researchers to formulate testable predictions. No such progress has been made by invoking the notions of goals and agency.

The agency perspective is rooted in the intuition that goal-directedness or purposive organization and behaviour must be an inherent attribute of an organism, not just a result of natural selection in previous generations (Igamberdiev, 2023; Newman, 2023; Noble & Noble, 2023a, 2023b; Odling-Smee, 2024; Rosslenbroich et al., 2024; Walsh, 2015). To justify this idea, one would have to show how it sometimes leads to different attributed "goals" than those that arise from natural selection, and presumably, how it leads to different predictions and explanations. If, by contrast, agency just means being a unit of selection, as in explicitly metaphorical evolutionary talk of agency (Dawkins, 1976; Dennett, 2017; Haig, 1997; Okasha, 2018, 2024), or if the two are completely co-extensive, then agency is hardly a neglected phenomenon requiring more scientific attention. Similarly,

if any goal-directed system is automatically an agent, this is compatible with a selection-based view of goal-directedness. In these cases, using the term "agency" without explicitly flagging it as a metaphor for natural selection is misleading insofar as it incorrectly implies that proto-cognitive attributes are a widespread feature of the biological world that scientists have failed to observe and study.

One potential deviation of goal-directed behaviour from the "goals" set by natural selection arises from the fact that humans, having elaborate social cognition and complex nervous systems capable of abstract and symbolic reasoning, are capable of setting their own goals and even creating new goals that have no direct relationship to fitness or selection—e.g., the arbitrary goals of sporting events and other games. Whether or not the human capacity to form representations of novel goals is itself an adaptation (Pinker, 1997), this kind of goal-directedness presupposes a degree of psychological and social complexity that is clearly not present in all species. It therefore does not license attributing agential goal-directedness to all organisms.

Another form of goal-directed behaviour that could be viewed as deviating from adaptation arises from the fact that organisms often possess proximate control mechanisms honed toward goals that are fitness components rather than overall fitness (Charlesworth & Hughes, 2000; Flatt, 2020; Stearns, 1992)—for example, mate-recognition systems or sensori-motor circuits for foraging. Like any other trait, these proximate mechanisms are subject to natural variation that is never entirely eliminated by the stochastic process of selection, and they can also be plastic in their development. When these mechanisms break down, misfire, or otherwise deviate from the previously selected outcome, an organism may appear to pursue goals that are contrary to its reproductive success, e.g., attempting to mate with a non-conspecific (Coyne & Orr, 2004; Gröning & Hochkirch, 2008; Noor, 1995). Similarly, when there is rapid environmental change, e.g., due to human activity, animals may respond to environmental cues that lead them to select worse habitats that reduce their fitness compared to other available habitats. Known as an "ecological trap," this phenomenon occurs when formerly reliable environmental signals of habitat quality become decoupled from current adaptive value (Gates & Gysel, 1978; Hale & Swearer, 2016; Robertson & Hutto, 2006; Schlaepfer et al., 2002). For example, some insects lay their eggs on horizontal artificial surfaces such as glass panes or car hoods, apparently mistaking them for water (Watson, 1992; Wildermuth & Horvéth, 2005; Wyniger, 1955). Deviations in environmental cues and in the perceptual mechanisms that respond to them can give rise to apparent goal-directed behaviours that run counter to reproductive success. On close scrutiny, however, such phenomena do not license anchoring goal-directedness in an organism's inherent agency. The operation of the maladaptive mechanism is only goal-directed at all due to past selection, and the mismatch between apparent behavioural goals and reproductive success is explainable by a combination of mechanistic variation and changing selective environments rather than purposeful planning. Natural selection is responsible for the goal-directedness (adaptedness) of behaviours like mate-finding, foraging, or egg-laying even if the behaviour is responsive to environmental cues rather than being a deterministic outcome of genetic programs, and even if the cues no longer accurately signal adaptive value.

It is important to recognize that the attribution of non-fitness-related goals to an organism can only be empirically grounded in the psychological case, where investigators can ask another human being to report on their internal cognitive states. For systems that lack the capacity to report on such states, the attribution of goals is empirically unmoored and arbitrary (see Figure 1). Is it the goal of a given stem cell to differentiate? (Levin, 2021, 2022; Manicka & Levin 2019) Or, if the stem cell fails to differentiate and dies, was that really its goal? In order for goal-attributions to explain anything, goals would need to be linked to some empirically detectable feature of the system other than the actual outcomes of its behaviour. Otherwise, these explanations would be circular and uninformative. It is not clear that this can be done without reference to natural selection.

It is not enough to say that goals are attractors or stable end-states (Aaby & Desmond 2021; Walsh 2015), or that systems exhibiting "persistence and plasticity" are goal-directed (Fulda, 2023; Lee & McShea, 2020; Nagel, 1979)—which is known as the "systems view" of goal-directedness. In this context, "persistence" means the tendency of a system on a trajectory to return to that trajectory following perturbation. "Plasticity" is here understood in an unusual sense as the tendency of an entity to converge on a specific trajectory from a variety of initial conditions (more often termed "canalization" or "robustness"). Multicellular organisms have a persistent and "plastic" tendency toward death over time, but attributing the goal of death to them is not biologically meaningful and does not advance our understanding of their biology. Many living things have a persistent and "plastic" tendency to be found in contact with the Earth's crust due to gravity. Is it their goal to be close to the ground? Does any object with mass—living or nonliving—also share this goal? These questions are not answerable because the notion of an inherent system goal does not generate empirically meaningful contrasts (see Okasha, 2023). As Okasha (2023, p. 244) notes, the fundamental problem with the "systems view" of goal-directedness is that "the goal toward which a process is directed, if any, is heavily underdetermined by the process's actual behaviour." In other words, from the same observed behaviour (e.g., mitosis, quiescence, autophagy), one can attribute many hypothetical goals, but there is no empirical criterion for telling which goal-attribution is correct.

In a central paper of the agency literature, Sultan et al. (2022, p. 8) explicate goals of biological agents in the following way: "A goal is simply a state that a system reliably tends to attain or maintain by making adaptive responses across a range of conditions." Yet the reference to adaptation is conspicuously ambiguous between individual and population levels. Is this just ordinary adaptation by natural selection? If not, how do we know which system responses are "adaptive" and which are not? It is not enough to assess this based on which responses seem beneficial or harmful to the individual according to human intuition. Many organisms reproduce at the expense of their own survival (Stearns, 1989; Williams, 1957). For example, in the *Antechinus* genus of small marsupials, males engage in frenzied mating during breeding season to an extent that leads to anaemia, elevated parasite load, hepatic necrosis, and haemorrhaging gastrointestinal tracts (Griffiths, 2009; Wingfield & Sapolsky, 2003). They die shortly after breeding season (Woolley, 1966), whereas males experimentally isolated from mating survive longer (Bradley, 1985). Human observers would likely find this behaviour

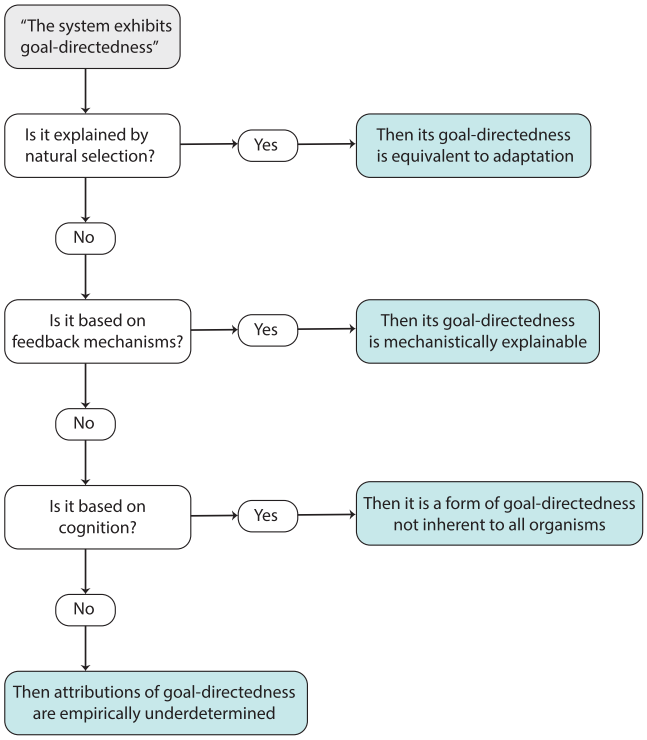


Figure 1. A decision tree illustrating a set of dilemmas surrounding agential goal-directedness. Goal-directedness, we maintain, is either explainable by selection, by natural selection plus proximate feedback mechanisms, or it is based on mental representations of goals, which only some animals possess. Outside of these alternatives, it is not clear that attributions of goal-directedness can be empirically grounded.

to be self-destructive. But is it "adaptive?" This cannot be decided in an empirically tractable way except by looking at whether males engaging in the behaviour tend to have more offspring than males that do not.

We suggest that there are two kinds of goal-directedness. Biological goal-directedness is adaptation and is explainable by natural selection. Cognitive goal-directedness is something different, and regardless of whether or not it is a direct product of selection, it is only present in some lineages (perhaps very few) with complex nervous systems. This distinction leaves no residual phenomenon of goal-directedness, common to yeast and ferns and mammals, that needs to be captured by a notion of biological agency. The idea that there are distinctive agential explanations (Sultan et al., 2022; Walsh, 2015) based on organisms' pursuit of goal-states seems therefore to either be a repackaging of adaptive explanations based on natural selection, or a proposal to explain biological phenomena in psychological or cognitive terms. The main upshot of the notion of agency is thus to suggest a parallel between biological and cognitive goal-directedness, which is encouraged by some researchers (Levin, 2022; Levin & Dennett, 2020; Rama, 2024; Shapiro, 2011, 2021) and disavowed by others (Fulda, 2020; Sultan et al., 2022).

One reason given for encouraging the parallel between biological and cognitive goal-directedness is that it appears to aid in understanding how cognitive agency has evolved out of simpler ancestral forms (Levin, 2019; Levin & Dennett 2020). For example, one can avoid positing sharp discontinuities or emergence events by picturing cognitive agency as being on a continuum or gradient (Levin, 2019, 2021; Seifert et al., 2024; Watson, 2024) stretching back in time, with, say, bacteria also having cognitive states but to a lesser degree (Margulis, 2001; Reber et al., 2023). A "gradualist" view of agency may even seem more consistent with evolutionary gradualism (Levin, 2022). The absurdity that follows from this reasoning can be appreciated by shifting examples. The avian capacity for flight did not evolve in a sudden saltational jump (Feo et al., 2015; Padian & Chiappe, 1998; Prum et al., 2015). But it is not useful to say that the wingless theropod ancestors of birds could also fly, only to a lesser degree. Saying so does not help to explain the evolution of flight. More generally: the evolutionary emergence of a complex trait is not explained by imagining that same trait to be present earlier in evolution to lesser degrees. Rather than explaining something about the complex trait (e.g., cognitive goal-directedness), one has merely re-described the earlier evolutionary form in terms of the complex trait, giving the illusion of understanding. It should be concerning that the same "gradualist" reasoning against emergence and discontinuity has been used to support panpsychism, the idea that even elementary particles possess consciousness to some degree (Goff, 2017; Wright, 1964).

Agency and mechanistic explanation

Several authors have proposed that biological agency provides a form of explanation distinct from, and complementary to, the causal-mechanistic style of explanation that characterizes much of biology (Rosslenbroich et al., 2024; Sultan et al., 2022; Uller, 2023; Walsh, 2015; Watson, 2024). The nature of mechanistic explanation is a large and widely discussed issue (Salmon, 1984; Gllenan & Illari, 2018; Craver & Tabery, 2024). It generally involves decomposing a system into parts, perturbing its properties and parts to discover how they interact as a system, and using this information to explain some system behaviour. To motivate the idea that mechanism is not enough, many proponents of agency conflate mechanism with molecular or genetic reductionism, and deploy general anti-reductionist arguments as vindications of agency (Ball, 2023; Noble & Noble, 2023a, 2023b; Potter & Mitchell, 2022; Sultan et al., 2022; Uller, 2023; Walsh & Sultan, 2024; Watson, 2024). We believe this is a mistake.

Sultan et al. (2022) identify two features of agential systems that purportedly call for non-mechanistic explanations: goal-directedness (discussed above) and context-sensitivity. Context-sensitivity is essentially plasticity or dependence on the environment, observed in organisms and their component parts. When a mechanism is context-sensitive, it generates different behaviours under different conditions. In this situation, citing the mechanism without the context will not explain the difference between the behaviours. Instead, Sultan et al. (2022) argue, this requires a system-to-component direction of explanation, or downward causation, which they regard as a non-mechanistic characteristic of agential systems.

This conclusion does not follow. Context-sensitivity is typically addressed not by switching to a different style of explanation, but by simply expanding the scope of the original mechanism to include more context. If there are causal influences from the context, mechanistic investigation can be refocused there. For example, stem cells in different tissues differentiate into one cell type or another depending on extracellular signals they receive from the surrounding tissue (Chacón-Martínez et al., 2018). The fact that a given stem cell differentiates into a given cell type rather than another is not

explained solely by genetic mechanisms within the stem cell, but also by extracellular signals. Such examples lie squarely within the standard mechanistic approaches to biological research.

When context-sensitivity involves downward causation, or causal influence from a variable at a higher level of organization to one at a lower, this does not imply "agency" in any other sense of the term. Consider action potential propagation in neurons (Hodgkin & Huxley, 1952; Woodward, 2021a). Ion channel proteins control the passage of ions across the cell membrane and thereby influence the electrical potential of the cell. At the same time, the cell potential influences the gating of the ion channels. This is an example of downward causation from a cell-level variable (cell voltage) to a protein-level variable (ion channel gating). Yet nothing would be gained by saying that cell voltage possesses agency. The downward causation that can be found in action potential propagation is thoroughly mechanistic, though it is a complex mechanism involving nonlinear feedback across different scales.

Another example of downward causation is the influence of tissue mechanics on cell states and gene expression during development (Busby & Steventon, 2021; Collinet & Lecuit, 2021). Mechanical properties of a tissue such as stiffness and elasticity influence the rates at which cells move past each other during morphogenesis, which can influence the timing of signal propagation between cells and its transduction to gene expression. Different degrees of mechanical tension and compression in a cell's environment can cause different genes to be expressed via threshold effects on mechanotransduction transcription cofactors YAP and TAZ (Panciera et al., 2017). Mechanical properties of tissues are themselves influenced by genetic effectors of the cellular actomyosin complex and adhesion proteins (Gilmour et al., 2017), giving rise to complex feedback across scales, which can be modified by natural selection to yield different modes of morphogenesis (Braun & Keren, 2018). Here again, it is not clear what would be gained by ascribing agency to mechanical properties of tissues or attributing the latter to the agency of the organism as a whole.

Many of the phenomena that have not yielded to reductionistic approaches are now studied using the tools of complexity science, which focuses on emergent dynamics of systems with many components, interactions, and feedback relationships (Anderson, 1972; Ladyman & Wiesner, 2020). Even when dealing with emergent processes, however, as Ladyman & Wiesner (2020, p. 7) write, "complexity science always involves describing a system by describing the interactions and relations among its parts." In this sense, it remains mechanistic rather than teleological. For example, to understand the emergent dynamics of a flock of birds flying, it is necessary to study how the local feedback interactions between individual animals give rise to the group-level swarm behaviour (Bialek et al., 2012). The fact that a given bird exhibits different flying behaviour in a group compared to solo flight would not be explained by invoking agency at the level of the group. The latter is at best an optional re-description of the context-sensitive flight behaviour of individuals.

These examples highlight why we should not think of mechanistic explanations as only bottom-up ("component-to-system") as suggested by Sultan et al. (2022), nor of mechanisms as exclusively genetic or molecular. This is not just a verbal issue concerning different definitions of mechanism. Variables at higher levels of organization that exert downward causal influence—e.g., cell voltage or tissue mechanics—are identified and studied using the same basic principles of causal discovery that are used in molecular studies: controlled perturbation of system variables followed by observation of effects on system behaviours. The examples of downward causation that we actually understand are mechanistic in this sense. Recognizing these phenomena, and rejecting the most extreme forms of molecular reductionism, therefore does not require embracing the view of organisms as biological agents.

Even if one allows explanations based on agency, it is difficult to see how such explanations could be useful for understanding an ordinary biological process—e.g., wound healing. To explain why a wound heals following injury, the statement that it is because the system possesses agency and pursues the goal of healing wounds is not useful from a scientific point of view. This is because agency is not an experimentally meaningful property that can be subjected to tests as to whether its presence or absence influences wound healing. The "goal" of wound healing is not something that can be detected or measured, but would have to be inferred and attributed ex post facto based on the system's actual behaviour (see *Agency and goal-directedness*). This procedure cannot predict that wound healing fails in pathological cases (e.g., tumorigenesis), nor can it explain why such malfunctions do or do not happen. In the context of modern biological research, wound healing is understood to be explainable in terms of complex positive and negative feedback mechanisms in which a wide array of signalling molecules mediate the progression through cell- and tissue-level processes, from wound detection to haemostasis, inflammation, cell proliferation, re-epithelialization, and tissue remodelling (Rodrigues et al., 2019; Singh et al., 2017). These feedback mechanisms are tuned to parameter values conducive to survival and reproduction because of natural selection.

Between mechanistic explanations and adaptive ones (Stearns, 1982; Tinbergen, 1963), there is no obvious role for a distinct form of explanation based on agency. Proximate organismic traits have evolved that exhibit goal-directedness, for example, foraging behaviour or cellular pH homeostasis. How they work is explained mechanistically, and their adaptiveness—to the extent that they are adaptive—is explained by natural selection.

Agency as self-determination

Perhaps the most central feature attributed to agents is self-determination, as seen in reflexive expressions like the following:

- "Biological agency—the capacity of living systems [...] to participate in their own development, maintenance, and function" (Sultan et al., 2022, p. 1);
- "Organisms themselves actively shape their own structure and function" (Sultan et al., 2022, p. 4);
- "We do not adequately understand the components of an agential system until we understand the ways in which the system regulates its structures, activities and relations in pursuit of the system's stable endstates" (Sultan et al., 2022, p. 8);
- "Constructive development refers to the ability of an organism to shape its own developmental trajectory by constantly responding to, and altering, internal and external states" (Laland et al., 2015, p. 6);

- "Typical descriptions of organismal dynamics treat organisms and their component parts as objects—organisms are the passive vessels of internal biochemistry at a nexus with the external thermodynamics of the environment, being separate from and passive to the conditions under which they develop and evolve" (Nadolski & Moczek, 2023, p. 3);
- "[Agency is] the ability of the entity ('self') to continuously (though sometimes transiently and provisionally) demarcate itself from its environment ('non-self') and actively constitute and reconstitute its boundary" (Newman et al., 2024).
- "Agency—a set of properties closely related to decision-making and adaptive action which determine the degree to which optimal ways to relate to the system (in terms of communication, prediction, and control) require progressively higher-level models specified in terms of scale of goals, stresses, capabilities, and preferences of that System as an embodied Self-acting in various problem spaces" (Levin 2022, p. 42, capitalization in original).

These are not parenthetical or ornamental expressions but are put forward as defining what biological agency *is*. Here, self-determination is contrasted with external determination. One form of external determination is the way physical systems are thought to passively conform to the boundary conditions imposed upon them (Yates, 1987). Another is the determination of phenotypes by genes, a methodological principle of Modern Synthesis biology and contemporary evolutionary and developmental genetics that is said to deprive organisms of agency (Noble & Noble 2023a, 2023b; Walsh, 2015; Walsh & Rupik, 2023).

An initial difficulty with the notion of self-determination centres on the self. It is not clear how to interpret expressions such as "the capacity of living systems [...] to participate in their own development." Development is the process of an organism going through the stages of its life cycle. It is not something separate from the organism. So how can an organism *fail* to participate in its development? If we suppose that the development of a given organism is fully determined by a set of underlying molecular factors, it is still the development of that particular organism rather than of another entity. It is also difficult to interpret the statement that "typical descriptions [...] treat organisms [as] separate from and passive to the conditions under which they develop and evolve" (Nadolski & Moczek 2023, p. 3). If this refers to environmental conditions, it is an ordinary question of the relative causal importance of internal versus external factors. If it refers to internal conditions, however, the statement veers into obscurity. How can an organism be separate from, or passive to, a process of development of *itself*?

It is instructive that this kind of language becomes intelligible if we switch to the mode of psychological agency in human contexts. For example, consider the statement: "medical patients should participate in their own treatment." The contrast between participation and passivity is meaningful here because the treatment involves interventions or procedures that are distinct from the patient, the patient is a human, and the patient has some choice about which options to pursue. When we apply this language to the relation between organism and development, some other source of distinctness and some biological grounding of choice is needed for it to make sense.

The apparent notion underlying the quotations above seems to be that the "self" of self-determination is the organism as a whole (Nadolski & Moczek, 2023; Newman et al., 2024; Sultan et al., 2022). Let us now examine the idea that physiological and developmental processes are caused by whole organisms exhibiting some form of choice or decision-making.

Self-determination as whole-organism causation

Attributing causal responsibility for events to the organism as a whole seems to be appropriate largely for phenomenological descriptions of organism behaviour—e.g., "the antelope runs from the lion to avoid being killed." Once we inquire more deeply, however, we often discover that it is not the whole system that is causally responsible for a behaviour, but a mechanism or sub-system within it. For example, circadian rhythms are system-level behaviours in some sense, but in mammals they are largely controlled by a population of oscillating neurons in the suprachiasmatic nucleus (Moore & Eichler, 1972; Stephan & Zucker, 1972). The yeast cell cycle is a whole-cell behaviour, but progression through stages is regulated by a subset of genes and proteins in the cell (Moris et al., 2016). If the primary cause of an organism's behaviour is a partial mechanism within the system, is this self-determination or external determination? Between the extremes of whole-organism behaviours and the expression of individual genes, there is a variety of intermediate causes of system behaviour whose status as self-determination or external determination is not clear. The same lack of clarity also afflicts any attempt to map the contrast between organisms as active agents versus as passive objects onto specific biological events (Walsh, 2015).

To say that it is "the system as a whole" (Potter & Mitchell, 2022; Sultan et al., 2022) that regulates or controls some component process can sometimes be a convenient figure of speech, but on close scrutiny it is not a well-formed causal statement (see Woodward, 2021a, 2021b). A defensible form of holism would be, for example, that the parts of cells are organized in a way that metabolically maintains the cell through time, making many of their parts interdependent (Kauffman, 2000; Moreno & Mossio, 2015; Rosen, 1991). This is not the same as attributing causal responsibility for events to the entire system. Consider how that type of claim could be empirically tested. It would require perturbing the whole system, as opposed to parts or properties of the system. Experiments one can perform on whole organisms like yeast cells—as opposed to parts (e.g., proteins and membranes), or properties (e.g., temperature or mechanical states)—would be limited to perturbations like destroying the cell in its entirety, moving it, or putting it under mechanical pressure. These perturbations have nonspecific effects on cell behaviours like differentiation, endocytosis, or mitosis, compared to specific effects of partial mechanisms in the cell and its environment. It is not possible to use whole-organism perturbations to test the causal hypotheses that it is either the whole system or its parts that influence some behaviour, because one cannot perturb the system as a whole while not perturbing its parts.

What *can* be perturbed to yield causal information are properties of an individual, like temperature, pH, or camouflage; behaviours, like meiosis or foraging; or parts, like transmembrane proteins or antennae. These aspects can often be varied independently, and variations can be linked to other changes in a system (i.e., dependent variables) to verify a causal relationship. By contrast, consider the following statement: "The

Box 2: Alternative conceptions of agency

The critical arguments of this paper are intended to apply to biological agency as defined earlier in the *Introduction*. However, what we refer to as "biological agency" represents just one out of a variety of concepts of agency that have been developed in different areas of scientific literature. Below we list some examples of alternative conceptions and contexts of discussion of agency (see Okasha, 2024 for further elaboration). The conceptual heterogeneity surrounding agency is an additional difficulty for implementing it in empirical research.

1. In the field of artificial intelligence research, the idea of an intelligent agent is invoked to describe any system that senses its environment and alters its behaviour in response (Russell & Norvig, 2016; see Okasha, 2024), which may include non-biological engineered systems such as thermostats or chatbots.
2. In psychology and cognitive neuroscience, researchers refer to the experience of controlling one's own actions as "sense of agency" (Ciaunica et al., 2024; Haggard, 2017; Roessler & Eilan, 2003). This is not considered a feature of biological agency.
3. Some authors describe as "agents" systems such as free-living cells in which metabolic interdependencies between components allow the system to maintain itself far from equilibrium (Hofmeyr, 2021; Jaeger, 2024a, 2024b; Kauffman, 2000; Moreno & Mossio, 2015). These approaches define agency in terms of cellular phenomena that are explainable without having to invoke agency, unlike other approaches that invoke agency as an explanation for system behaviours. This interpretation is supported by the fact that the precursor theories this literature relies on (e.g., Rosen, 1991) make no mention of biological agency. Hence, we suggest that the notion of agency does not play an indispensable role in this strain of work.
4. In some areas of economics, an agent or rational actor is characterized as one exhibiting utility-maximizing behaviour (Okasha, 2024; Ross, 2010). This description of behaviour is compatible with different explanations of the behaviour, such as adaptation by natural selection or conscious planning in the case of human beings.
5. Some work has proposed that single cells engage in "learning" (Dussutour, 2021; Gunawardena, 2022; Tang & Marshall, 2018; Wright et al., 2023). Despite not substantively relying on biological agency (as in #3 above), this work can be seen as supporting a cognitive perspective on simple organisms. On close examination, however, more explicit frameworks (e.g., Gunawardena, 2022) define learning in terms of statistical concepts such as mutual information between cellular and environmental states—which is compatible with the mechanistic view advocated here—but also in terms of internal representations of the environment, which may be just as difficult to link to detectable features of cells as agency.

system as a whole, as it pursues its goals, modulates the activities of its parts and processes in ways that bias the system toward the attainment of the goal in predictable (and empirically explicable) ways" (Sultan et al., 2022, p. 8). Any specific modulation of parts and processes can only be tested by identifying a specific part or property of the system that is to be treated as an independent variable, perturbing it, and looking for change in a specific dependent variable. In that case, it is not the system as a whole that is doing the modulation, but a part or process that is in effect being studied mechanistically.

Self-determination: "choice" versus multistability

Central to the idea of agential self-determination is that a behaviour or process must be internally caused (Barandiaran et al., 2009; Dretske, 1988; Moreno & Etxeberria, 2005; Moreno & Mossio, 2015; see Okasha, 2024). Yet any complex system is influenced by a combination of internal and external factors. The tidal heating of moons may be influenced by gravitational attraction as well as the composition and viscosity of their interiors (Henning, 2009), but we do not say that the existence of internal influences on tidal heating is indicative of agency or goals in celestial bodies. Internal causes of system behaviour are thus not distinctive of biological systems or biological "agents." More than internal causation, self-determination seems to require a repertoire of system behaviours, or "choices," that can be made in response to environmental conditions.

What it means to have a repertoire of choices is clear enough in human psychological settings. In the setting of cyanobacteria, algae, and sea anemones, it is far from clear, because it requires knowing how to map psychological expressions onto biophysical reality. We suggest that, instead of pursuing the analogy to cognitive decision-making, the biological ability to switch between different behaviours in a repertoire should be understood as multistability, defined in the language of dynamical systems theory as the presence of multiple attractors in a phase space (Strogatz, 2015). Multistability is a common feature of dynamical systems and is also not unique to biological organisms. Classic non-biological dissipative structures such as the Belousov-Zhabotinsky reaction and Bénard convection cells are multistable systems that switch between emergent dynamical regimes depending on the combination of internal states, external inputs, and inherent thermal stochasticity (Glansdorff & Prigogine, 1971; Nicolis & Prigogine, 1977).

To illustrate multistability in a simple biological system, consider the *lac* operon. *Escherichia coli* and many other bacteria are able to switch from a metabolic regime adapted for the digestion of glucose to one that can digest lactose, thanks to a cluster of genes known as the *lac* operon. When lactose is present and and glucose levels are low, the *lac* operon is switched on (de-repressed) via two regulators that detect ambient lactose and glucose levels—*lac* repressor and catabolite activator protein (Ozbudak et al., 2004; Santillán et al., 2007). This form of multistability (bistability) has likely evolved as an adaptation to the environmental variability of food sources in which glucose is prioritized.

We are free to describe the shift in metabolic regimes mediated by the *lac* operon as a "choice" or "decision" that the bacterium makes in pursuit of its "goals" (e.g., Ben-Jacob, 2009; Shapiro, 2011; see Reber et al., 2023). But the same phenomena are more usefully described in the language of mechanistic complexity science and natural selection (i.e., multistability of metabolic regimes and adaptive dynamics) (see Ozbudak et al., 2004; Robinson et al., 2024; Santillán et al., 2007) because this connects our observations to a testable body of models and theory with a substantial record of empirical success. Moreover, if we describe the metabolic switching as agential, it is not clear how to avoid attributing the same form of biological agency to Bénard convection cells and Belousov-Zhabotinsky patterns, which exhibit perhaps greater system-level behaviour and multistability than the *lac* operon.

As noted above (in *Agency and non-mechanistic explanation*), proponents of the agency perspective have suggested that embracing agency is an alternative to molecular reductionism. We have provided reasons to believe that multiscale feedback mechanisms capable of complex dynamics provide a better alternative to molecular reductionism than embracing the scientifically problematic notion of agency. Similarly, some have suggested that agency and something like "free will" in cells is an alternative to physical and genetic determinism (Levin, 2022; Newman et al., 2024). Here again, we see other unconsidered possibilities. Rejecting agency does not carry with it any commitment to determinism. Multistable dynamical systems with stochastic influences have a repertoire of behaviours that need not be strictly programmed or determined by prior states. "Agential behaviours" in cells and simple muticelled aggregates can be fruitfully explained in this way, whereas the reification of apparent agency, we suggest, is cryptically cognitive and scientifically inert.

Biological agency is a cryptically cognitive concept

The central idea of biological agency is a form of organismic self-determination that is goal-directed and non-mechanistic (Moczek & Sultan et al., 2023; Sultan et al., 2022). Against the background of an appropriately nuanced framework of mechanistic complexity science—one that includes nonlinear dynamics, multistability, feedback across multiple scales, emergent behaviours, and even downward causation—the idea of agential self-determination seems to differ from ordinary mechanistic causation only in the aspect of goal-directedness. But goal-directedness, at least in organisms without complex nervous systems and advanced cognition, is nothing other than adaptation, which is explained by natural selection. So, again, between mechanistic causation and natural selection, there seems to be no distinctive explanatory role for biological agency. The only known process that is goal-directed but not directly explained by selection, and self-determining but (seemingly) non-mechanistic, is conscious cognition in individual organisms like humans with complex nervous systems. This supports the interpretation that biological agency is in fact cryptically cognitive—i.e., a psychological style of explanation applied to organisms not normally regarded as having a mind.

We suggest that the above difficulties with mapping self-determination, goal-directedness, and agential explanations onto biological systems stem from the fact that these are psychological concepts that are primarily meaningful in social contexts where intentionality, cognition, and the notion of a person are assumed. Personal agency or self-determination is a matter of freedom, and is contrasted with coercion or manipulation. For organisms without complex nervous systems adapted for social interaction, there is no clear biological analogue of the self or the person that can be empirically investigated.

The fact that past psychological approaches to biological science were never successful (e.g., Binet 1889; Haeckel, 1878) does not inspire confidence that they will start to become so. The most fundamental problem with psychologizing more basic biological systems, such as bacteria (Shapiro, 2011) or plants (Ferretti et al., 2024), is that it is empirically unproductive. We are free to attribute inherent goals to systems, to ascribe causal responsibility for events to whole systems, or to describe the shift between multistable states as choice. But the same phenomena are better described in terms meaningful to mechanistic biology, complexity science, and evolutionary biology. These concepts connect our inquiries to a rich framework of methods, models, and data that have successfully driven discovery in empirical research for many decades. The psychological idiom does not do this. It is a stopping point for investigations of how biological systems work. It does not generate new data, and does not identify targets of experimental intervention for purposes of verification and causal understanding.

The psychology of agency attributions

The above analysis has focussed on understanding what biological agency means and whether viewing biological systems as agents is justified scientifically. However, there is an additional question of how attributions of agency work cognitively in the minds of human observers. Rather than being separate issues, findings from experimental psychology on how humans perceive and judge natural systems to exhibit agency, and why they seek teleological interpretations when they do, can help to explain why these ideas persist independently of their scientific grounding.

There is an extensive literature in developmental psychology, cognitive science, and related fields on attributions of goal-directedness, agency, and teleological explanations (e.g., Atran, 1994; Douglas et al., 2015; Keil, 1992; Kelemen, 1999a; Leslie, 1994; Piaget, 1929; Roberts et al., 2021; Rutherford & Kuhlmeier, 2013; Tomasello et al., 2005; Westfall, 2023). Work promoting the agency perspective in biology has not, to our knowledge, reckoned with the challenges posed by this literature. One general finding has been that humans have a seemingly inbuilt cognitive bias referred to as "hypersensitive agency detection," which leads them to see purpose and intention in nature where it does not exist (Barrett, 2004, 2011; Douglas et al., 2015; Kelemen, 1999a, 1999b; Okasha, 2023; Rosset, 2008). This bias is exhibited in the classic Heider-Simmel illusion (see Figure 2) (Abell et al., 2000; Heider & Simmel, 1944; Scholl & Gao, 2013). Subjects are shown a cartoon in which two triangles and a circle move in and out of a container and relative to one another. Observers standardly attribute goals and intentions to the shapes and conjure a socio-teleological explanation of the scene (e.g., "the big triangle is aggressively chasing the small one," or "the small triangle is helping the circle"). The display is considered an illusion, despite the fact that it is experimentally contrived, because what participants strictly observe is a configuration of abstract shapes moving in two dimensions, and abstract shapes cannot possess psychological attributes. The Heider-Simmel illusion is illustrative of the "intentionality heuristic" or "intentionality bias" (Dennett, 1987; Kelemen, 1999a; Roberts et al., 2021) and shows how easily attributions of intentionality are elicited in the human visual processing system (Scholl & Gao, 2013).

According to intention-based theories of teleology, teleological explanations have their psychological origin in the intentionality heuristic, which is honed for use in social contexts from an early age, but becomes "promiscuously" overextended in service of the broader need to make sense of the world (Barrett, 2004; Kelemen, 1999a, 1999b; Roberts et al., 2020, 2021; Rosset, 2008). These theories suggest that when observers attribute goals to a system or propose a teleological

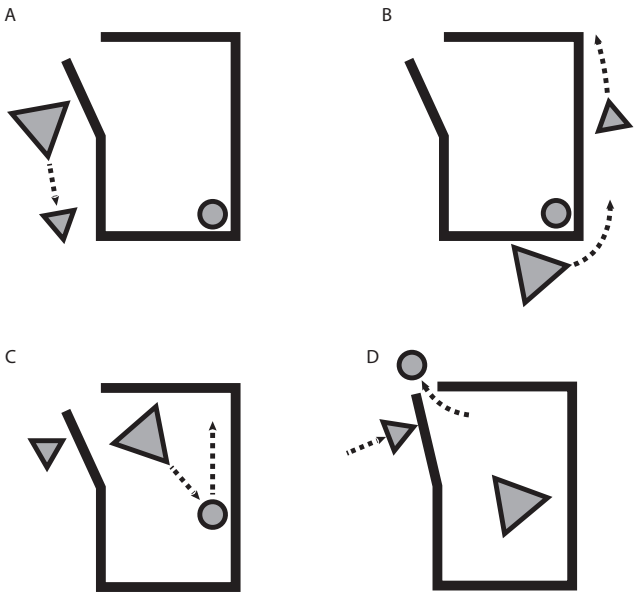


Figure 2. A reproduction of stills from the classic Heider-Simmel (1944) animation. The majority of subjects ascribe goals and intentions to abstract shapes based on their movement patterns, despite the lack of human-like or animal visual features, and despite the fact that triangles and circles do not have goals or intentions.

explanation, they rely on the intuitive recognition of an analogy between a system behaviour and human behaviours guided by intentions. In this view, different natural systems may get classified as goal-directed systems because "the system behaves as if it were goal-directed in the sense of having, or stemming from, a conscious mental representation of a goal" (Okasha, 2023; p. 244; cf. Baker et al., 2009).

Indirect evidence for the intentionality-based theory is found in statistical associations between endorsement of teleological explanations, agency detection, and other intention-related attributions. For example, Roberts et al. (2020) (cf. Kelemen & Rosset, 2009; Roberts et al., 2021) compared rates of endorsement of unwarranted teleological explanations of natural phenomena (e.g., "The Earth has an ozone layer in order to protect it from UV light") and warranted teleological statements (e.g., "Schools exist in order to help people learn new things"). Study participants were asked to judge such statements as true or false. Responses under speeded conditions (<3,200 ms) were used to assess implicit teleological endorsement, and responses under unspeeded conditions were used to assess explicit teleological endorsement. The study found higher explicit endorsement of unwarranted teleological explanations among subjects who reported belief in the existence of supernatural agents with intentions. Interestingly, nonreligious subjects exhibited a greater disparity between implicit and explicit endorsement across speeded and unspeeded conditions than did religious subjects. The finding that subjects who explicitly reject unwarranted teleological statements nonetheless implicitly endorse such statements under speeded conditions supports the idea that teleological thinking is a persistent heuristic that can be inhibited with explicit reasoning (Roberts et al., 2020).

Other studies point to the same conclusion. For example, a positive association was found between belief in supernatural and paranormal phenomena and belief in conspiracy theories (Darwin et al., 2011; Swami et al., 2011). These beliefs are positively associated with individuals' "sensitivity of agency detection" (Douglas et al., 2015), as measured by the individual differences in anthropomorphism scale (Waytz et al.,. 2010) and responses to questions about the Heider-Simmel animation (e.g., "Did you think the behaviour of the shapes was the result of conscious decisions?") (see Douglas et al., 2015). Other studies found that rates of endorsement of scientifically unwarranted teleological statements are modulated by youth and education level (Casler & Kelemen, 2008) and by neurological illness (Lombrozo et al., 2007).

These associations do not, on their own, entail that viewing organisms as agents is unjustified. Instead, they support the hypothesis that humans possess an intentionality heuristic that is prone to over-extension, and that can be reined in through cognitive development and explicit reasoning. This hypothesis may explain why many people, including scientists (Kelemen et al., 2013), seek teleological explanations and attribute agency to living systems even when this is not scientifically justified. It is also consistent with our observation that features of biological agency such as agential goal-directedness and self-determination are conceptually unclear and difficult to map onto biological reality, but are readily comprehensible in psychological terms.

Discussion

Pre-scientific humans are thought to have relied on the personalistic concepts available from social life to describe and explain events in the world around them (Atran, 1994, 1998; Gelman & Legare, 2011). Given that modern biology evolved out of an earlier "folk biology," it is not surprising to find that mentalistic notions like agent, soul, mind, etc., have historically been invoked to explain goal-directed behaviours in non-human organisms, just as is done with humans (Aristotle [350 BC], 1931; Atran, 1998; Gelman & Legare, 2011). Contemporary advocacy of biological agency can be interpreted as recasting the framework of folk biology with a scientific veneer in the effort to "supplement" modern mechanistic and evolutionary biology. We have made the case that this is both unnecessary and undesirable.

From the point of view of an experimenter trying to understand a system, adopting a biological agency perspective has utility only in situations where nothing is known about how the system works, as in pre-scientific folk biology. Attributions of agency provide extremely basic predictions, e.g., that an organism will tend to avoid damaging stimuli, whereas an ordinary material object will not. At present, however, we are not in the cognitive situation of pre-scientific humans. We have highly sophisticated theories and research programs for explaining complex adaptive behaviours of biological systems. These are based on modern evolutionary biology, particularly on natural selection as a mechanism for explaining goal-directedness, and on causal-mechanistic investigation, which is based on observation, controlled experimental perturbation, data collection, and statistical inference. Importantly, the practice of explaining goal-directedness as adaptation by natural selection does not require commitment to adaptationism (Orzack, 2024) about every trait an organism exhibits. Nor does the practice of seeking and giving mechanistic explanations require commitment to genetic reductionism or determinism. When adaptive and mechanistic approaches are in place, explaining a given biological process in terms of the agency of the organism is merely a psychological re-description that does not contribute additional insight to

our understanding of the development, ecology, or evolution of the organism in question.

We are far from understanding the full complexity of basic processes like eukaryotic gene regulation, mitosis, wound healing, morphogenesis, or the evolution of novel body parts. A touchstone of the empirical, mechanistic approach is to acknowledge this incompleteness, and to work toward piecemeal progress through the cyclical process of observation, hypothesis-formation, experimental intervention, modeling, and confirmation or revision of ideas. In the course of scientific advance, it is possible that a psychological style of explanation could turn out to be useful for biology. But it would need to provide explanations and predictions that link to data so that the ideas can be tested and verified. Despite claims that "agency is an empirical property" (Sultan et al., 2022, p. 1), this is what work promoting the idea of biological agency is lacking. Our aim in insisting on testability is not to return to a positivist view of science (Carnap, 1936). Testability instead serves the egalitarian stance that claims made by a speaker should be confirmable in principle by others rather than being taken on authority or by non-rational forms of persuasion. Empirical tests are necessary for transforming a concept into not just a "perspective" but rather a progressive research program (Lakatos, 1978).

Biological agency is not adequately motivated empirically. It is not clear how it could become so, because its theoretical basis depends on flawed reasoning: (1) the misunderstanding or neglect of natural selection as an explanation for goal-directedness; (2) the promotion of teleological explanations in science and misunderstanding of causal-mechanistic explanation as inherently reductionistic; and (3) confusion about self-determination and whole-organism causation. Once these problems are recognized, it becomes evident that the phenomena that agency is being invoked to explain can be explained in terms of complex multiscale feedback mechanisms evolving under natural selection.

The cumulative outcome of the preceding is to pose a challenge to advocates of the biological agency perspective. Show concretely what work this idea can do for biological research that cannot be done better by current modes of explanation. Until this is done, biological agency is merely a concept without a research program.

Data availability

This article does not present new data.

Author contributions

James DiFrisco (Conceptualization [Equal], Writing—original draft [Lead], Writing—review & editing [Equal]), and Richard Gawne (Conceptualization [Equal], Writing—original draft [Supporting], Writing—review & editing [Equal])

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Conflicts of interest

The authors have no conflict of interest to declare.

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