# Towards a unified framework for biological agency: “Individual Playful Memory”

**Abstract.** In recent decades, agency has resurfaced as a prominent concept for conceiving of biological phenomena, both in philosophy and biology. While the long-dominant reductionist framework, centred on genes, minimised the epistemic role of organisms and rendered ‘organicism’ obsolete, the Extended Evolutionary Synthesis has reintroduced agency to account for organismal spontaneity and highlight previously overlooked processes, particularly organism-environment interactions. However, its definition varies across and within disciplines, whether it is employed to understand development, organisation, or evolution, or applied to genes, cells, organisms, or even natural selection. This ambiguity hinders distinguishing its appropriate from inappropriate uses and establishing a cohesive theoretical basis for its various manifestations. This paper reviews the literature on agency from philosophy, evolutionary theory, developmental biology, and behavioural ecology. It identifies three core capacities that unify the concept of agency: Individuality, Playful flexibility, and Memory (IPM). These capacities interact in diverse ways, with their influence varying depending on the process and context. These quantitative differences give rise to qualitatively distinct forms of agency: autonomous organisation, goal-directed choice, and inventiveness. Drawing on the IPM framework, this paper explores the relationships between these forms of agency and argues that this approach can rationalise and formalise our understanding of agency while accommodating its diverse expressions.

**Keywords:** agency; organisation; goal-directedness; inventiveness; evolution; behavioural ecology

Over the past decades, agency has resurfaced as a central concept in philosophy of biology, and in biological theory. While the long-dominant framework of the Modern Synthesis, centred on genes, minimised the epistemic role of organisms and rendered ‘organicism’ obsolete, the Extended Evolutionary Synthesis (EES) has reintroduced the concept agency. This concept aims to capture the spontaneity of living beings and illuminate processes left underdetermined by the reductionist perspective, particularly organism-environment interactions. Nonetheless, the definition of biological agency is far from uniform across and within disciplines, varying according to its context and application—whether used in discussions on development, organisation, evolution, or in reference to genes, cells, organisms, or even natural selection. It serves varied purposes: in some cases, it is merely metaphorical, while in others it plays an operational role, being incorporated into biological theories or even acquiring ontological significance. Moreover, the concept is shared by researchers across a broad spectrum of disciplines: beyond the multiple domains collaborating within the EES, agency is also invoked in fields such as animal studies to explore nonhuman capacities and prompt ethical reflection. Given this wide array of uses, definitions of agency tend to be shaped opportunistically to fit the argument at hand, suggesting the existence of multiple concepts linked only by their shared terminology. Each concept has a narrow scope and a precise application; conflating its different uses can lead to confusion and risks the concept becoming widely applicable yet operationally meaningless.

However, the lack of a unified conceptual methodology extending beyond the EES to integrate fields such as behavioural ecology and animal welfare studies raises several issues. First, despite the use of the same word indicating a commonality of meaning, this meaning remains globally undefined. As a result, the term is often divorced from its vernacular signification. Second, without establishing shared criteria for agency, it becomes challenging to differentiate between the erroneous and justified uses of the concept. Thus, its operational value is diminished. Finally, in the absence of a common definition, agency functions as an umbrella term shared by several disciplines, but whose equivocality impedes the integration of knowledge from different fields.

This paper seeks to address these issues by synthesising the disparate definitions of agency in order to identify unifying criteria. Through a literature review, three main categories of agency are identified: organisation, choice, and invention. It is then argued that these distinct types of agency share a set of core characteristics: Individuality, Playful flexibility, and Memory (IPM). Finally, this paper demonstrates how these characteristics help to address key challenges, such as elucidating the commonalities among diverse forms of agency, enhancing the understanding of their distinctions, and clarifying their conceptual and biological articulation.

# 1. Agency or agencies?

The concept of agency has multiple definitions both across and within disciplines, and a first challenge is to determine whether there is any consistency despite this diversity.

## 1.1 Agency in biology

The term agency has traditionally been used in the social sciences and humanities to reflect on the rationality or irrationality, moral responsibility or irresponsibility of agents, typically humans (Shapiro 2005; Emirbayer and Mische 1998). However, over the past decades, agency or at least a form of “agential thinking” (Godfrey-Smith 2009) has increasingly permeated the field of biology. It is true that biologists do not frequently engage with the concept of agency itself. And, when they do, it seldom receives in-depth theoretical scrutiny. Nevertheless, even if agency is not a primary object of biological study, it is still present in three notable ways. First, it is used as a rhetorical device to communicate core biological concepts, especially within evolutionary studies. In this case, agency serves as a heuristic metaphor but also reveals an implicit agential mode of thinking at work in the theory. Second, behavioural ecologists invoke organisms'—most often animals'—agency to reflect on scientific practices. Here, agency is explicitly advanced as a concept to be incorporated into biological methodologies. Finally, introduced as a conceptual tool to correct or complement theoretical models, *i.e.*, to move beyond a gene-centred perspective on development and evolution by integrating the roles of other living systems, particularly organisms[1]. The agency-based approach serves to address theoretical gaps in the orthodox theory (Sultan, Moczek, and Walsh 2022), specially where genetic processes fail to both predict developmental, organisation or evolutionary outcomes and account for their unpredictability. n this context, definitions of agency are often drawn from philosophical discourse or co-developed in collaboration with philosophers.

### 1.1.1 'Agential thinking' in evolution

An agential perspective is often used by evolutionists to convey their findings. In these instances, agency rarely becomes the subject of deep theorisation. More often, it assumes a metaphorical role: it is *as if* the subject of study were acting as an agent. Here, agency is understood teleologically: one speaks as if the object under study were an agent because it seems to be goal-directed. This approach to agency has been applied to a wide range of biological processes and entities. For instance, the action of natural selection is often described in agent-like terms, as if nature itself were striving to optimise for the most suitable traits (Dawkins 1989; Dennett 1995). Similarly, genes are sometimes depicted as metaphorical agent, pursuing their own interests, most famously in Dawkins' *Selfish gene* (Dawkins 1989). Aligning with a more intuitive understanding of agency (see section 2.1), the concept is also widely applied to organisms, which are often portrayed as intentional, even rational, agents, striving to optimise their chances of survival and reproduction (Grafen 2008; 2014). For example, it is said that the lion kills cubs that are not its own, because it *realises* that the mother won't have any sexual activity while lactating (and actually does not ovulate), and it *wants* to increase its chances of reproduction (infanticide interrupts lactation in mothers and allows ovulation to resume).

In all these cases, agency functions as a practical, if anthropomorphic, metaphor rendering biological discourse more accessible: it offers a pedagogical framework for discussing biological functions. Agency here is merely expressing the adaptationism prevalent in evolutionary explanations, and according to which all traits and behaviours are contributing to the fitness of the whole (Okasha 2018). Yet, this form of heuristic agential thinking has been strongly criticised as being, in most situations, a misapplication of the concept, especially when applied to natural selection, and genes, and often even to organisms. While it seems useful in selected scenarios (especially when the agents are high-cognitive organisms), it usually leads to more confusion than clarity (Okasha 2018; Tahar 2023), misrepresenting evolution as a linear progress, genetics as a programme, and organisms as rational, goal-directed agents.

### 1.1.2 Agency for biological practice

In contrast, there are cases where agency is adopted as a concept with true operational implications in scientific practices, shedding light on genuine attributes of biological entities. This is particularly evident in behavioural ecology (also labelled ethology), where agency is

[1] It should be noted that these functions are not mutually exclusive (Uller 2023).

employed to critically assess the scientific validity and ethical dimensions of experiments. It is mostly—but not exclusively[2]—applied to animals, and it aims at expressing their subjectivity and spontaneity, prompting us to reconsider the ethical implications of our scientific practices. A particularly illustrative example of these operational implications is the controversy that arose from a widely mediatised study involving a game of hide-and-seek between researchers and rats (Reinhold et al. 2019). The study demonstrated the rats' capacity for learning, spontaneously engaging in play, and even initiating new behaviours. However, despite these demonstrations, the rats were ultimately euthanised to analyse the neural mechanisms underlying their behaviours. This decision sparked considerable controversy, with several researchers advocating for the recognition of the rats' agency as a basis for ethical reconsideration, a recognition made necessary by the very study that killed them (Webb, Woodford, and Huchard 2020).

Typically, animal behaviours' studies will use the concept but not provide a detailed theory (e.g. Warkentin 2009; Webb, Woodford, and Huchard 2020). But some do outline criteria for identifying agentive behaviours in experiments or observations, encompassing the animals' natural behaviours, social interactions, and their responses to experimental conditions (McFarland and Hediger 2009; Špinka 2019; Sueur, Zanaz, and Pelé 2023). Agency then refers to the animals' ability to control an action (Couchman 2012; Kaneko and Tomonaga 2011), resist to some experimental settings (Sueur, Zanaz, and Pelé 2023), or even manifest creativity (McFarland and Hediger 2009; Špinka and Wemelsfelder 2011).

Importantly, recognising animal's agency has implications beyond ethical considerations, challenging the scientific validity of certain practices. For rigourous research, it is crucial to limit interference with the subjects under observation, while allowing their agency to express as freely as possible (Sueur, Zanaz, and Pelé 2023; Webb, Woodford, and Huchard 2019). Therefore, experimental designs should allow animals to express their agency, avoiding undue stress or overly restrictive conditions.

### 1.1.3 Agency for biological theory

The concept of agency has also recently been used in theoretical biology to challenge the dominant reductionist, genocentric approach. In this context, agency is not merely a pedagogical tool or an instrument for practical and ethical purposes, but a fully-fledged concept to be integrated in theoretical models to address some gaps in the orthodox framework. Its application in biological theory is particularly prominent in two complementary domains: the study of biological systems where it highlights the specificity of biological development and organisation (Nadolski and Moczek 2023; Newman 2023; Watson 2023), and in evolutionary theory (Kauffman and Clayton 2006; Laland, Odling-Smee, and Feldman 2019). In the former, the concept of agency serves to acknowledge the role played by the developmental and physiological feedback processes allowing biological systems to both self-regulate and produce adaptive novelties (Sultan, Moczek, and Walsh 2022). In the latter, agency designates the active role played by organisms in ecological dynamics and selective pressures (Bateson 2004). As such, it is employed within the framework of the Extended Evolutionary Synthesis, which complements the selectionist narrative by introducing new processes, such as niche construction (Kylafis and Loreau 2008; Deffner 2023), emphasising the epistemic role of organism-environment interactions (Baedke and Fábregas-Tejeda 2023). These two areas of research are not mutually exclusive. On the contrary, the agentive approach aims to highlight the intertwining of developmental (embryogenic and lifelong) processes, and evolutionary ones, conceiving of organisms as both the 'subjects' and 'effects' of evolution (Lewontin 1983).

[2] Agency is also invoked to question scientific practices concerning other entities, both biological and non-biological—such as plants, organoids, or even artificial intelligence. However, it is typically philosophers, rather than biologists, who engage with these grey-area cases " See for instance (Birch 2024) or (Verma 2024).

In theoretical biology, a great deal of discussion is devoted to the definition of agency, usually based on philosophical research. Most of the time, these definitions integrate flexibility, self-regulation, autonomy, adaptivity, and goal-directedness, with these characteristics often overlapping each other. The theoretical definitions tend to closely align with those found in the philosophy of biology, with biologists either directly adopting these philosophical definitions (Nadolski and Moczek 2023; Newman 2023) or collaborating with philosophers to develop them (Kauffman and Clayton 2006; Kylafis and Loreau 2008; Sultan, Moczek, and Walsh 2022). Hence, the distinction between biological and philosophical concepts of agency becomes somewhat irrelevant, especially when the concept is used to structure theoretical models.

## 1.2 Agency in philosophy of biology

Mirroring the distinctions in theoretical biology, philosophy recognises two main notions of agency: one rooted in organisational theory and the other in evolutionary theory.

### 1.2.1 Organisation

Agency is frequently invoked to capture the specificity of organisms and of their relationships with the environment distinguishing them from other (non-living) systems. This specificity is most evident in the coordination and orientation of their activities towards internal goals, such as maintenance, survival, and reproduction, but it encompasses several other key characteristics of organisms: their individuality, their ability to self-initiate actions, the normativity of their activities, and their adaptability to both internal and external changes (Barandiaran, Di Paolo, and Rohde 2009; Moreno and Mossio 2015; Virenque and Mossio 2024).

While this concept of agency primarily applies to organisms, it can be extended to lower-level entities such as cells, when their activities exhibit characteristics typically associated with agency (Skewes and Hooker 2009; A. Soto, 2024, personal communication).

Recognising these agentive characteristics is increasingly seen as pivotal r complementing gene-centred theories of heredity, development, and organisation. Specifically, it offers a framework for understanding the internal feedback processes within biological systems, through which gene-environment interactions shape both their robustness and flexibility. Although this concept of agency is primarily aimed at understanding the organisation of these systems, the inclusion of variability (Jaeger 2024), phenotypic plasticity or adaptability (Virenque and Mossio 2024), bridges the gap between the organisational and evolutionary approaches (see 4.2.1).

### 1.2.2 Evolution

In recent years, the role of organisms in shaping evolutionary processes has garnered growing recognition, particularly because of their influence on selective pressures through processes like niche construction (Aaby and Desmond 2021). This shift in perspective has led researchers to import the concept of agency into evolutionary theory (Walsh 2015). In this context, a biological entity is considered an agent, when its activities or behaviour alter its ecology, thereby influencing the evolutionary trajectory of its population (e.g. Corning 2014). While this entity is typically an organism, it can also extend to include groups or populations. Rather than focusing on the agent's inherent properties, as in the organisational approach, this perspective highlights their long-term effects, insisting on the agent's active role in ecological and evolutionary dynamics. This perspective contrasts with traditional evolutionary theory, where organisms are seen as passive recipients of genetic determinism and natural selection.

Instead, the agentive approach contends that what organisms do—their interactions with their environment—actively shapes their ecology and can alter the evolutionary fate of their population and, potentially, other species.

*Choice*

Denis Walsh (2015) made a substantial contribution to defining agency from an evolutionary perspective. According to him, all organisms can be considered agents, because they experience ecological conditions as affordances to which they respond based on their adaptive repertoire and with respect to their internal goals. In other words, the active role played by organisms is rooted in their capacity to *select* responses to conditions, in alignment with their goals, which requires both behavioural flexibility and purposiveness. Consequently, agency is closely linked to the ability to make choices, even when those are deemed unintentional—an idea further developed by several other researchers (see Corning et al. 2023; Desmond 2023).

*Inventiveness*

A distinct form of agency emerges in the phenomenon of invention. An invention is a novel behaviour, that neither the organism nor any member of its group has previously exhibited. Unlike choice-based agency, invention does not necessarily require goal-directedness but instead relies on inventiveness—an organism's ability to self-initiate a new behaviour whose novelty can be attributed to the organism itself (*i.e.,* it is neither genetically determined, environmentally induced, nor socially learned) (Tahar 2023). While such agency is well-documented in humans, its presence in non-human animals is an expanding area of study, and and whether it extends to non-animal organisms remains an open question. This growing interest is due to the potential evolutionary impact of invention. Indeed, when an invention becomes an innovation—meaning it spreads within a population and integrates into its culture—it can influence ecological dynamics and, consequently, selective pressures (Sol 2003). Moreover, it can initiate a "Baldwin effect", wherein a newly acquired behaviour, emerging through individual inventiveness, becomes a driver of natural selection, inducing genetic evolution (Baldwin 1896)[3].

Although biological definitions of agency vary, they likely share underlying commonalities that justify the use of a single term. The challenge is to synthesise these different concepts to identify the principles that unify them. In Section 2, I examine these shared features, beginning with those included in the everyday meaning of agency.

# 2. What do the different definitions of biological agency share?

The widespread use of the term "agency" across diverse contexts and definitions suggests that scholars from different fields share at least a broad understanding of the concept. As noted above, this understanding is partly rooted in the social sciences and humanities. This

[3] Let's imagine that an individual invents a behaviour that enhances its fitness—by granting access to a new food source, for instance—and that this behaviour is subsequently transmitted through social learning within the population. While this transmission ensures the retention of the beneficial behaviour, the learning process incurs cognitive and energetic costs. Therefore, if a genetic mutation arises in the population that reduces this cost, it will be favoured by natural selection (i.e., individuals carrying the mutation will leave more offspring than others).. The invention will thus have created new selective pressure. This is the Baldwin effect. For a more detailed account, see (Bateson 2004).

means that applying it to non-human organisms (or other biological systems) requires some *de-anthropomorphising* or *de-intellectualising*—a requirement emphasised in most papers (among others: Walsh 2015; Sultan, Moczek, and Walsh 2022; Uller 2023) and analysed by Okasha (2023). However, the persistence of the word across its varied applications suggests that researchers do not typically tend to devise a *sui generis* concept, completely divorced from this common understanding (Okasha 2024). Therefore, while keeping in mind the risk of anthropomorphism, analysing the vernacular meaning of agency should help us to identify some of its essential properties.

## 2.1 Everyday meaning of agency

In everyday language, agency refers to the capacity of an individual to act and exert influence over something else. This concept encompasses both the agent—which possesses the ability to (α) self-initiate an action—and the consequences of this action: for agency to be acknowledged, the action (β) must yield tangible effects (planned by the agent, or not) (Merriam-Webster 2025; Oxford English Dictionary 2025). Refining this definition further, an entity is considered an agent only if it (γ) has some control over the action it initiates. Moreover, it must serve as both the cause and the *raison d'être* of that action. In other words, the action would either differ or not occur at all if the agent were different, which means that (δ) the action depends on the agent's singularity and flexibility. This definition implies that agents are not agents all the time, in all situations. For instance, while humans in full command of their faculties are typically recognised as agents, someone experiencing involuntary actions—such as hiccups or stumbling—is not considered to be exercising agency in those moments.

By clarifying the fundamental criteria of agency, this initial definition helps eliminate certain uses of the concept. For example, natural selection itself does not initiate or influence anything: it is merely the result of the individuals' struggle for survival and their consequent differential reproduction. Therefore, it does not qualify as an agent. Similarly, while genes, as carriers of information, exert influence, they do not self-initiate actions; their influence is contingent upon their so-called "interpretation", within an organism's biological context, which disqualifies them as agents. Conversely, organisms can be considered agents, though not in all situations. Consider cows that release methane. They initiate the belches releasing methane and impacting climate change, but this process is not under their control, nor does it vary significantly between individuals. Hence, in this scenario, cows are not agents.

While this preliminary definition is broad and does not explain the mechanisms underlying agency or the characteristics of agentive actions, it does help discard unjustified uses of the term. One could argue that the various uses of "agency" in biology share only this everyday meaning and may therefore coexist without requiring further integration. However, a more compelling hypothesis is that a deeper conceptual unity underlies these definitions, forming the basis for a cohesive theory of biological agency. This paper adopts the latter perspective, seeking to explore the possibility of a unified theoretical framework.

## 2.2 Synthesising the scientific definitions

To develop a unified conceptualisation of agency in biology, I conducted a literature review, compiling definitions from theoretical biology, philosophy of biology, and behavioural ecology. Relevant articles were identified through data mining, using the keyword 'agency' in combination with 'biology', 'evolution', 'ecology' 'organisms', or 'animals'. This diverse body of literature allowed me to distinguish three main categories of phenomena to which agency is applied: organisms' behaviour, the organisation of biological systems, and the influence of organisms on ecological and evolutionary dynamics.

### 2.2.1 Agency in understanding behaviour: the ethological approach

The concept of agency as applied to the behaviour of living organisms—primarily animals but also plants (Gilroy and Trewavas 2023; Sandford 2024; Sultan, Moczek, and Walsh 2022), and even bacteria (Arias Del Angel et al. 2020)—encompasses several key characteristics across different studies:

(1) The agent is considered an individual (Sueur, Zanaz, and Pelé 2023; Wemelsfelder 1997; Arias Del Angel et al. 2020). However, this individuality is not isolated: agency is inherently relational, contingent upon the agent's interactions with its surroundings (Carter and Charles 2013; Read and Szokolszky 2024; Arias Del Angel et al. 2020).

(2) Agents experience their surroundings as affordances, meaning they do not merely respond to objective stimuli but engage with their environment subjectively. In other words, they have an internal experience, and an individual memory: they record their experiences either physiologically or cognitively, or both (Steward 2009; Sueur, Zanaz, and Pelé 2023; Warkentin 2009).

(3) The relationship between the agent and its environment can be asymmetrical, *i.e.*, the agent can self-initiate some actions (Read and Szokolszky 2024; Steward 2009; Wemelsfelder 1997).

(4) Agents exercise a degree of control over at least some of their actions. For instance, bacterial agents can *modulate* biomaterials (Arias Del Angel et al. 2020), while animals choose whether to follow commands (Scott 2009), and resist undesirable conditions—for instance, by attempting to escape captivity (Couchman 2012; Kaneko and Tomonaga 2011; Warkentin 2009).

(5) Agency is recognised through volition, reflected in preferences or choices of resources, habitat, or behaviours (Blattner, Donaldson, and Wilcox 2020). For instance, the controversial 2019 study (Reinhold et al. 2019) was interpreted as evidence of rats' agency, as it demonstrated their ability to engage in hide-and-seek without direct rewards, suggesting intrinsic motivation. In other words, through such behaviours, agents exhibit internal goals or desires (Špinka 2019; Sueur, Zanaz, and Pelé 2023; Warkentin 2009).

(6) Agency also manifests through behavioural flexibility, meaning an agent's actions are not purely automatic but emerge dynamically through interactions with the environment (Gilroy and Trewavas 2023; Wemelsfelder 1997; Sultan, Moczek, and Walsh 2022).

(7) In some cases, agents exhibit 'surprising' behaviour, at odds with their usual repertoire: thereby manifesting creativity (McFarland and Hediger 2009; Špinka and Wemelsfelder 2011).

(8) Agents have a tangible impact, whether on experimental conditions, their surroundings, or even their own destiny (Carter and Charles 2013; Sueur, Zanaz, and Pelé 2023).

### 2.2.2 Agency in understanding biological systems: the organisational approach

The organisational approach, as shared by biologists and philosophers, defines agency through distinct characteristics. As with the ethological perspective, the concept applies to various biological entities but is primarily used to describe organisms (animals, plants, bacteria). An analysis of the literature reveals the following key features for the organisation concept of agency:

(A) The agent is an individual (Barandiaran, Di Paolo, and Rohde 2009; Gontier 2023).

(B) This individual is a self-organising system. In other words:

   a. It exhibits a form of closure (Moreno and Mossio 2015; Uller 2023),

   b. derived from its self-generated structure: the system is autopoietic (Moreno and Mossio 2015; Skewes and Hooker 2009).
(C) Agents are capable of initiating activities, actions, and interactions (Moreno and Mossio 2015; Newman 2023; Skewes and Hooker 2009).
(D) Agency is characterised by autonomy. In other words:
   a. Agents generate their own internal norms (Barandiaran, Di Paolo, and Rohde 2009; Moreno and Mossio 2015; Skewes and Hooker 2009);
   b. which define internal goals towards which their activities are oriented (Moreno and Mossio 2015; Newman 2023; Watson 2023).
(E) Agents are adaptive, flexible systems, capable of adjusting their organisation and behaviour in response to internal or external changes (Skewes and Hooker 2009; Virenque and Mossio 2024)
(F) This adaptability is enabled by memory: agents retain past experiences which transform their organisation. Their organisational processes are thus historical (Moreno and Mossio 2015; Watson 2023).
(G) Agents' activities have causal effects both on themselves and on their surroundings (Moreno and Mossio 2015; Newman 2023).

It is important to note that certain terms, such as 'goals' are used differently across conceptual frameworks. When studying behaviour, goal-directedness refers to organisms actively pursuing their *desires* (5 in section 2.2.1). In contrast, within the organisational approach, goal-directedness refers to an agent's activities being oriented toward *internal goals* (such as maintenance, or reproduction) (D in this section).

### 2.2.3 Agency in understanding the role of organisms in evolution: the evolutionary approach

Finally, agency is also used to explore the influence of organisms' activities on evolutionary dynamics. In this context, agency is defined by the following features:
(i) The agent is an individual (Tahar 2023; Walsh 2015).
(ii) Agents experience their conditions as affordances, which implies internal experience and individual memory (Tahar 2023; Walsh 2015).
(iii) Agents are able of self-initiating actions (Aaby and Desmond 2021; Tahar 2023).
(iv) They possess some degree of control over their actions (Aaby and Desmond 2021; Trewavas 2023).
(v) Many scholars argue that agency requires goal-directedness: agents are individuals acting according to their own goals (Corning 2023; Desmond 2023; Walsh 2015). Agency is then defined by the ability to make choices according to these goals (Desmond 2023; Kauffman and Clayton 2006; Walsh 2015).
(vi) Agents interact with their dynamic surroundings through adaptive responses, demonstrating behavioural flexibility (Tahar 2023; Walsh 2015).
(vii) In some cases, agency is expressed through inventions that can become innovations (Tahar 2023). In other words, agents may occasionally transcend their genetically and culturally determined repertoire by inventing new behaviours, which can then spread within a population.
(viii) Agents' self-initiated actions can influence ecological and evolutionary processes (Aaby and Desmond 2021; Kauffman and Clayton 2006; Laland, Odling-Smee, and Feldman 2019; Trewavas 2023).

The challenge now is to synthesise these different conceptualisations of agency to identify their commonalities and distinctions, ultimately working towards a unified theoretical framework for biological agency.

## 2.3 Organising the definitions

Some elements of agency definitions describe the characteristics of agentive actions, while others pertain to the agents' inherent properties.

### 2.3.1 Agentive actions

Regarding the nature of an agent's actions—how agents enact their agency—there is a clear consensus (Figure 1):

*Agentive actions are initiated by the agent itself.* (α; 3; C; iii)

*Agentive actions have consequences.* (β; 8, G, viii)

Additionally, while not a *sine qua non* condition for organisational agency, it is often the case that:

*Agentive actions are within the agent's control. In other words, the agent not only triggers the action, but also exercises control over its execution.* (γ; 4; iv)

While most definitions describe agentive actions as goal-directed, the ambiguity surrounding the meaning of goal-directedness (see the end of section 2.2.2) warrants setting this aside for the moment.

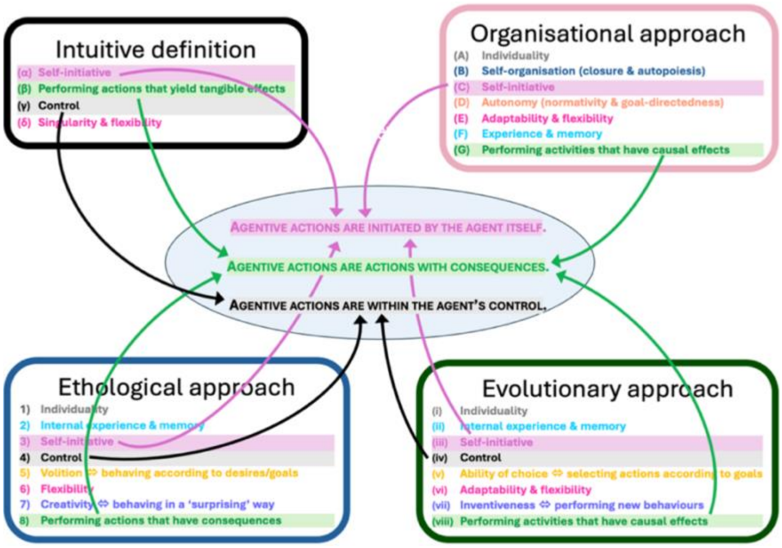


Figure 1. Properties of the agentive actions. Colour scheme of figures subject to editing. Suggestions welcome.

### 2.3.2 Biological agent

A more complex challenge lies in identifying the properties enabling agents to perform agentive actions. To address this, I have drawn upon the remaining elements from the three perspectives under study, focusing on those consistently present across all definitions of biological agency (Figure 2).

One of the most significant criteria is individuality:

*An agent is an individual (which may include collective entities, provided they act as a unified whole).* (1; A; i)

Another shared characteristic is flexibility. Regardless of the specific approach to agency, agents are understood as capable of a range of behaviours or activities, making them inherently flexible. Flexibility is indeed foundational: Flexibility is foundational: it underpins volition in ethology, adaptability in organisational theory, and both choice and invention in evolutionary approaches. Sometimes referred to as "adaptive improvisation" (Soen, Knafo, and Elgart 2015) or even "play" (Kortmulder 1998; G. Longo 2023, personal communication; Tahar 2023; Wemelsfelder 1997), such flexibility does not imply goal-directedness. It is characterised as playful precisely because it lacks intrinsic directionality—allowing agents to explore and engage with both internal and external conditions in an open-ended manner.

*An agent is flexible in its activities and behaviours: capable of playfully engaging with its internal and external conditions.* (6; E; vi)

However, for flexibility to result in controlled actions rather than random behaviours, it must be channelled. This channelling arises from the agent's internal experience, shaped by its unique embodied perspective and individual memory. It is important to note that memory — the capacity to record information for future use—does not necessarily require a brain (even in organisms *with* a brain, like humans, see Finley 2025). For example, planarian flatworms trained to traverse rough surfaces in exchange for a reward retained the learned behaviour even after being decapitated and regenerating from their tails, suggesting that their tail cells registered past experiences (Shomrat and Levin 2013). Similarly, brainless slime moulds have been observed overcoming their aversion to caffeine to reach previously enjoyed oatmeal, demonstrating memory-dependent behaviour (Boisseau, Vogel, and Dussutour 2016).

*An agent is a subjective entity, registering its experiences through an individual (physiological or cognitive) memory.* (2; F; ii)

I synthesise these three criteria—Individuality, Playful flexibility, and Memory (IPM)— as the fundamental components of biological agency:

*An agent is an individual characterised by playful (non-directional) flexibility, and by a memory that channels and directs it into structured actions.*

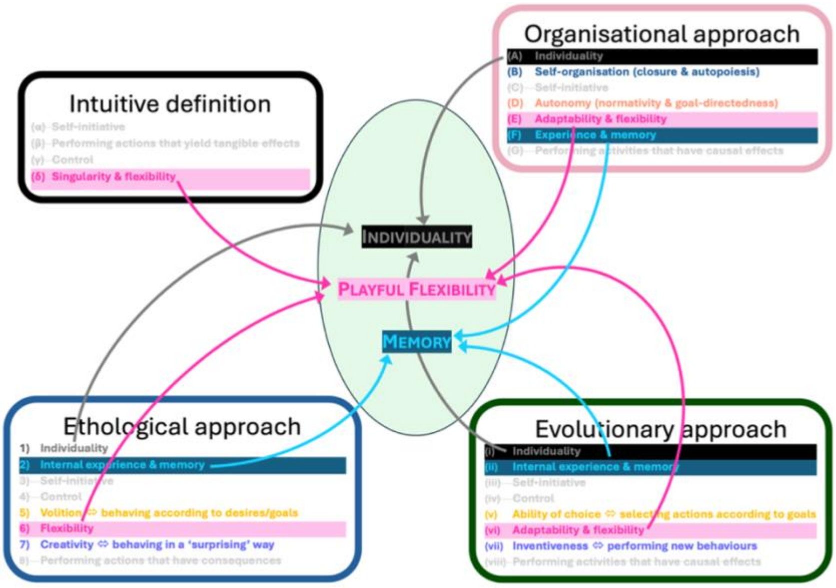


Figure 2. Core characteristics of biological agency (IPM)

Individuality, Playful flexibility, and Memory constitute both the necessary conditions for agency and the criteria by which it can be recognised. Whether they are also sufficient conditions for biological agency remains an open question. Nevertheless, this question is likely theoretical, as most biological entities meeting these three conditions also exhibit other properties associated with the organisational, ethological, or evolutionary concept of agency. It is also worth noting that, in line with Occam's razor, I have excluded goal-directedness from these foundational criteria. The directionality observed in agentive actions is sufficiently accounted for by the channelling of flexibility through memory, rendering explicit references to goals unnecessary. However, as Section 3 will show, goal-directedness remains relevant for explaining some properties of more specific forms of agency.

What about the remaining criteria, not incorporated into this synthesis? These criteria delineate distinct forms of agency, which will be examined in section 3.

# 3. The different forms of agency

## 3.1 Autonomous organisation, goal-directed choice, inventiveness

Having established the foundational elements of biological agency (IPM) we can now explore the additional characteristics put forward by the different definitions. These characteristics give rise to more specific forms of agency.

### 3.1.1 Autonomous organisation

The organisational concept of agency introduces several features beyond IPM, forming a distinctive mode of agency. These features fall into two main categories: (B) self-organisation, which encompasses closure and autopoiesis, and (D) autonomy, which includes normativity and internal goals. These elements are interrelated: self-organisation gives rise to internal norms that guide the agent's activities. Together with IPM, they define a first form of agency: *agency as autonomous organisation*.

### 3.1.2 Goal-directed choice

Across the different approaches, certain features overlap. This is the case of volition, in ethology, and choice, in evolutionary approach. The difference between these terms lies less in their meaning—both pertain to goal-directed actions—than in their role within different theoretical frameworks. Indeed, volition is primarily used when focusing on animals, not only in scientific contexts but also to support ethical considerations in experimental settings (Sueur, Zanaz, and Pelé 2023; Webb, Woodford, and Huchard 2019), and in everyday interactions (Blattner, Donaldson, and Wilcox 2020; Carter and Charles 2013). The focus on volition seeks to acknowledge animals' moral agency (McFarland and Hediger 2009), or potential citizenship (Kymlicka and Donaldson 2014). Choice, in contrast, is more common in **evolutionary biology**, which tends to adopt a more theoretical stance (although the boundary between theory and ethics remains porous). The shift away from volition, exemplified by Walsh's notion of "unintentional choice" (2015), likely reflects an effort to avoid anthropomorphism and maintain scientific rigour[4]. Despite these differences in terminology, both volition and choice refer to an agent's ability to select actions based on internal goals or desires. This capacity constitutes a second form of agency: *goal-directed choice*.

### 3.1.3 Inventiveness

The ethological concept of creativity and the evolutionary concept of inventiveness appear to be synonymous. While ethologists focus on the observer's surprise, evolutionary theorists highlight deviations from an organism's known behavioural repertoire**.** However, both perspectives describe the same capacity: the agent's ability to produce new, unexpected actions,

[4] Interestingly, anthropomorphism is frequently debated in ethology (see among many others: Arbilly and Lotem 2017; Burghardt 2006; Horowitz and Bekoff 2007) but often treated as a caricatured scarecrow in philosophy.

behaviours, and relationships with the environment. Unlike choice agency, inventive agency does not require goal-directedness. Although inventiveness can occur in goal-directed activities, such as problem-solving, it may also emerge without a clear purpose, especially in play (Bateson 2014; Burghardt 2015). This capacity for invention constitutes a third form of agency: *agency as inventiveness*.

Despite their distinct properties, these three forms of agency share the foundational elements of agency (IPM). However, Individuality, Playful flexibility, and Memory vary in degrees and importance across these forms. Similarly, while all agentive actions involve the agents' initiative and control, and yield tangible consequences (see section 2.3.1), these characteristics express differently in autonomous organisation, goal-directed choice, and inventiveness.
Section 3.2 will examine these distinctions in greater detail.

## 3.2 Comparison: the different types of agentive actions

The three forms of agency involve different types of agentive actions, distinguished by their main target and by the degree of control the agent exerts over them (Chart 1).

| *Performance of the agentive action* | Autonomous organisation | Goal-oriented choice | Inventiveness |
|---|---|---|---|
| Self-initiative | + | + | + |
| Locus of the direct impact | Agent | Relationship with the environment | Agent & its relationship with the environment |
| Control | + | ++ | +++ |

Chart 1. Performance of the agentive action

### 3.2.1 Target of the action

In autonomous organisation, agentive activities are primarily oriented toward the agent itself. This explains why organisational theory emphasises *self*-organisation, *self*-maintenance, and *self*-constitution. The impact on the agent is direct, while any effect on the relationship with the environment or on ecological and evolutionary dynamics is indirect.

In goal-directed choice, actions predominantly affect the relationship between the organism and its environment, whether through habitat selection, resource use, and social interactions. Occasionally, the environment itself becomes the direct target. For example, the construction of dams by beavers is a behaviour primarily aimed at transforming the environment. However, outside of humans, such actions only have indirect effects on the agent, and evolutionary dynamics.

Finally, invention influences both the agent and its relationship with the environment. The agent expands its behavioural repertoire, enabling new interactions with the environment. For instance, in Jerusalem, rats invented a technique for opening pinecones, which spread and became an innovation (Zohar and Terkel 1991). This invention affected both the rats' behavioural repertoire, widening it, and their interaction with the environment, allowing them to exploit a new food resource, and even to invade a new habitat (pinecone forests). As with goal-directed choice, inventions could affect the environment directly, although empirical evidence remains limited. Except when the agent is human, it seems that the influence of invention on ecological and evolutionary dynamics remains mostly indirect.

### 3.2.2 Control over the action

The degree of control an agent exerts over its actions varies across the different types of agency. In autonomous organisation, control originates from the *agent's internal conditions*, which the agent contributes to shape, even though they are also heavily constrained by genetics and environmental factors.

In goal-directed choice, the agent exerts control by *selecting* one behaviour from a range of possible actions. Although the execution of the behaviour is determined by this choice, its structure is largely predefined by the organism's existing repertoire, which is shaped partly by individual experience (Memory) but primarily by past selection. Thus, while the agent controls the specific execution of the action, it does not fully control its overall structure.

In invention, by contrast, the agent determines both the performance and the structure of the behaviour, as the action is not part of its initial repertoire. The agent *invents* the behaviour: in other words, it is both the triggering and the structuring cause of its action (for this distinction, see Dretske 1997).

These differences in the control reflect deeper distinctions in the nature of the agent itself.

## 3.3 Comparison: the different types of agents

While the three forms of agency—autonomous organisation, goal-directed choice, and inventiveness—share the foundational characteristics of Individuality, Playful flexibility, and Memory (IPM), these elements are expressed differently across each form.

### 3.3.1 IPM in the three forms of agency

Memory plays a consistent role across the three forms of agency (depending on the specific action being performed). However, the significance of Individuality and Playful flexibility varies in their expression. (Chart 2).

For example, high Individuality is crucial in autonomous organisation, where cohesion (closure and self-organisation) is essential. In contrast, goal-directed choice and inventiveness necessitate less unity, and can be performed by less cohesive groups.

Playful flexibility is most prominent in inventiveness. Although this flexibility is channelled by individual experience, and sometimes contextual factors (especially in problem-solving), inventiveness demands the greatest freedom from genetic and environmental constraints. Choice, while also involving Playful flexibility, operates under tighter constraints; flexibility is channelled not only by the agent's experience but also by its goals and typical behavioural repertoire. In autonomous organisation, flexibility is even further narrowed, as it is directed by the unity of the cohesive, self-oriented goal—the agent itself.

Each form of agency also possesses distinct characteristics beyond IPM, which define their specificity. A key question is whether these forms are interconnected and, if so, how they relate to one another.

| *Agent* | Autonomous organisation | Goal-oriented choice | Inventiveness |
|---|---|---|---|
| Individuality | ++ | + | + |
| Playful flexibility | + | + | +++ |
| Memory | + | + | + |

Chart 2. The role of IPM in different types of agency

### 3.3.2 Connections between the three forms of agency

On the one hand, the characteristics specific to autonomous organisation—self-organisation and normativity—provide a foundation for both goal-directed choice and invention. In other words, both choice-agency and inventive agency require a self-organised, normative agent. However, this agent may exhibit these characteristics to a lesser extent than what is required to constitute a fully autonomous organisation. For example, while groups may meet the criteria for goal-directed choice and inventiveness their typical lack of closure and self-organisation makes them less suitable—though not theoretically disqualified—as candidates for autonomous organisation.

On the other hand, the characteristics of goal-directed choice and invention do not overlap. Goal-directed choice is not a prerequisite for autonomous organisation or invention, nor is invention necessary for autonomous organisation or choice. They represent *diverging* types of agency: invention involves creating new behaviours, whereas choice consists of selecting from pre-existing options. Nevertheless, they share some characteristics: like goal-directed choice, invention requires the agent to transcend automatic responses to the environment. Additionally, in some cases, invention can be goal-oriented, especially in problem-solving scenarios.

### 3.3.3 Agents

A key question remains: which entities exhibit these forms of agency?

In theory, any system—biological or non-biological[5]— that demonstrably possesses IPM could manifest agency, either as autonomous organisation, goal-directed choice, or inventiveness. However, while agency is not restricted to specific types of entities, some are better suited than others to expressing particular forms of agency.

Autonomous organisation, with its emphasis on closure and autonomy, is most likely to manifest in organisms, especially multicellular organisms, which exhibit higher levels of self-organisation.

Goal-directed choice is evident when organisms could have acted differently, meaning alternative actions were conceivable. While this form of agency is more easily shown in organisms, it can also be exhibited by cells or groups, under certain conditions.

Invention in theory, could occur across a broad range of entities, but it is predominantly observed in highly flexible individuals, whose behaviour can be studied over extended periods, *i.e.*, with a relatively long lifespan. Indeed, Researchers need long-term population-level observations to recognise a behaviour as an invention, which has led to most documented cases being attributed to animals. However, recent studies on plants, demonstrating their remarkable flexibility, suggest this capacity may be more widespread than previously assumed.

This analysis demonstrates that there is no hierarchy among the three forms of agency: they differ in how they express IPM and are defined by distinct characteristics. However, this does not imply that different forms of agency cannot be rigorously assessed and compared. Indeed, Charts 1 and 2 can be used to identify and quantify agentive actions or to specify an individual's agency. Moreover, this discussion highlights that the different types of agency, despite their distinct processes, are not mutually exclusive and may coexist within the same entities, particularly in organisms. Section 4 will explore how the underlying processes interact to shape the different forms of agency and how these forms relate to one another within the same agent.

[5] This is beyond the scope of our study, but we have no principled argument against attributing agency to non-biological entities like artificial intelligences.

# 4. How do these forms of agency interact?

To understand how different processes contribute to each form of agency and how these forms interact, the most instructive case study is the organism, as it is the biological system where all three forms of agency are most likely to coexist.

## 4.1 Agency in the organism

### 4.1.1 Autonomous organisation

An organism constitutes an autonomous organisation, sustaining itself through self-directed processes of development and maintenance (Figure 3). These processes are enabled by IPM, but also by certain emerging characteristics of the system: autopoiesis (the system is self-generating with structural closure) and autonomous (it establishes internal norms and defining its own goals). However, the organism is not isolated: its agentive activities are influenced by environmental factors and historical constraints, including past natural selection, prior developmental stages, and earlier agentive processes (Montévil 2022; Montévil and Mossio 2015). This form of agency may or may not influence selective pressures and evolutionary processes (see section 4.2.1).

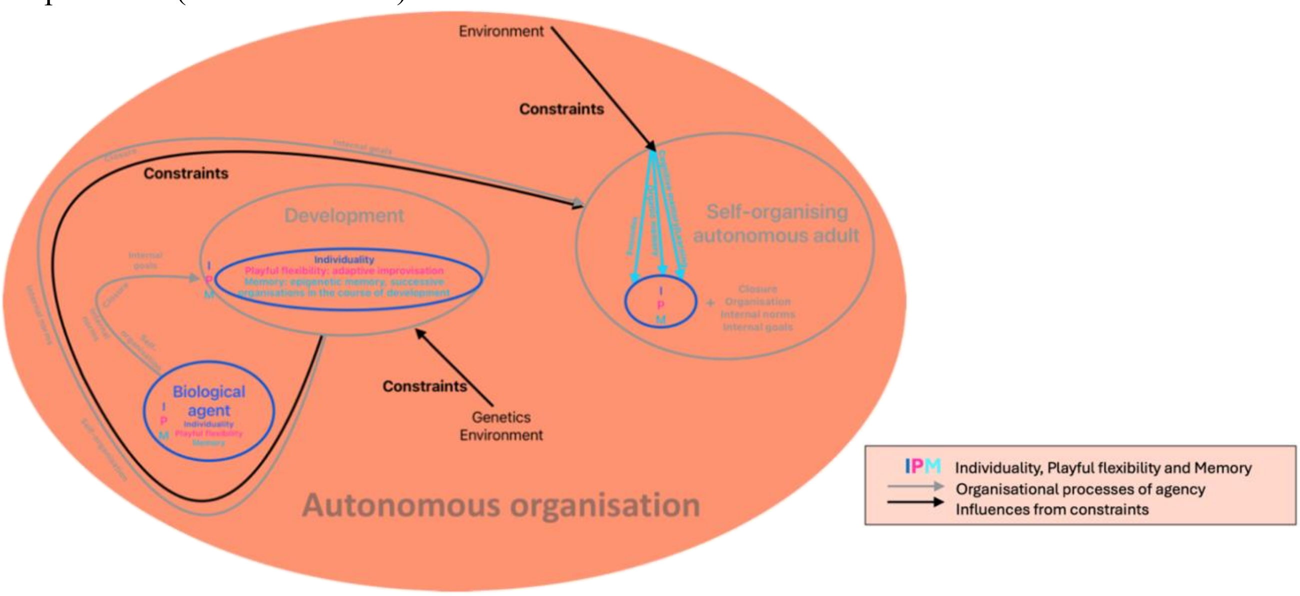


Figure 3. Autonomous organisation

How does this form of agency interact with others? Along with IPM—that operates across all levels of agency—organisational processes help build the agent's behavioural repertoire, though this repertoire which is also influenced by genetic, environmental, social, and cultural constraints. Organisational processes also influence the organism's goals; however, these goals are largely imposed by environmental factors, particularly those related to survival and reproduction. Combined with environmental pressures, the behavioural repertoire and natural goals can constrain the organism's actions so strongly that it may never exercise its capacity for choice (or deliberation Desmond 2023). Thus, while the properties of organisational agency enable goal-directed choice and inventiveness (see section 3.3.3), they do not necessarily lead to them nor do they guarantee their exercise (Figure 3b). In many cases, organisms remain 'just' autonomous organisations, their actions being otherwise fully determined.

But sometimes, autonomous organisations *do make choices.*

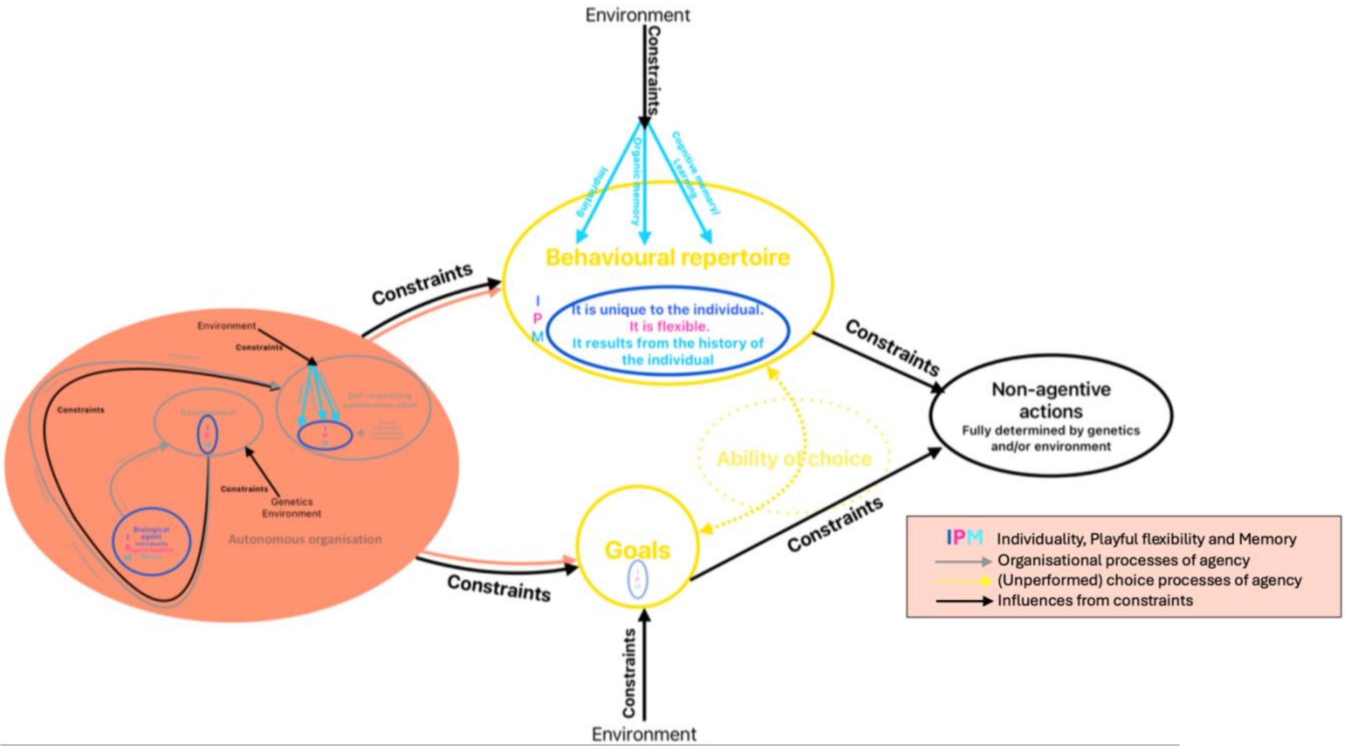


Figure 3b. Autonomous organisation without any other forms of agency

## 4.1.2 Goal-directed choice

Some organisms possess the ability to select behaviours from their repertoire, according to their goals (Figure 4). When they do, they are not mere autonomous organisations but express a distinct form of agency: goal-directed choice. Here, IPM intervenes both in the definition of goals[6], in the constitution of the repertoire and in the choice itself. Autonomous organisation processes also contribute to enable this form of agency. However, as mentioned above, an organism may still react automatically to its environment rather than exercising choice. The expression of goal-directed choice depends not only on the agent but also on environmental conditions—stressful situations that demand quick, risk-free actions make it less likely to manifest.

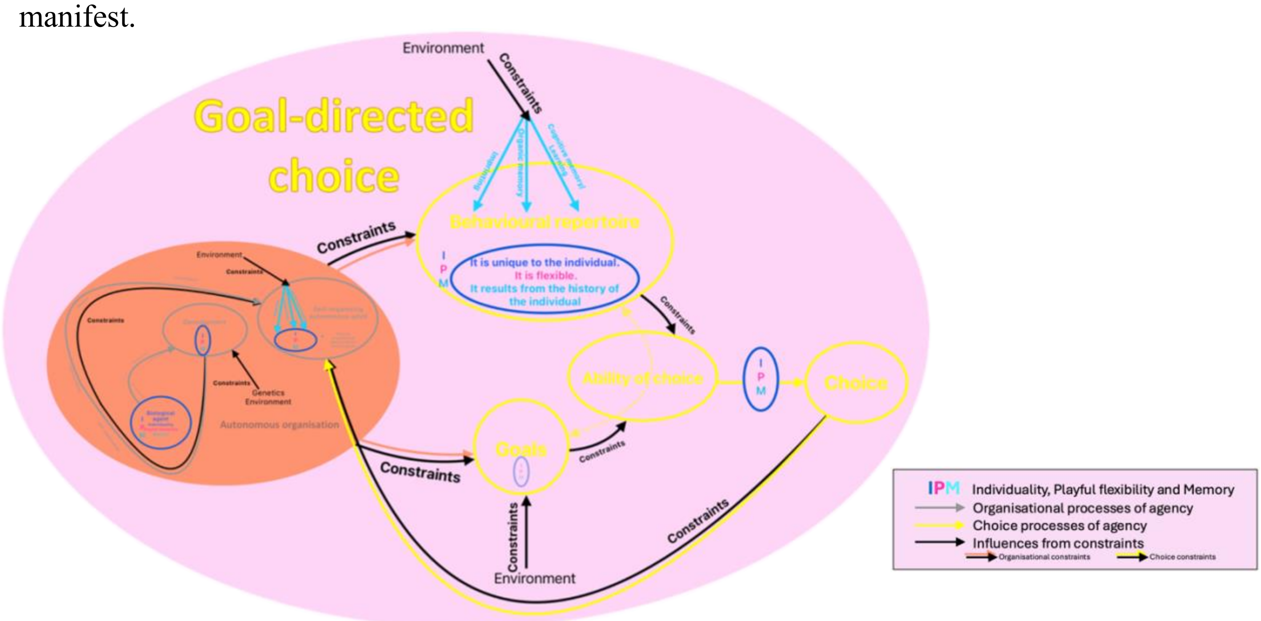


Figure 4. Goal-directed choice

[6] It is true that IPM influence is moderate within the goals, as the survival and reproduction imperatives determine the general goal-direction. Nevertheless, IPM plays a role in shaping specific goals, reflecting individual differences.

Just as organisation processes enable agency as choice, choices themselves in turn influence the system's organisation. For instance, food choices can affect immunity or gene expression, and selection of ecological partners can sometimes significantly affect individuals' phenotype, especially during early development[7]. While most choices impact the organism's ecological interactions, they do not necessarily have evolutionary consequences.

### 4.1.3 Inventive agency

Some organisms exhibit inventive agency (Figure 5), generating novel behaviours beyond their existing repertoire. While inventiveness is constrained by organisational processes, it is not necessarily governed by the same mechanisms as goal-directed choice. However, in some cases, inventiveness is channelled by goals—especially when facing environmental challenges or in problem-solving situation induced by researchers—then sharing some processes with choice agency.

Like choice, invention feeds back into and transforms the organism's organisation. It also directly transforms the behavioural repertoire by introducing new patterns. This, in turn, may or may not affect evolutionary dynamics.

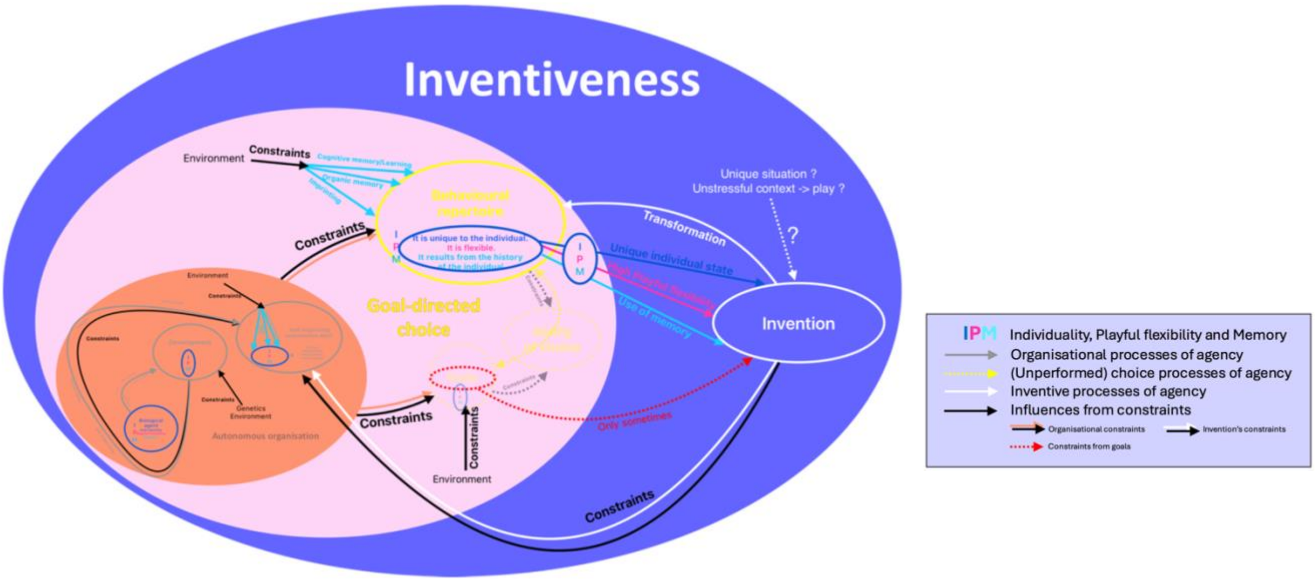


Figure 5. Inventiveness

*Why do organisms invent rather than selecting from the existing repertoire?*

Invention likely occurs in scenarios where no immediate, functional behaviour is required, allowing the organism to take risks and experiment. This aligns with the observed link between play and inventiveness: many non-human inventions are first observed during play. Research indicates that play promotes inventiveness and potentially adaptability across species (Bateson 2014; Burghardt 2015; Špinka, Newberry, and Bekoff 2001). The absence of a specific goal seems to free flexibility from efficiency constraints, enabling true inventiveness. Conversely, it could be argued that "necessity is the mother of invention" (Reader and Laland 2003): in emergencies, or unexpected situations, where typical behaviours fail, organisms are compelled to invent. Both perspectives may hold merit, as to this day, determining when and why individuals deviate from routine to explore new behaviours remains a challenge. A plausible hypothesis, reconciling these views, is that practising inventiveness when it is not

[7] For instance, the symbiosis between the squid and the bacterium *Vibrio fischeri* enables the squid to develop a luminescent organ it cannot develop otherwise (Pradeu 2011).

immediately necessary develops an agent's capacity to depart from habitual behaviours and try new ones, when necessity arises.

While Figure 3 primarily serves the organisational approach, Figures 4 and 5 cater to ethological and ecological perspectives. However, these three models offer limited insight into the long-term evolutionary implications of agency.

## 4.2 Agency in evolution

What makes a biological agent an *evolutionary* one? For an individual to act as an evolutionary agent, it must be the cause of its action, but that action must also exert a tangible effect on the environment and selective pressures, impacting long-term evolutionary dynamics. How can each of the three forms of agency contribute to ecological and evolutionary processes?

None of these three forms of agency *necessarily* drive evolutionary change. Some organisms may be agents, because they are autonomous organisations, because they make choices, or even because they invent behaviours, without their activities significantly altering the longer-term dynamics of evolution. However, in some cases, these activities are pivotal in shaping evolutionary trajectories.

### 4.2.1 Autonomous organisation and evolution

When autonomous organisation does not significantly affect selective pressures, forms are largely replicated generation after generation (assuming stable conditions). However, in some instances, organisational activities can also influence agent-environment interactions, potentially sparking evolutionary shifts or tempering the effects of selective pressures (Figure 6). It is known, for example, that phenotypic plasticity can prevent a species from extinction or allow a population to pursue new evolutionary directions (West-Eberhard 2003). In such cases, autonomous organisation exerts a causal influence on evolutionary dynamics, making the organism an evolutionary agent.

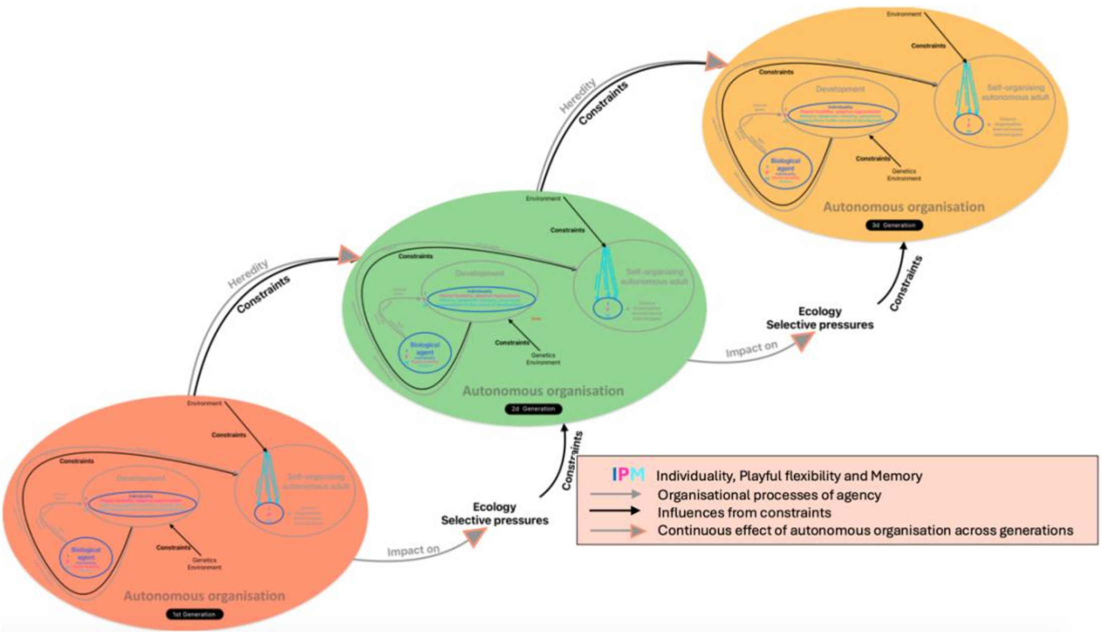


Figure 6. Autonomous organisation and evolution

### 4.2.2 Goal-directed choice and evolution

Organisms' choices regarding habitats, resources, and partners contribute to niche construction, affecting their interactions with the environment (Aaby and Desmond 2021; Deffner 2023). These choices can also influence reproductive success and transform the ecology, even when the environment is not the primary target of the action (Kylafis and Loreau 2008). For instance, the foraging paths chosen by ants have consequences for the entire ecosystem, as ants drop part of their harvest along the way. This choice likely has long-term effects, thereby contributing to shaping selective pressures. However, not all choices lead to lasting effects—this is especially true of choices made by individual agents. For example, if an individual or small group migrates on its own and fails to survive, their quick death will prevent their choice from having long-term effects. In such cases, they are agents, but not evolutionary ones. Conversely, if they survive and reproduce, their initial choice may have shifted the evolutionary trajectory of the entire species (Zelnik, Solomon, and Yaari 2015). Indeed, for a choice to be evolutionarily significant, its effects must persist across generations (Aaby and Desmond 2021; Laland, Odling-Smee, and Feldman 2019). This can occur through ecological change, social conformity, or both. When this happens, the agent (or, more often, agent*s*) initiates a new evolutionary dynamic and thus qualifies as an evolutionary agent (Figure 7).

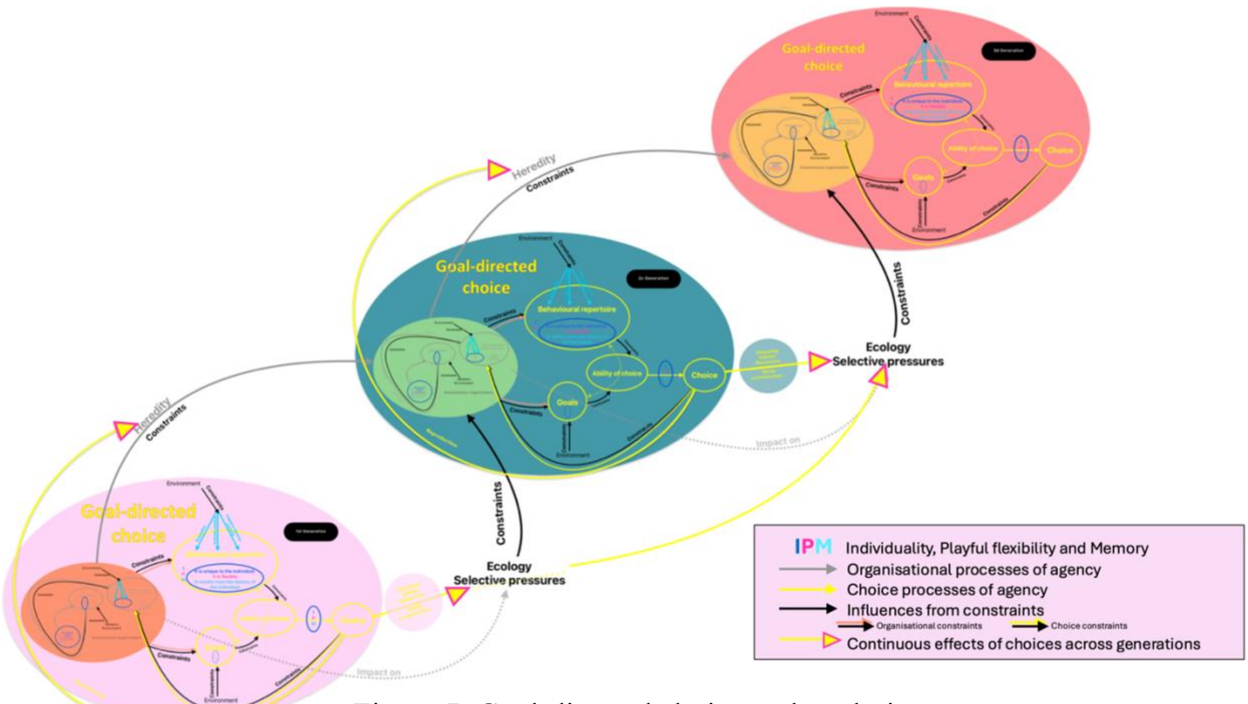


Figure 7. Goal-directed choice and evolution

### 4.2.3 Inventiveness and evolution

Inventions are rare and difficult to observe. However, the emergence of an inventor suggests conditions conducive of inventions, whether in the environment, the population, or the species. This suggests that invention may arise across multiple generations within the same population. Nonetheless, as other forms of agentive action, inventions do not necessarily have an evolutionary impact, as they rarely spread widely enough to cause large-scale effects. The inventor is then an agent, but not an evolutionary one. However, when inventions do spread (usually through social learning[8]), become innovations and change the way things are done (Bateson and Martin 2013), they can have long-term effects, on both organisms, their interaction with the environment, and the broader ecology (Bateson 2004; Sol 2003) (Figure 8).

[8] This means that innovations (*i.e.*, inventions that spread in a population) require social interactions, and may be restricted to only a certain set of biological entities—social animals?

A prime example is orcas in the Aleutian Islands, which innovated by including otters in their diet. This dietary shift disrupted the entire ecosystem: with fewer otters preying on urchins, urchin populations surged, devastating kelp forests crucial for local biodiversity (Estes et al. 1998). Even if the orcas later revert to their previous diet, this innovation will likely have lasting evolutionary consequences.

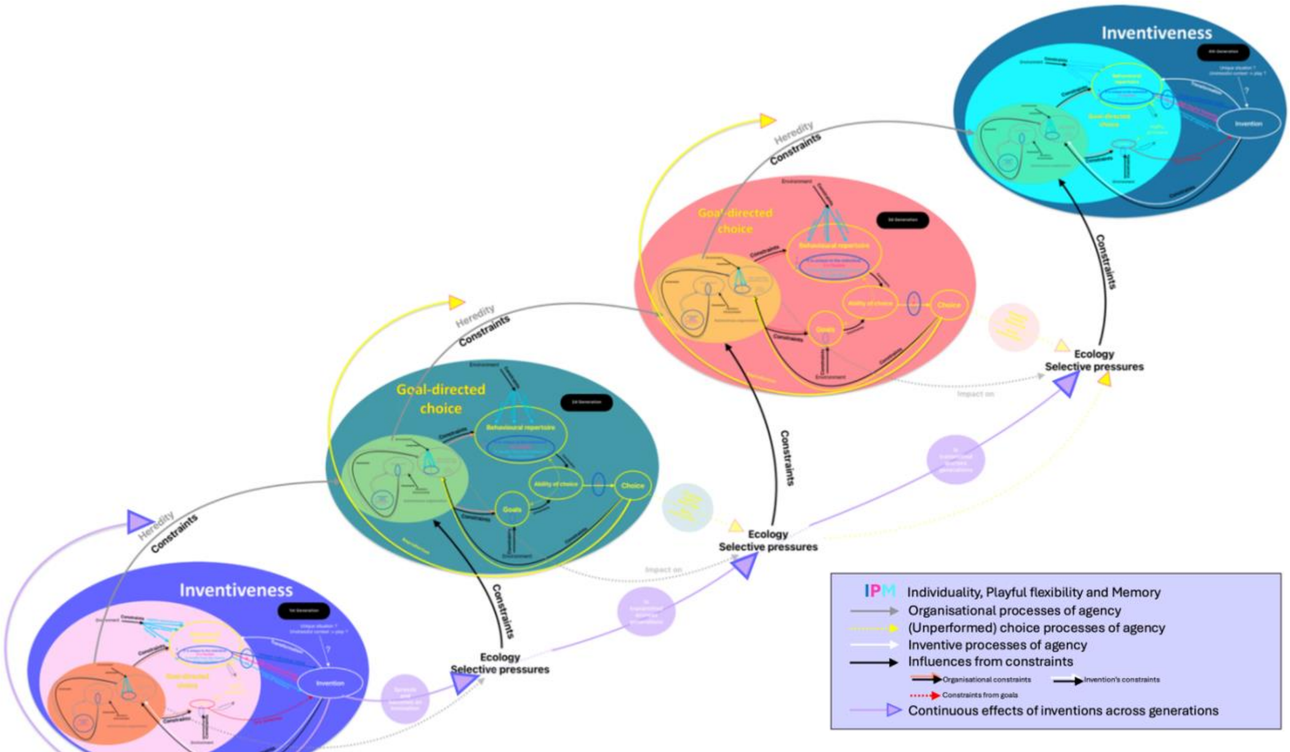

Figure 8. Inventiveness and evolution

The long-term effect of innovations is even more pronounced when they are consistently transmitted through generations. In such cases, both the inventor and those adopting and spreading the behaviour can be considered evolutionary agents, as they contribute to altering long-term selective pressures.

This is why, to fully grasp the evolutionary significance of these three forms of agency, it is crucial to acknowledge both the role of individual memory in channelling agentive processes and stabilising their outcomes, and the historical continuity which enables these processes and their effects to persist and exert long-term effects. Biological agents shape a continuous history, generation after generation, through which they can influence evolutionary trajectories.

# 5. Remaining challenges

This paper has proposed a framework for understanding biological agency, offering a basis for future interdisciplinary discussion and collaboration. However, while it represents an initial step towards integrating different definitions of agency, substantial theoretical and empirical work is still needed to clarify both the nature of agency and the processes enabling it. In conclusion, I will highlight three pressing challenges: (1) a theoretical difficulty, intrinsic to the definition of agency; (2) an epistemological challenge, that calls into question key assumptions in evolutionary theory; and (3) an empirical problem regarding the biological mechanisms underlying the various forms of agency.

## 5.1 A theoretical difficulty: Where does agency end?

A major theoretical obstacle lies in defining the precise boundaries of agency. As discussed earlier, agents do not *always* act agentively; agency is expressed only in certain types of actions. But does it extend solely to the direct target of those actions, *i.e.,* what the agent controls? If so, organisms would not be considered agents of the broader consequences of their actions, which complicates the idea that they can be agents of evolutionary change. For instance, an ant choosing a foraging path has no control over the seeds falling, yet this seed dispersal alters the environment and may have evolutionary consequences. Is the ant not an agent of these effects? Likewise, a cow belching does not control the resulting increase in atmospheric methane—it is not an agent of this change. But suppose cows were to spontaneously innovate by altering their diet (*i.e.*, without human intervention), thereby reducing methane emissions, this would influence their ecosystem and potentially alter selective forces; would the cows still not be considered agents of this evolutionary shift?

If agency includes all consequences of an action, organisms risk being seen as agents of nearly all ecological and evolutionary changes—rendering the concept too broad to be operational in ecology and evolutionary biology. Conversely, if agency is restricted to what an individual directly controls, even humans would rarely qualify as agents of evolutionary or ecological change, since most consequences of our actions lie beyond our ability to predict or control them.

A potential solution is to distinguish between more and less direct consequences and associate them with different degrees of agency. For example, if cows changing their diet started competing with a new species for this novel resource, they could be seen as more the agents of this shift in selective pressures than of the secondary ecological consequences of reduced methane emissions due to the new diet.

## 5.2 An epistemological challenge: rethinking the evolutionary framework

Recognising the role of agency calls for an adjustment to current evolutionary theory, which largely treats the development and behaviour of biological systems as the inevitable predetermined consequences of interactions between genetics and natural selection. Within this framework, living beings appear as passive entities, and our inability to prognosticate evolutionary trajectories remains unaccounted for. This results in an under-determination of evolution's inherent unpredictability, often dismissed as mere gaps in knowledge rather than a fundamental feature of biological processes.

As argued in this article, and supported by the EES, the concept of biological agency can make up for these shortcomings. Integrating agency allows us to account for the unpredictability of evolutionary and evolutionary dynamics, and thus compensate for some explanatory shortcomings in the current framework, without discarding its valid contributions (Sultan, Moczek, and Walsh 2022). Moreover, considering organisms as potential agents in evolution and incorporating organisational and behavioural studies could bridge some gaps between explanations of different biological processes.

However, current theoretical models remain inadequate for fully integrating agency into evolutionary explanations. Producing such models requires moving beyond deterministic views that reduce biological entities to passive recipients of genetic and selective forces and adopt an agency-based approach that acknowledges individual specificity and historicity, treating unpredictability as their necessary consequence. Agency is gaining ground in organisational studies, ethology, and ecological approaches, but, despite being increasingly advocated within the EES, its epistemic role in evolutionary theory remains largely underappreciated. The dominant view still regards the dynamics of biological systems as irrelevant to the study of evolution, despite their role in long-term evolutionary processes (Chenard and Duckworth 2021). Therefore, addressing this challenge demands not only the development of new theoretical models but also acknowledging the broader epistemological shift it relies on—one that moves away from the reductionism that has dominated evolutionary theory in recent decades, while preserving its key insights.

## 5.3 An empirical problem: how to elucidate the mechanisms underlying agency?

While this paper provides a theoretical structure that connects the different concepts of agency, and outlines avenues for interdisciplinary collaborations, it only constitutes an initial step. Indeed, our understanding of the mechanisms enabling different forms of agency is still limited, and experimental research on the topic is still scarce.

Especially, the physiological, organisational and cognitive processes underlying IPM remain largely abstract within the framework proposed here. Although research in organisational and developmental biology has improved our comprehension of individuality, the mechanisms governing flexibility and memory are still poorly understood. What makes an individual flexible? Is flexibility an intrinsic property of all living entities, or does it require specific organisational, physiological, or cognitive capacities? Is behavioural flexibility continuous with phenotypic plasticity? Similar uncertainties surround memory. While extensive research exists on brain-related memory—some addressing the role it plays in agentive behaviours (Toates 2004)—little is known about how memory operates in brainless organisms or about memory processes occurring outside the brain in species that possess one. Empirically investigating these mechanisms, understanding their interplay in enabling agency, and determining how they give rise to different forms of agency are critical areas for future research.

Such progress requires interdisciplinary collaboration across both theoretical and empirical biological fields, from neurobiology and molecular biology to behavioural ecology and broader approaches such as evo-devo. These disciplines must work together to establish a theoretical foundation that enables the coordination of empirical findings and clarifies how the different mechanisms they study interact to produce agentive behaviours. This research is still in its infancy, but the growing body of literature on agency and the increasing cross-disciplinary engagement suggest a shift in our theoretical framework—one that calls for continued efforts to refine concepts, clarify mechanisms, and foster integration across fields.

The present paper contributes to this effort by reviewing the existing literature on biological agency across various biological and philosophical fields and synthesising their conceptual findings. This has led to the identification of three core capacities—Individuality, Playful flexibility, and Memory (IPM)—that unify the concept of agency and can serve as conceptual tools for integrating the diverse processes examined in different agency-based approaches. The IPM framework provides researchers with a means to connect their fields of study, investigate how different forms of agency—autonomous organisation, goal-directed choice, and inventiveness—emerge across various entities, and assess their influence on biological processes occurring at different timescales. By helping to rationalise and formalise the study of agency while accommodating its diverse manifestations, I hope this framework will facilitate the interdisciplinary collaboration necessary for integrating the concept into epistemological models, clarifying its causal significance, and advancing our understanding of the mechanisms underlying its manifestation.

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