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How an Agential Account of Biological Individuality Can Come Apart from Concepts of the Organism

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Abstract

This paper aims to connect the problem of biological individuality with the increasing interest in minimal accounts of biological agency. Generally, the concept of biological agency merely acts as another way to describe the organism and not as an individuality concept in its own right. This paper develops two main claims. (1) We should have an agential account of biological individuality in addition to an evolutionary and an organismal one. (2) This concept of *agential individuality* comes apart from concepts of the organism (and evolutionary individual), motivated by the case of eusocial insects, like the honey bee *Apis mellifera*.

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1. Introduction

When considering the problem of biological individuality, philosophers tend to defend an evolutionary and/or a physiological organismal account (see Hull 1978; Gould and Lloyd 1999; Clarke 2010; Godfrey-Smith 2009; Pradeu 2013, 2016). Yet, these accounts of the biological individual fail to discuss the more active and goal-directed nature of living entities. Recently, there has been a resurgence in research looking into agency and cognition as a means to understand and describe biological entities. Much of this research moves away from the traditional brain-centred domain of the cognitive sciences, exploring the *minimal cognitive* processes that enable living systems to sense, process, store, and act on information (see Levin 2019; Keijzer 2021; Moreno and Mossio 2015; Sultan et.al 2021; Lyon et.al 2021; Bechtel and Bich 2021; Walsh 2015).

Despite the growing interest in such minimal accounts of agency, apart from a few notable exceptions (see Levin 2019; Arnellos and Moreno 2015), there has been little work done to consider agency in the context of biological individuality. Generally, the concept of biological agency merely acts as another way to describe the organism and not as an individuality concept in its own right (see Lyon 2021; Moreno and Mossio 2015, Sultan et.al 2021; Bechtel and Bich 2021; Walsh 2015).

I will defend two main claims. First, we should have an agential account of biological individuality, in addition to an evolutionary and an organismal one. The term 'agent' is used broadly, to capture the active, cognitive nature of living entities. The claim of *agential individuality* developed in this paper is one broad enough to describe more than just animals with nervous systems, while also allowing us to demarcate the main agential individual from the lower-level minimal agential processes of its parts. Second, this concept of agential individuality comes apart from the concept of the organism (and the evolutionary individual).

Ultimately, I defend a three-pronged pluralistic approach to the problem of biological individuality, which includes evolutionary individuals, organisms, and agential individuals as connected but ultimately distinct individuality concepts. While the extensions of these three concepts often overlap, they can and do come apart in interesting ways.

Before introducing and defending the above claims in Sections 3 and 4, I will address the problem of biological individuality more generally, with a focus on the organism concept. This paper draws inspiration from the curious case of eusocial insects, like the honey bee *Apis mellifera.*

2. The Organism Concept

2.1 Eusocial Insects

Eusocial insects are often touted as stereotypical non-paradigmatic cases when considering the problem of biological individuality. The archetypical example being the European honey bee (see Queller and Strassmann 2009; Clarke 2010; Godfrey-Smith 2013; Folse and Roughgarden 2010). Such eusocial insects live in highly integrated colonies with a distinct division of reproductive labour (Crespi and Yanega 1995; Nowak et.al 2010). In the case of the honey bee, the colony has three reproductive castes—one fertile female queen, approximately 20,000-40,000 functionally sterile female workers, and 200-400 fertile male drones (Elekonich and Roberts 2005, 362-63). The queen is the only female that reproduces within the hive, while the workers perform all the non-reproductive labour, including nursing brood, caring for the queen, foraging, guarding etc. (Johnson 2010; Page 1980). The reproductive division of labour between the female bees is irreversible but not genetically determined (Maleszka 2008, 188; Grout 1949, 39-40). The other reproductive caste, the male drones, live within the hive until spring when they leave to mate with new queens. The drones will either die during mating or be kicked out of the colony before winter (Grout 1949, 56-58; Winston 1987, 41, 201-03).

Eusocial insects are characterised by their high degree of integration and self-organised division of labour. The honey bee hive is often referred to as a superorganism for this reason. Moreover, some scholars working on the problem of biological individuality consider the honey bee hive to be an individual in its own right (see Queller and Strassmann 2009; Godfrey-Smith 2013; Pradeu 2013; Clarke 2010; Folse and

Roughgarden 2010). However, this claim of hive individuality is complicated when we start to tease apart the problem of biological individuality itself.

2.2 The Problem of Biological Individuality

Despite the biological individual being central to many fields in biology, there is still little agreement about what criteria underlie the concept itself. Particularly for non-paradigmatic cases, like eusocial insects, it is a question of how we distinguish biological individuals from other biological entities like social groups or parts (Clarke 2010). The problem has both spatial and temporal components. Not only can we ask whether a collection of spatial parts, like cells, is one individual, but we must also consider a biological individual's temporal boundaries—when and how does a new biological individual come into existence?

The problem of biological individuality is often concerned with describing two kinds of biological individual—evolutionary individuals and physiological organisms. Evolutionary individuals are those entities that are defined by evolutionary criteria—by being a member of an evolutionary (or Darwinian) population and being capable of forming lineages that are subject to the forces of natural selection (Godfrey-Smith 2013, 5; Hull 1978; Gould and Lloyd 1999; Clarke 2013). In contrast, organisms are defined by physiological criteria. They are a collection of diverse parts that are physiologically bound in particular ways—such as spatial boundedness, cooperation, metabolism, or immunological policing mechanisms etc. (Gould and Lloyd 1999; Queller and Strassmann 2009; Godfrey-Smith 2013; Dupré and O'Malley 2009; Pradeu 2010). Some authors, such as Godfrey-Smith (2013) and Pradeu (2013), explicitly defend such a split; however, other authors like Clarke (2013) use the terms synonymously.

While many paradigm cases will be both evolutionary individuals and organisms, the concepts describe different criteria and therefore come apart. If we are going to consider whether the honey bee hive is a biological individual, we should actually ask whether the honey bee hive is an evolutionary individual and/or if it is an organism.

The honey bee hive can easily be considered an evolutionary individual. Due to the obligatory reproductive division of labour, lineage formation occurs at the level of the hive. The queen and drones pass on the genetic information, with the workers acting as facilitators for this reproduction (Godfrey-Smith 2013, 9-10; Seeley 1989; Wilson and Hölldobler 2005).

It is less clear whether we should consider the honey bee hive an organism. If we adopt more conceptual, abstract iterations of the organism concept, the honey bee hive can be considered an organism rather than a social group. According to Queller and Strassmann's (2009) definition of the organism, some biological entity is an organism if there is a high degree of actual cooperation and a low degree of actual conflict between its parts. This is the case for the honey bee hive. The authors do state that the honey bee hive is an organism in its own right, being the "largest unit of near-unanimous design" (3145). A materially neutral interpretation of Pradeu's 'Immune Individual' definition of the organism also has a similar result. (Pradeu 2013, 91).

However, we are left with a problem. On certain interpretations, such as those defended by Queller and Strassmann (2009)[2] and Godfrey-Smith (2013), the organism concept includes an "exclusion principle". Such an exclusion principle states that an organism cannot be a proper part of (as opposed to merely contained within) a larger organism.

Godfrey-Smith (2013) proposes a graded version of this exclusion principle. If lower-level parts are metabolically subsumed by a higher-level organism, then the lower-level parts must have a lower degree of organismality. Conversely, if a part of some biological whole retains a sufficient degree of physiological autonomy, the degree to which it is a functional part of the larger organism is diminished (13). Although lower-level parts may possess some organismal properties, by being a true part of a larger organism, they are no longer an organism to the same degree.

If we accept such a graded exclusion principle and accept that the honey bee hive is an organism, then the honey bee itself cannot be an organism to the same degree. The bee

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[2] Queller and Strassmann (2009) seem to defend both an exclusion principle (3145) and state that organisms can be parts of larger organisms (3149)

loses organism points by being a part of the hive organism. This means that either the hive or the honey bee is the primary organism. It cannot be both.

There is something problematic about the conclusion that the honey bee is not an organism to a significant degree if the hive is. This problem becomes clear if we compare our social honey bee with solitary bees like the blue-banded bee (*Amegilla spp.)*. Unlike our social honey bee, the blue-banded bee lives a solitary life, finding food, reproducing, nesting, and tending to her brood autonomously (Cardale 1968; Dollin 2000, 52). When comparing reproductive strategies, the solitary bee and the social bee are vastly different. However, if we look at their physiology, the solitary bee and the social bee are comparable, with similar anatomical and physiological structures and functions (Winston 1987, 13-44; Tomlinson et.al 2015). The blue-banded bee is an organism according to every definition of the concept; yet, according to more abstract conceptions of the organism, like those described above, the social honey bee is not.

One solution is to adopt a *materially restricted* organism concept. Rather than having an abstract concept of the organism, like that described by Queller and Strassman (2009), the organism would be a very particular sort of biological entity, defined by specific biological substances, functions, and/or processes (Okasha 2022, 15). This would be much like how we conceptualise other particular biological entities, like the gene. Rather than being defined by the abstract ideas of 'units of inheritance', contemporary definitions of the gene emphasise the material makeup and functional output of a gene, as being made of nucleic acid (be it DNA or RNA) and producing RNA and/or a protein as a part of a gene regulatory network (see Portin and Wilkins 2017, 1361-62). A similar biologically restricted organism concept would allow us to identify and demarcate such entities without relying on abstract concepts like cooperation or integration.

What processes and/or functions define the organism? Organisms are the quintessential *living* entity. As such, we can turn to characterisations of life to help define the organism. Despite some disagreement, metabolism is generally considered central to the definition of life. To be alive is to metabolise (Parke 2023; Dupré and O'Malley 2009). Metabolic chemical reactions are the fundamental processes that maintain life, by transforming energy from the environment into usable energy for the living entity, allowing it to persist over time (Dupré and O'Malley 2009, 2).

However, metabolic reactions alone are not enough to characterise the organism. The organism is an entity that has a *centred metabolic network.* Single biochemical reactions form large and complex metabolic networks where different reactions produce different metabolites according to the needs of the whole, allowing it to persist over time. These metabolic networks operate at the level of single cells, while also being scaled up to form complex multicellular metabolic networks (Ma and Zeng 2003).

As opposed to the mere sharing of metabolites, centred metabolic networks have a cohesive and interconnected network topology, that is dominated by a few highly connected reactions and substrates, with the majority of nodes having very few connections. These are known as *scale-free networks*. Jeong et.al (2000) found such scale-free metabolic networks in all of their 43 study organisms across all three domains of life. Despite differences in detail, this scale-free network structure remains consistent between organisms, regardless of size or lineage (Jeong et.al 2000; Ma and Zeng 2003; Gao et.al 2021).

As such, an organism could be defined as a cooperative collection of biological parts that are unified by a centred metabolic network, self-maintaining and resisting the forces of entropy by turning energy from the environment into usable energy for the whole organism. They are metabolic wholes.

3. An Account of Biological Agency

What is not captured by this metabolic concept, is how organisms acquire the resources that fuel these metabolic networks. To facilitate metabolism, living entities must have other processes that connect internal metabolic reactions to the environment. These are active and causal processes.

Recently, more scholars have defended the importance of having an account of biological agency, defining the concept with various degrees of breadth and permissibility (see Sultan et.al 2022; Moreno and Mossio 2015; Levin 2019; Keijzer 2021; Bechtel and Bich 2021; Lyon et.al 2021; Walsh 2015; Godfrey-Smith 2016). Broadly, the notion of biological agency is based on a goal-directed capacity that living entities must have, to facilitate their own self-maintenance, allowing them to survive in and interact with a complex and changing world. This adaptive goal-directedness is minimally cognitive. Shettleworth (2010) describes cognition as:

> …the mechanisms by which animals acquire, process, store, and act on information from the environment. These include perception, learning, memory, and decision-making (2010, 5).

Although Shettleworth is focused on animal cognition, this definition could be extended to all living entities that can sense and interpret information from the environment.

One framework that captures this idea of minimal cognition is Keijzer's (2021) *cobolism*. Keijzer defines cobolism as the basic cyclic processes that work to provide the resources for and facilitate the fundamental metabolic processes that allow the entity to persist (151). Unlike some interpretations of minimal cognition or agency, Keijzer distinguishes between the more fundamental metabolic processes and the minimal cognitive (cobolic) processes that facilitate them. Other authors, like Bechtel and Bich (2021), Moreno and Mossio (2015), and Arnellos and Moreno (2015) make a similar distinction. This is a distinction between the centred energy production networks that define the organism and the cognitive processes that facilitate and mediate them. I will refer to these facilitative cognitive processes as *cognitive control processes*.

Such cognitive control processes can be multiply realised by different biological mechanisms. These cognitive processes facilitate the more fundamental transformation of energy by connecting the internal state of affairs with the environment, to provide resources for metabolism. Such processes could include sensorimotor control, development of structural features, growth, information processing and storage, behavioural adaptation, and even representational cognition (Keijzer 2021, 151-52). As such, biological agency could be defined as the collection of the cognitive control processes that facilitate metabolic reactions. While the metabolic and cognitive control processes are linked, they are different in kind.

3.1 Where is the Agent?

Although we have an account of *biological agency* we do not have an account of the *agential individual.* While this more minimal account of agency allows us to identify agency in single-celled entities, it makes it difficult to attribute agency to multicellular individuals and identify the main agent that interacts with the environment. For example, in multicellular organisms, there will be cognitive control processes at multiple levels—at the level of cells, cell groups, organs, and the organism—each of which can be considered agential (Keijzer 2021, 152-54).

This is not a bug but a feature. Many biological processes need to occur simultaneously in a multicellular individual without top-down control. This can only happen if there is local cognitive control that allows such self-organisation. Consider the local changes that occur due to an immune response (see Atlan and Cohen 1998). There needs to be various cognitive processes occurring locally, capable of sensing, processing, and interpreting local information to prevision resources. There need to be agential processes the whole way down.

Nonetheless, we still want to say that there is a primary agential individual—a coherent whole that is the main interactor with the environment which persists over time. To have an account of agential individuality, we need to be able to distinguish between the agent and the environment. Rather than a multicellular entity merely being a collection of many agents, porous to the environment, an agential individual has both internal coherence and spatial and temporal boundaries. Many authors rely on the organism concept to find these boundaries. The concept of biological agency merely acts as another way to describe the organism and not as an individuality concept on its own (see Lyon 2021; Moreno and Mossio 2015, Sultan et.al 2021; Bechtel and Bich 2021; Walsh 2015).

Although the minimal cognitive control processes that define *agency* are linked to metabolism, this does not mean that the *agential individual* is the *organism*. The difference here is between how lower-level processes are related and how we find the boundaries of the organism or agential individual. Although cognitive control processes *do* facilitate metabolism, the spatial and temporal boundaries of the organism and the agential individual are not necessarily the same.

For example, Keijzer leaves room for cobolic processes that could extend beyond the metabolic boundaries of the organism, such as "social forms, symbiosis, and extensive forms of niche construction" (2021, 153). In principle, there is not a definitive reason to rule out such processes as being considered within the boundaries of the agential individual, even though they extend beyond the metabolic boundaries of the organism. Hence, we cannot rely on the organism concept to identify the agential individual. To identify the agential individual, we must consider how sub-agent agential parts are arranged and how we find the main agent.

Levin (2019) addresses a similar problem. Levin acknowledges that all complex agents are made up of sub-individual agents and posits that we can have an account of the individual based on goal-directedness and sub-agential organisation. Levin argues that the main agent or '*Self',* as he puts it, is at the level where the networks of communication between cells are "working together toward a unified goal [to] create and maintain specific, large structures" (6), demarcating between the main agential individual and sub-agent agential processes.

A defining feature of the agential individual is goal-directedness. The boundaries of the agential individual can be found by identifying where such unified goals are. This idea of goals is a naturalistic one. It does not rely on the entity being conscious or aware of such goals. Goals are merely a means by which some entity orients toward some state of affairs (Levin 2019, 2).

According to Levin (2019), "what defines a coherent, unified Self out of its constituent components and the surrounding environment is the set of parts that operate toward reaching a specific goal-state" (7). This idea of a *goal-state* is more than the collective alignment of the goals of parts. Rather, it is emergent goals specific to the entire integrated system. Levin (2019) leaves this notion of a goal-state relatively vague. Yet, when considering agency in the context of the problem of biological individuality, we can restrict this notion of goals to biologically grounded *existential goals*. Borrowing a term from Lyon (2020), I consider existential goals as the goals that ground the ongoing persistence of an agential individual—for example, survival and possibly reproduction (146-147). For a multicellular entity to be an agential individual, the cognitive control mechanisms of the parts (i.e., cells) must be ultimately aimed toward the persistence of the whole. For example, there are mechanisms within a multicellular individual that encourage the death of parts, such as programmed cell death, to facilitate the ongoing survival of the whole system (Elmore 2007). When a part no longer does this, then it may no longer be a part of the agential individual.

Although lower level parts may have agential processes and even local goals, there is only one main agential individual. These agential individuals are the primary causal entities that interact with the environment and that persist over time, even when parts change.

Note that *persistence* for an agential individual does not necessarily mean *staying alive* in a strictly metabolic sense. As will be discussed below, such existential goals may extend beyond the living organism, focusing on the persistence of a non-metabolic agential individual.

4. How the Concepts of the Organism and the Agential Individual Come Apart

The concept of the organism and the agential individual come apart. As such, we cannot rely on one concept when trying to find the extensions of the other. While organisms are defined as being the largest unit that has the right kind of physiological unity between its parts, in this case having a centred metabolic network, an agential individual is a cognitive entity, in which all minimal cognitive control processes are directed toward fulfilling the unified existential goals of the whole. Although the minimal cognitive control processes that define biological agency may be linked to the metabolic processes that define the organism, the spatial and temporal boundaries of the agential individual and the organism can differ.

This is, in part, because the metabolic organism concept described above is firmly grounded in particular biological processes; whereas, the concept of the agential individual can be multiply realised by a variety of different cognitive control processes, some of which may extend beyond the metabolic boundaries of the organism. If the ongoing persistence of such cognitive control processes is bounded within the existential goals of the agential individual, then the boundaries of the agential individual will include more than just the metabolic organism.

Of course, in many cases, the extensions of the two concepts will be the same. Nonetheless, because the two concepts are both grounded by different criteria and have different boundary conditions, they can come apart.

4.1 Consider the Bees

Eusocial insects, like the honey bee and the hive, are one case where these two concepts come apart. If we take the concept of the organism to describe a physiological entity based on having a centred metabolic network, then the bee is the organism and not the hive. This resolves the problem described in Section 2, where, under a more abstract organism concept, the solitary bee is an organism and the social bee is not. What is different between solitary bees and social bees is not their underlying physiology, the difference is in their existential goals. While the solitary bee is entirely focused on her own survival and reproduction, the social bee's primary goals are the survival and reproduction of the hive. This is not to say that there are no agential processes and organism-level goals for the honey bee; however, the needs and goals of the hive are more important than the bee's, *according to the bee.*

One of the perplexing things about eusocial insects like the honey bee is that their robust and flexible division of labour is self-organising, much like how the complex systems within a body are self-organising (Bonabeau et.al 1997). Like cells in a body, the bees need to have some agential properties for this self-organisation to function. Nonetheless, the hive's goals are more important to the bee than the bee's own survival. This places the main locus of agency at the level of the hive. To say that the worker bee, and even the queen, is an agential individual in the same way as our solitary bee is misleading. Defining what bees do within the hive as merely social dramatically underplays how interconnected the colony is. The bees are organisms with agential properties but not agential individuals. (Note: the male drones complicate this account of hive-level agential individuality and further discussion is warranted. Although drones can be seen as fulfilling the reproductive goals of the hive, it is not clear whether the hive's goals are more important *to the drone* than the drone's own existential goals.)

The lesser-known honeypot ant is another clear instance where these two concepts come apart. Honeypot ants are also eusocial, with an obligatory reproductive division of labour (Conway 1994, 51; Keller and Gordon 2009, 106-08). Like the honey bee, honeypot ants make a kind of ant honey, which is used to feed the rest of the colony.

However, the honeypot ants do not store this honey in wax combs like bees. Instead, up to 50% of the worker caste stores the honey in their abdomens (Conway 1991). These workers, known as *repletes*, then spend their lives hanging from the roof of the nest, supplying the rest of the colony with food. Repletism has convergently evolved in several ant lineages, with dozens of known species adopting such a strategy (Sawh 2022, 8-10). One such species is the Australian *Camponotus inflatus* (Conway 1994).

Much like the difference between the social honey bee and solitary bees, the main difference between the honeypot ant and other solitary insects is that the colony is the main agential individual rather than the ant. These replete workers act like cells in a body—in this case much like adipocytes that store fat in mammals (Keller and Gordon 2009, 107-08; Zwich et.al 2018, 1-2). The replete sub-caste are behaviourally and morphologically adapted to act as living food storage for the ongoing persistence of the colony (Sawh 2022, 7-10). Nonetheless, even though the ants live their lives entirely for the benefit of the colony, the ants are still organisms as they are the largest physiological units with a centred metabolic network. Their bodies still convert energy from the environment into usable free energy that keeps them metabolically alive. However, their entire lives are dictated by the goals of the colony. These ants are organisms but not agential individuals.

5. Conclusion

Ultimately, this concept of agential individuality fits into a broader three-pronged pluralist approach to the problem of biological individuality; in which, there are three main kinds of biological individuals—evolutionary individuals, organisms, and agential individuals. While many biological individuals will fulfil the criteria of being all three, these individuality concepts can and do come apart in interesting ways.

By adopting this three-pronged pluralistic framework of biological individuality, we can approach non-paradigmatic cases with more clarity. A particular case may be non-paradigmatic merely because it is indeterminant whether it fulfils any of the criteria for being a kind of biological individual. Conversely, it could also be because these three different concepts of biological individuality are coming apart in unintuitive ways, like with eusocial insects. The honey bee hive fulfils the criteria for being an evolutionary individual and an agential individual but not the criteria for being an organism.

Moreover, the temporal boundaries of these three biological individuality concepts may differ, even for our paradigm individual organisms. An entity might become an evolutionary individual, before an organism, before an agential individual. It may be that many cases that complicate discussions of biological individuality do so because they fulfil the criteria of being one kind of biological individual but not others.

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