## Author

Alan C. Love

*aclove@umn.edu*

*Department of Philosophy and Minnesota Center for Philosophy of Science*

*University of Minnesota*

*Heller Hall #746, 271 S 19th Ave, Minneapolis, Minnesota*

## Source

"Reflections on the Study of Biological Agency and its Evolution"

*Spontaneous Generations* Volume 11, Issue 1 (Spring/Summer 2023)

doi.org/10.4245/spongen.v11i1.13757

https://spontaneousgenerations.com

## Editorial Offices

Institute for the History and Philosophy of Science and Technology

Room 316 Victoria College, University of Toronto

91 Charles Street West, Toronto, Ontario, Canada

M5S1K7

Founded in 2006, Spontaneous Generations is an online academic journal published by the Institute for the History and Philosophy of Science and Technology, University of Toronto. There is no subscription or membership fee. Spontaneous Generations provides immediate open access to its content on the principle that making research freely available to the public supports a greater global exchange of knowledge.

# Reflections on the Study of Biological Agency and its Evolution

Alan C. Love

Department of Philosophy and Minnesota Center for Philosophy of Science

**Abstract**

What is biological agency? Is it relevant for evolution? How should it be studied? Using Michael Tomasello's recently published *The Evolution of Agency* as a point of departure, this essay emphasizes the ability to undertake inquiry with multiple working characterizations of agency rather than a single consensus definition. These characterizations should be empirically interrogated using well-justified investigative systems and the choices for individual models should be explicitly indicated (e.g., focusing on social interactions surrounding foraging but ignoring parenting). Additionally, the availability of different types of models, such as feedback control versus dynamical systems, should be acknowledged and explored. The result is a possibility space of different research projects where the diverse epistemic issues at stake are open to scrutiny and evaluation, thereby potentially fostering novel ways of studying the many dimensions of biological agency and their evolution.

**Key Words**

*Agency; definitions; Extended Evolutionary Synthesis; modeling practices; organisms; scientific models*

A key plank in the platform of the Extended Evolutionary Synthesis is the evolutionary significance of organismal agency manifested in exploratory behavior and plasticity (Laland et al., 2015). According to one recent perspective, introducing considerations of agency explicitly helps to bridge explanatory gaps related to phenotypic variation, trait transmission, and the origin of novelty (Sultan et al., 2022). However, debates about the need to implement this kind of recommendation frequently yield conflicting viewpoints based on divergent modeling choices. For some researchers, the agential behavior of organisms and its causal impact on the environment—and thereby natural selection—is minimized or absent from our models of evolutionary change (Laland et al., 2011); for other researchers, these features are captured already—though perhaps conceptualized differently—in extant models of the standard theoretical toolkit (Scott-Phillips et al., 2014). Instead of attempting to somehow tip the balance in one direction or the other for these debates, it seems warranted to step back and reflect more broadly on how biological agency and its evolution might be studied. Although it does not guarantee a path out of the impasse of divergent modeling choices, growing attention to agential (or agent-like) phenomena across areas of biology (e.g., Arias Del Angel et al., 2020), as well as the centrality of agents and goals as working concepts in evolutionary biology (Okasha, 2018), suggest it may be a prerequisite. To circumscribe my remarks, I focus on a recently published book where these reflections are highly salient: *The Evolution of Agency* (Tomasello, 2022).

## Where Not to Begin

It might be tempting to think that the first step in the study of biological agency is to define clearly and unambiguously what it is. However, this is likely to immediately bring investigative efforts to a halt. There are many ways to construe agency that have been the subject of long discussions and no consensus definition currently exists (Schlosser, 2019). The nature of agency is controversial, and the concept is contested, like many others in the biological sciences (e.g., gene, species, homology). We can appreciate this by contemplating other areas of inquiry where we know better from experience. For example, who would argue that we cannot study species and their evolution until we have clearly defined 'species'? Good work can be done without a consensus amid a healthy variety of species concepts that are extant in the discourse of evolutionary and population biology.

Despite the unproductivity of formulating a single consensus definition, there is certainly warrant for a *working characterization*. "Agency is thus not about all of the many and varied things that organisms do—from building anthills to caching nuts—but rather about *how* they do them. Individuals acting as agents direct and control their own actions" (Tomasello, 2022, p. 2). This characterization is helpful because it draws our attention to core components (what does it mean to "direct and control"? What counts as an "individual"?). A characterization such as this does not rule out other ways of formulating the concept of agency, such as via autonomy and organization (Moreno & Mossio, 2015), but it does help inquiry get started. What forms can "control" take? How might we measure them? In what systems would we do the measurements? What kinds of models of control should we deploy or modify? How do we undertake decisions of approximation, abstraction, and idealization in those models? "Scientists infer psychological agency when the organism acts flexibly towards its goal even in novel contexts" (Tomasello, 2022, p. 27). Maybe, but what counts as a goal? How do we understand their representation? (Tomasello holds that, for biological agents, "goals and reference values are internally represented as desired situations" [Tomasello, 2022, p. 36] and sees them as "off-line perceptions of the world—perceptually imagined situations" [Tomasello, 2022, p.38].) And what is a 'novel' or novel-enough context? A good working characterization prompts scientific work to answer these types of questions.

One impact of addressing these issues is the recognition that some existing efforts are focused elsewhere. "The scientific challenge is to identify the underlying psychological organization that makes such individual direction and control possible. Answering this challenge yields a kind of photographic negative of the usual picture in evolutionary psychology: backgrounding what is usually focused (the adaptive specialization of species) and focusing what is usually backgrounded (the agency of individuals)" (Tomasello, 2022, p. 2-3). Importantly, the point is not that evolutionary psychology cannot get at a notion of agency or that there is only one way to approach characterizing the relevant psychological organization of an individual. Rather, this framing concentrates our attention on the relevant unit of investigation (individual organisms rather than populations or species) and what our models should attempt to capture in this circumstance ("underlying psychological organization that makes such individual direction and control possible").

**Choosing an Investigative System**

The subtitle of Tomasello's book is *Behavioral Organization from Lizards to Humans*. This signals what investigative systems are taken to be pertinent, though the justification for that choice should be explicit. "To explain in the end specifically human agency—as I wish to do—we need an account that traces the evolutionary steps in agentive behavioral organization from creatures who make few and highly constrained decisions to creatures who quite often decide for themselves what to do" (Tomasello, 2022, p. 3). For some readers, this formulation might raise alarm bells. Isn't it inappropriately teleological to conceptualize humans as the apotheosis of some capacity like agency? More than 50 years ago, Hodos and Campbell (1969) stated this worry explicitly in their challenge to comparative psychology's unacknowledged use of a *scala naturae*: "The concept that all living animals can be arranged along a continuous "phylogenetic scale" with man at the top is inconsistent with contemporary views of animal evolution" (Hodos & Campbell, 1969, p. 337). However, this criticism presumes that there is a single conception of agency in view that is applicable to all taxa, and that the goal of Tomasello's inquiry is a general theory of biological agency and its evolution. Tomasello explicitly indicates that the latter is not his aim: "our question is how human agency evolved" (Tomasello, 2022, p. 22). His focus is on the evolutionary lineage of vertebrates that yields human agency. It could just as well have been the evolutionary lineage of vertebrates that produced "avian agency," or the invertebrate lineage of mollusks resulting in "cephalopod agency." "I will not be considering species that branched off from reptiles in nonhuman directions, some of whom display great intelligence and agency. …that is a story for someone else to tell" (Tomasello, 2022, p. 44). This is a form of lineage thinking that is perfectly respectable as far as it goes (Jenner, 2022) and does not presume a teleological orientation of

the evolutionary process to humans as the preeminent outcome.

Although Tomasello might escape the basic charge of relying on a scala naturae for his study of the evolution of biological agency, Hodos and Campbell raise another issue that hits closer to the mark. "Comparative psychologists have failed to distinguish between data obtained from living representatives of a common evolutionary lineage and data from animals which represent divergent lineages. …The rationale for such a study is based on the assumption that the living animals that have been selected are sufficiently similar to the ancestral forms that some inferences about the ancestral forms can be drawn" (Hodos & Campbell, 1969, p. 337; p. 342). Tomasello needs the former for his investigation, but his approach relies primarily on the latter. His systems of choice are *C. elegans*, lizards, squirrels, chimpanzees, and humans. A key motivation for these choices is the existence of experimental literature on how they forage or make decisions when rewarded with food (Tomasello, 2022, p. 137). "Three lines of experimental evidence support the proposal that squirrels and other mammals operate in this general way" (Tomasello, 2022, p. 53). However, there is no discussion of the difficulties associated with interpreting these and other experiments cited (e.g., Hanus & Call, 2011), or justification for anthropomorphic interpretations of animal behavior, especially those applied to non-primates.

It is not that data from animals that represent divergent lineages are uninformative; they can speak to general mechanisms related to agential capacities. And sometimes Tomasello seems interested in this: "a systematic theoretical account of the evolution of individual decision-making and behavioral control" (Tomasello, 2022, p. 6). However, they offer nothing specific to his primary explanatory target: "to reconstruct the evolutionary pathway to human psychological agency" (Tomasello, 2022, p. 9). More comparative phylogenetic effort is required to determine ancestral character states (Jenner, 2022, Ch. 10). Some confidence for this strategy emerges from how Tomasello conceptualizes the possibility space for the agential capacities that have evolved: "the general organizational architecture of agency comprises only a few basic types and they are highly conserved across related species …what we are concerned with here is the organization of mammals' most basic modes of psychological functioning… and that, by hypothesis, is generally similar across mammalian species" (Tomasello, 2022, p. 25; p. 44). Possibly, but not something that a methodology can presume at the outset.[1]

**Agency With Respect to What?**

If agency is characterized as having capacities of control over actions, then what actions are pertinent? Squirrels might need to scratch themselves when they itch, but this is unlikely to be an action that yields deep insight about the evolution of agency. More pertinent would be *evolutionary relevant* actions, those connected to survival and reproduction, such as eating and mating or staying alive and fostering offspring. Tomasello concentrates on how these actions involve forms of social interaction: eating other organisms, mating with conspecifics, escaping predators, and investing in progeny. Types of uncertainty with respect to the way others behave in these interactions encourage the evolution of agential control capacities.

As a consequence, one might think that studying the evolution of agency in the lineage leading up to humans would require being attentive to these different forms of social interaction. Interestingly, Tomasello concentrates almost uniformly on securing calories—from tracking prey to hunting in groups—and ignores dimensions of reproduction, whether mates or offspring. He holds that, "foraging ecology is key for the evolution of many cognitive skills" (Tomasello, 2022, p. 21). Ecological challenges in the form of unpredictability are defined in terms of foraging for food: "selection pressures leading to behavioral agency arise when a population of organisms moves into an ecological niche rife with unpredictabilities, for example, clever prey and predator species … early mammals had to deal with complexities created by enhanced competition with group mates for food and other resources" (Tomasello, 2022, p. 39; p. 44).[2]

The neglect of reproductive behaviors that involve social interactions is a critical oversight when studying the evolution of agency. Tomasello is engaged in a form of adaptive thinking rather than reverse engineering. Instead of starting with a trait

and ascertaining its function, he begins with an environmental test that must be met. "I start with the problem (ecological challenge) and attempt to determine—on the basis of empirical observations from behavioral experiments—what mechanisms might have been designed [evolutionarily] to solve it" (Tomasello, 2022, p. 13). However, foraging is not the primary environmental challenge faced by organisms. Tomasello holds that a "separate executive tier of psychological monitoring and control" evolved in early mammals, but the ecological challenges related to social interactions in foraging may not be the most relevant for fostering this evolutionary change. Further, it is much more plausible that simultaneously occurring ecological challenges related to social interaction in reproduction (especially offspring care), which require an executive tier to manage shifting between different types of ecological challenges dynamically (i.e., multiple problems), would select for additional executive control.[3] Since other vertebrates face this same dual ecological challenge (i.e., survival and reproduction), the most interesting factor to change substantively in early mammalian evolution may have been parenting rather than foraging (Broad et al., 2006). Similar concerns arise for claims about the origin of a new executive tier of behavioral control in primates (Tomasello, 2022, Ch. 5).

## Types of Models

A long tradition of inquiry into goal-directedness, especially prominent in cybernetics, emphasizes that the behavior of agents is persistent and plastic; agents act to achieve a goal, even under negative conditions or in the face of obstacles ('persistence') and these actions are flexible in what is done and when, even in response to unpredictable environmental changes ('plasticity') (Nagel, 1977). This tradition suggests that feedback control models should be the foundation for representing the behavior of agents, perhaps supplemented with decision-theoretic principles and organized in a nested fashion ('hierarchical modularity') to achieve executive function or higher order behavioral control. Tomasello adopts this modeling strategy throughout his analysis, but he goes one step further: "It is not just that a feedback control system happens to be a good model for generating flexibly intelligent agentive behavior; *it is the only type of model possible*" (Tomasello, 2022, p. 19). The claim is not an offhand remark and appears repeatedly: "pretty much the only organizational architecture used is feedback control organization … there are not so many other possibilities" (Tomasello, 2022, p. 122; p. 128).

It is not at all clear that this is the only type of model possible to try and capture capacities relevant to agentive behavior. Consider one alternative possibility: dynamical systems models (Brauer & Kribs, 2016). Although complementary in many ways to feedback control systems, this modeling approach is distinct. Importantly, these models can capture agent-like behavior in aggregates of interacting components or individuals, but without the same modeling requirements. (Both types of models also can represent behavior we might not want to call agentive—thermostats are well-modeled as feedback control systems but not typically thought of as agentive.) Tomasello notes that the three core elements of feedback models for behavior are a reference goal, some form of empirical sensing, and a mechanism for comparing empirical input and the reference goal that then guides behavioral decisions. Dynamical systems models need not have the first element; instead, through rules of component behavior determined by empirical input, they can yield behavioral flexibility (e.g., avian murmuration). Three core elements of dynamical systems models are a representation of the state of the system, its state-space depicting all possible system states that can obtain, and a state-transition function that describes system state-change over time (Busemeyer, 2006). Thus, in these models, present states of the system are dependent on past states of the system, though not in the form of learning and memory that we might associate with feedback control models. Similarly, dynamical systems models can represent persistence and plasticity. One can certainly argue about how well or with what precision these models represent and predict agent-like behavior, but these models are not somehow outside the realm of possibility for studying biological agency.

## Parting Thoughts

The aim of our discussion has been to reflect on

how to study agency and its evolution in living systems, in part as a prerequisite to entering the contested space of whether agency reorients standard evolutionary theorizing. We do not emerge from these reflections with a ruler for measuring the evolutionary significance of organismal agency or standards to ascertain whether it bridges explanatory gaps, even though Tomasello seems to take a side in these debates: "agentive action is not just an object of natural selection but also a causal force in the process of evolutionary change" (Tomasello, 2022, p. 41). However, our analysis has secured several salient footholds for ascending in this direction. The study of biological agency and its evolution should include an explicit working characterization that is empirically interrogated and recognize the possibility of different investigative projects oriented around distinct and potentially conflicting working characterizations (as seen in other areas of biology). Although it is legitimate to concentrate on how human agency emerged evolutionarily, lineage thinking does not excuse the difficult work required to select an investigative system from which to gather data. The justification for drawing data from extant animals that purport to represent an ancestral behavioral architecture cannot simply be the existence of experimental studies. Living representatives of the common evolutionary lineage in view are required; careful comparative methodology is a necessity.

Studies of the evolution of agency should take into consideration behavior relevant to both survival and reproduction. If foraging is singled out and parenting is ignored, then this should be flagged as an idealization because reproductive behavior and the uncertainty related to it are relevant for the control capacities being scrutinized. And if there are reasons to consider one as more important than the other, that rationale should be made explicit. Additionally, feedback control models are not the only device in the modeling toolkit for representing agential behavior that facilitates predicting, explaining, or manipulating it. Keeping in view the full array of resources available for studying agency directly addresses the concern about the existence of divergent modeling choices; any differences arising from these can be documented and analyzed.

Could we just give up on agency? Tomasello doesn't think so. "We may not need agency to explain the actions of Venus flytraps or bacteria, only the same energetic principles that only the same energetic principles that explain their growth, reproduction, and other life-sustaining functions. But to explain how organism behave flexibly and efficiently in novel environmental circumstances, we need a new behavioral principle" (Tomasello, 2022, p. 133). Maybe we do, and others seem to agree, at least in broad outline (Walsh, 2015). Yet unless we attend to the above considerations, it is likely that different approaches to modeling agential phenomenon in living systems will continue to yield divergent perspectives that seem justified from within each research tradition committed to conceptualizing these phenomena in their own distinct way. A better route forward would be interdisciplinary conversations where the diverse epistemic issues at stake are brought forward and evaluated to avoid simply talking past one another, and thereby potentially foster novel ways of studying the many dimensions of biological agency and their evolution.

## Notes

1. There also are blatant non-sequiturs. For example: "Just as only a few basic Bauplans for animals' bodies have survived the test of evolutionary time, so only a few basic Bauplans for behavior organizations have survived the test of evolutionary time" (Tomasello, 2022, p. 122). Apart from being a problematic inference (e.g., functional organization is typically thought to be more variable than structural organization), most comparative biologists recognize more than thirty Bauplans (not just a "few").

2. This is pervasive. "Extant great apes have retained their ancestral psychological adaptations for diverse and flexible foraging environments. However, at some point before the extant species diverged, there arose a new set of socioecological challenges, prompted by apes' growing predilection for fruits" (Tomasello, 2022, p. 70). "The initial step was early human individuals (before the emergence of *Homo sapiens*) coming to collaborate with one another in face-to-face interactions to pursue collaborative goals, especially in the context of foraging" (Tomasello, 2022, p. 91-2).

3. Tomasello recognizes this abstractly but does not contemplate it beyond foraging: "of special importance for issues of reflective cognitive control are situations in which a conflict exists between one goal and another" (Tomasello, 2022, p. 81).

## Bibliography


Arias Del Angel, J.A., Nanjundiah, V., Benítez, M., & Newman, S.A. (2020). Interplay of mesoscale physics and agent-like behaviors in the parallel evolution of aggregative multicellularity. *EvoDevo, 11*, 21. https://doi.org/10.1186/s13227-020-00165-8

Brauer, F., & Kribs, C. (2016). *Dynamical systems for biological modeling: An introduction*. Taylor & Francis.

Broad, K.D., Curley, J.P., & Keverne, E.B. (2006). Mother–infant bonding and the evolution of mammalian social relationships. *Philosophical Transactions of the Royal Society B: Biological Sciences 361*, 2199–2214. https://doi.org/10.1098/rstb.2006.1940

Busemeyer, J.R. (2006). Dynamical systems: Mathematics. In L. Nadel (Ed.), *Encyclopedia of cognitive science*. Wiley. https://doi.org/10.1002/0470018860.s00012

Hanus, D., & Call, J. (2011). Chimpanzee problem-solving: contrasting the use of causal and arbitrary cues. *Animal Cognition, 14*, 871–878. https://doi.org/10.1007/s10071-011-0421-6

Hodos, W., & Campbell, C. B. G. (1969). Scala naturae: Why there is no theory in comparative psychology. *Psychological Review, 76*, 337–350.

Jenner, R. (2022). *Ancestors in evolutionary biology: Linear thinking about branching trees*. Cambridge University Press.

Laland, K.N., Sterelny, K., Odling-Smee, J., Hoppitt, W., & Uller, T. (2011). Cause and effect in biology revisited: Is Mayr's proximate-ultimate dichotomy still useful? *Science, 334*, 1512–16. https://doi.org/10.1126/science.1210879

Laland, K.N., Uller, T., Feldman, M. W., Sterelny, K., Müller, G. B., Moczek, A., Jablonka, E., & Odling-Smee, J. (2015). The extended evolutionary synthesis: its structure, assumptions and predictions. *Proceedings of the Royal Society B: Biological Sciences, 282*, 20151019. https://doi.org/10.1098/rspb.2015.1019

Moreno, A., & Mossio, M. (2015). *Biological autonomy: A philosophical and theoretical enquiry*. Springer.

Nagel, E. (1977). Teleology revisited. *Journal of Philosophy, 74*, 261–279.

Okasha, S. (2018). *Agents and goals in evolution*. Oxford University Press.

Schlosser, M. (2019). Agency. In E. N. Zalta (Ed.), *The Stanford encyclopedia of philosophy*. https://plato.stanford.edu/archives/win2019/entries/agency/

Scott-Phillips, T. C., Laland, K. N., Shuker, D. M., Dickins, T. E., & West, S. A. (2014). The niche construction perspective: a critical appraisal. *Evolution, 68*, 1231–1243. https://doi.org/10.1111/evo.12332

Sultan, S. E., Moczek, A. P., & Walsh, D. (2022). Bridging the explanatory gaps: What can we learn from a biological agency perspective? *BioEssays, 44*, 2100185. https://doi.org/10.1002/bies.202100185

Tomasello, M. (2022). *The evolution of agency: Behavioral organization from lizards to humans*. MIT Press.

Walsh, D.M. (2015). *Organisms, agency, and evolution*. Cambridge University Press.