Looking for keys in model organisms: Interpreting and keying-up in basal cognition

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Abstract

In this article, I analyse what epistemic operations are involved in adopting novel model organisms in a given research field. To this end, I draw on the DEKI account of scientific representation, and extend it by introducing the notions of "interpretation-" and "key-sketches". These refer to the incomplete and heuristically-justified mappings between models and targets that are initially constructed while the model is being developed for a particular use. I substantiate this proposal by analysing three case studies coming from the emerging research area of basal cognition, where an established model organism is adopted for novel uses in the context of neuroscientific research.

1 INTRODUCTION

Contemporary life sciences are significantly shaped by the study of model organisms (for recent reviews see Ankeny and Leonelli 2020; Green 2024). Model organisms (henceforth, MOs) are non-human species which have been extensively studied across a range of biological phenomena with the hope of translating the results to "other organisms, particularly those that are in some way more complex than the original model, especially humans" (Ankeny and Leonelli 2020, p. 2). MOs have become a subject of philosophical interest in recent years, yet the current picture fails to capture the epistemic processes involved in establishing a novel model organism for a particular area of research.

In the course of the second half of the twentieth century, particular species of rats (*Rattus norvegicus*), mice (*Mus musculus*), monkeys (in particular, the genus *Macaca*), birds (e.g., *Gallus domesticus*), amphibians (e.g., *Xenopus laevis*), fish (e.g., *Danio rero*), invertebrates (e.g., *Caenorhabditis elegans*, *Drosophila melanogaster*), bacteria (*Eschierischia coli*, *Bacillus subtilis*), or plants (*Arabidopsis thaliana*), among others, have been selected, standardized (through selective breeding and inbreeding, and in some cases by direct genetic control) and thoroughly studied across a variety of biological subdisciplines. For example, *D. melanogaster* is commonly studied as a model of chromosomal crossover, and

the conclusions of such studies are extended to the whole group of sexually reproducing organisms. For rats, one of the most widely employed MO in biological research, some of its uses include studies of hippocampal activity during spatial navigation, extended to a number of other mammals, most importantly primates, or the genetic underpinnings of addiction, with results extended to humans (see Nelson 2013).

MOs have provided researchers not only with detailed understanding of their genotype, anatomy, development, etc., but also with specialized techniques for experimental intervention [e.g., optogenetics; see also Weber (2004), chapter 6]. MOs have achieved a special epistemic status also in virtue of the institutional infrastructure built around them, in particular the different databases that allow for a broad dissemination of results (both community databases and more formalized efforts such as The Arabidopsis Information Resource or databases of DNA sequencing produced as part of the Human Genome Project, see Ankeny and Leonelli 2020, p. 36).

Much of this translation from MOs to other organisms has been conceptualized by philosophers in terms of scientific representation. These accounts view "model" in the term "model organism" through the lens of philosophical accounts of theoretical models, including how they relate to targets. There are a number of philosophical accounts which attempt to evaluate and account for this putative representational status of model organisms. Most recently, the proponents of this view have focused on the DEKI account of scientific representation (see Ankeny and Leonelli 2020; Prieto and Fábregas-Tejeda 2025; Sartori 2023; for DEKI see Frigg and Nguyen 2020; Nguyen and Frigg 2022). This framework highlights key steps involved in the development of material models. DEKI is particularly useful for the study of model organisms as it explicitly aims to capture the role of model-target mismatches for model-based reasoning in science, which often escapes the alternative accounts of representation (such as the similarity (e.g., Giere 2004; Weisberg 2013) or isomorphism (e.g., French 2003; Van Fraassen 2008) views). Indeed, it is these mismatches—and the variety of epistemic practices they require from scientists—that will come to the fore in the case studies analysed later in the paper.

Nevertheless, the use of MOs involves a variety of other scientific practices: they are employed in the development of experimental tools (as a site for "preparative experimentation", see Weber 2004), as measurement tools (e.g., in toxicology, see Green 2024; though Sartori 2023, argues these uses do involve representational assumptions), or as specimens for a broader class of organisms (e.g., Currie and Levy 2019; Levy and Currie 2015; see also Bolker 2009). These uses have motivated some theoreticians to argue against the representational view, instead focusing on these instrumental uses (Weber 2014) or maintaining that MOs serve an epistemological function distinct from that of theoretical models (Currie and Levy 2019; Levy and Currie 2015).

While these debates have shaped the state-of-the-art discussion of model organisms in philosophy, for the purpose of this article it is enough to accept a more pluralist position, which would acknowledge both the instrumentalist uses Weber highlights, and the representational ones that are covered by Ankeny and Leonelli's account. I will focus on the latter, as they are particularly relevant for the case studies in section 3 and as such, I will work within the representational view of model organisms. In particular, in what follows I adopt the perspective embedded within the DEKI account of scientific representation, as mentioned above and described in greater detail in the following section.

The more epistemically-focused existing work centres practices involving *established* model organisms, and primarily addresses issues related to the justification of inferences drawn on the basis of model organism research and applied to other species or groups. This overlooks the fact that a number of related epistemic concerns appears already when a novel model organism is being introduced or adopted in a new area of research. In the current paper I want to focus on the epistemic practices involved in establishing a model organism as relevant to a particular set of questions. To this end, I will look at a number of cases drawn from the emerging research field of basal cognition. Basal cognition seeks to extend the standard focus of neuroscience by emphasizing the organisms with no nervous systems, or only a simple one (see Lyon et al. 2021). To analyse them, I will draw from the DEKI account of scientific representation which offers a useful formalism for highlighting key steps involved in the development of material models, and has been previously applied to model organisms (see Ankeny and Leonelli 2020; Sartori 2023; Prieto and Fábregas-Tejeda 2025). The emerging picture highlights the role of idealizations[1] involved in model organism research, and identifies widespread use of heuristic reasoning which escaped the attention of previous accounts.

The structure of the paper is following. In section 2 I offer a primer on the DEKI account of scientific representation, named so after the main components: denotation, exemplification, keying-up, and imputation. Concurrently I review the previous literature which used DEKI to account for the use of model organisms in biological research. In sections 3 and 4 I introduce and analyse three case studies of how model organisms are adapted to a novel domain, in this case basal cognition and neuroscience. Then, in section 5, I highlight the notions of "interpretation-" and "key-sketches" which emerge from that analysis and expand on the role of heuristics and idealizations in model organism research. I conclude in section 6 by highlighting the epistemic benefits of the proposed perspective.

2 DEKI ON MODEL ORGANISMS

The DEKI account (Frigg and Nguyen 2020; Nguyen and Frigg 2022) proposes four main components of scientific representations, which give it its name: denotation, exemplification, keying-up, and imputation. The framework has initially been applied to model organisms by Ankeny and Leonelli (most importantly in 2020), and their account was later on expanded by Sartori (2023). More recently, however, there's been an alternative interpretation offered by Prieto and Fábregas-Tejeda (2025), who differ in important respects from these previous attempts. However, the current paper is agnostic

1. For idealization, see Batterman (2009); Cartwright (1983); Jebeile and Kennedy (2015); Nowak (1980); Potochnik (2017); Weisberg (2007). For relation to abstraction, see Levy (2021); Portides (2021). For standardization, see Holmes et al. (2010). There are important epistemic distinctions between the three concepts, as exemplified in the cited papers. Nevertheless, all three involve a purposeful distortion of the target phenomena: either via direct introduction of falsehood (in the case of idealization), or exclusion of some of its elements (in abstraction, and in standardization) The latter is for instance the case in standardized experimental protocols, which aim to exclude diversity and variation inherent in the world. In all three, the distortion serves a positive representational function in scientific investigation. In this sense I will refer to the three operations together in various places throughout the paper. However, since the philosophical literature on the topic is extensive, I do not have the space to defend this view in detail.

with regard to main issues at hand in this debate, and for this reason I will attempt to synthesize these distinct positions into a coherent account, only marking the divergences in passing.

To give the overview of both the DEKI and its application to MOs, consider one of the standard case studies, the fruit fly (*Drosophila melanogaster*) used as a model in the study of chromosomal crossover during sexual reproduction. In this context, a specific interpretation function (I) is applied which allows the researchers to view some properties of the fly[2]—the biological processes involved in reproduction—as the mechanisms of chromosomal crossover (the domain Z). The actual, physical process of the exchange of genetic material (i.e., the properties the fly itself *instantiates*) is thus described in more abstract terms, as a particular "generalized conceptualization or theoretical description" (Prieto and Fábregas-Tejeda 2025, section 3.1) of the process, which constitutes the domain.[3] In terms of the DEKI, we take the fly to *exemplify* (more precisely, I-exemplify) features of that mechanism—and this exemplification is possible, as Sartori notes (2023, section 2.3) due to the large size of *Drosophila*'s chromosomes in salivary glands, which allowed for epistemic access to their properties early on in the history of genetics (see Levy and Currie 2015, for some historical notes on this case).

While the DEKI account is also useful for cases of targetless modelling, if a particular model does *denote* a *target*—as happens with the *D. melanogaster*, which is taken as a model for all sexually reproducing organisms—its use requires further epistemic steps. The exemplified features in such cases can be *imputed* to a target. This is done via a *key*, a crucial element, as the features of the model "rarely [...] hold directly in their target systems" (Frigg and Nguyen 2020, p. 174).

Keys can have a number of different forms. In some cases they are relatively simple. Identity keys connect strictly equivalent features of Z-models and targets. Conventional keys are used for instance in the standard way of depicting subway connections—e.g.,

2. Ankeny and Leonelli (2020) attribute the epistemic distinctiveness of model organisms to the fact that they have unique representational *scope*—in that they are models of a much larger group—and *target*—as models of "whole, intact organisms" (Ankeny and Leonelli 2020, section 6). Prieto and Fábregas-Tejeda (2025) strongly argue against the latter point, highlighting that this goes against a widespread practice of speaking about model organisms as models of a particular phenomenon, depending on a given research context. For this reason, these authors adopt a distinct view which sharply distinguishes the model from the model carrier. The "whole, intact organism" is the latter, but the model itself, and correspondingly, the representational target, is a (structured) set of features of some biological system, indexed to a particular research context (and interpreted within the domain). What this means is that in any representational use of a model organism, there is only a limited subset of relevant features in the model carrier which constitute the model—and in the system the model denotes, which constitute the target (these may include "whole-organism features", such as behaviours, as Prieto suggested in personal communication). While they succeed in accounting for some scientific practices involving model organisms, Sartori (2023, p. 11-12) also correctly notes that the "properties that a [model organism] exemplifies are usually inseparable, at least in a practical sense, from the rest of the [model organism]'s properties" and the epistemic advantage of the model organisms over some alternative models, such as organoids, hinges on the "holistic picture" they produce. While these are important considerations for understanding the epistemic status of MOs, they are not directly relevant to the goals of the current paper.

3. Sartori (2023, section 2.3) equates the domain with the genome (calling the *Drosophila* a genome-representation), which disregards the dynamic processes involved in chromosomal crossover, acknowledging only the end result. Prieto and Fábregas-Tejeda (Prieto and Fábregas-Tejeda 2025) more appropriately identify the domain in terms of chromosomal crossover (which results in the fly, in this particular context, being a chromosomal crossover-representation).

used in the London Underground. In that case, by convention the colours of individual lines map onto the distinct lines of the subway system, while the sequence of stops maps onto the sequence of stops of a given line. In science, conventional relations are at play in various methods which use colour coding of results (e.g., litmus papers). Simple mathematical keys include scaling keys, e.g., used to translate the distance on a map to the actual distance between the places. However, the keys can also be much more complex. For example, Frigg and Nguyen (2020, p. 175) consider an example of nonlinear transformation when a scale model of a ship is used to represent the forces that act on an actual ship at sea. They consider the resistance of the model ship when dragged through a tank. At the scale of the model, forces such as viscosity of the medium have a disproportionate effect compared to the target system, hence a more complex, nonlinear transformation is necessary. Other cases, e.g., in mechanics, involve limit keys (e.g., Nguyen and Frigg 2020). These associate mathematical limit values—which, by definition, cannot actually obtain—with their approximations as imputed to the target.

In the case of model organisms, the keys are regarded as split into two categories: *broad* and *local* (Sartori 2023, p. 5). For Ankeny and Leonelli (2020), the key "includes several factors such as principles (e.g., evolutionary conservation); the fit with other models such as simulations, diagrams, and mathematical models of development; and pragmatic factors such as the extent to which the objects chosen as models make the properties tractable and accessible" (Ankeny and Leonelli 2020, p. 27). As Sartori notes (2023, p. 5), this diverges significantly from the standard treatment of keys in DEKI, and essentially equates the key with the repertoire: a framework for a particular way of doing science, embedded in a conceptual, material, logistical, and institutional setting (Ankeny and Leonelli 2020, p. 40). Such a *broad* key loses the essential mapping component postulated in the DEKI. Hence, Sartori proposes to complement it with a *local* key, which precisely defines the mapping from exemplified features to the target, performing the primary role of the key within DEKI. However, in Sartori's account of model organisms, the local and broad keys supplement each other, scaffolding the justifications of factual correctness[4] of the model. Eventually, they should "reach a reflective equilibrium" (Sartori 2023, p. 11), but continue to serve different epistemic functions.

> An inference drawn from a representation is derivationally correct if the inferential steps that lead to the conclusion are correct with respect to the rules of the representation and only use premises that form part of the representation. The conclusion of an inference is factually correct if the conclusion is true of the representation's target.

While the first relies completely on the structure of the representation, including the interpretation and key, the latter requires going beyond the representation, e.g., studying the target phenomenon through experiment or observation. In the context of MOs, Sartori (2023) notes that also the repertoire can provide justification of the model's factual correctness, but that the local key is necessary for the justification of the derivations from model to target.

Some simple local keys in model organism research are at play when a dosage of a drug is adapted from an animal model, where it was tested, to humans, where it is to

4. Frigg and Nguyen (2022, p. 296) distinguish between "derivational" and "factual" correctness:

be used therapeutically (known as "human equivalent dose"). In such cases, an initial step of human testing of the substance is to translate the "no observed adverse effect level" dose from the animal to the human (as recommended e.g., by Food and Drug Administration 2005). This often can be simply done by multiplying the animal dose in mg/kg of body mass by a scaling factor—e.g., for rats, the dose is to be multiplied by 0.16 (see Food and Drug Administration 2005, Table 1). However, most uses of model organisms require more complex keys. For some such cases, Sartori (2023, p. 9) introduces the "functional identity key", which maps elements of mechanisms with the same overarching function in virtue of the identity of those elements contributions to the mechanism. For instance, Sartori argues that such a key is at play in the study of 3D organization of genome in *Drosophila* as translated to vertebrates. The largely different sets of architectural proteins in the two groups perform the same function (three-dimensional organization of the genome) and as such a functional identity key can be constructed to justify inferences between the model and the target (Sartori 2023, p. 9-10; see also Moretti, Stévant, and Ghavi-Helm 2020).

In the case of the fly as a chromosomal crossover-model, consider how the model was used to establish the "centromere effect", i.e., an inhibition of crossovers at and close to the centromere, the point where the two chromatids constituting the chromosome are linked (Beadle 1932). This effect was then identified in a number of other species, e.g., in humans (Ottolini et al. 2015). The inferences between the model (the fly) and the target (humans) are often implicit. For instance, Ottolini and colleagues note: "Centromeric crossovers interfere with segregation of sister chromatids in *Drosophila melanogaster* and budding yeast and are associated with an increased risk of aneuploidy in humans" (2015, p. 7, references removed). This draws a parallel between the known mechanism studied in the model and its likely consequence that is observed in humans. Since the description is relatively abstract, this can be taken as an identity key, where the identity of outcomes (abnormal number of chromosomes in a cell) is suggested to result from the same mechanism (the occurrence of centromeric crossovers resulting in the incorrect segregation of sister chromatids during cell division). If the description was offered on a more detailed level, the key would be better characterized as a functional identity key, as it is likely that the actual mechanism is different (e.g., involves homologous or analogous genes in different species).

3 CHOOSING AND KEYING-UP RESEARCH ORGANISMS

The model organism approach in biology has been extensively criticized by a number of authors. These criticisms highlight the limits of the study of biological systems via a relatively small set of highly modified, standardized, domesticated, lineages of a few species (e.g., Gilbert (2009); Bertile et al. (2023); see also Alfred and Baldwin (2015) and other articles in the collection Baldwin, King, and Alfred (2015); for criticisms in neuroscience see e.g., Manger (2008); Kaplan (2017); Keifer and Summers (2016)). Indeed, the case of *D. melanogaster* and its role as a model of the centromere effect usefully illustrates these limitations: while the effect is quite strong in *D. melanogaster*, a more recent study of closely related *Drosophila* species, *D. simulans* and *D. mauritiana*, indicated significantly greater rates of crossing over in central regions (see the review in Hawley et al. 2025). This interspecies variation is likely to have evolutionary consequences (Hawley

et al. 2025) and highlights the role of mechanisms which would not be identified through the study of only *D. melanogaster* (similarly in the case of crossover interference effects, when the occurrence of a crossover suppresses subsequent nearby crossovers, see the review in Housworth and Stahl 2003).[5]

There's a number of suggestions to alleviate the current situation: from increasing the diversity of studied model organisms, resigning from the ones that, we believe, are not "representative" (e.g., highly specialized), through considering the domestication and captivity effects by comparing laboratory and wild populations (but see Nemati 2024; Chrzanowska et al. 2025), to emphasizing the evolutionary and comparative considerations for justifying the inferences (e.g., Cisek 2019; Cisek and Hayden 2022; Cisek and Green 2024). These can impact how both broad and local keys are constructed and effectively offer a stronger foundation for inferences drawn on the basis of model organism research.

In fact, key construction is a complex process which "depends on a myriad of factors: the scientific discipline, the context, the aims, and purposes for which the model is used, the theoretical backdrop against which the model operates, etc." (Frigg and Nguyen 2020, p. 175). These factors are primarily associated with the repertoire, but through the mutual dependence between the broad and local keys, noted by Sartori [see above in section 2], some epistemic factors also contribute to the key construction. In the case of MOs, this process intersects in interesting ways with the selection of an appropriate organism for a particular research purpose [a topic discussed in detail by Dietrich et al. (2020); the criteria are summarized in Table 1; see also the social aspects analyzed by Lewis et al. (2013)].

To highlight this interdependence, consider the following three case studies drawn from the emerging basal cognition research tradition (e.g., Levin and Dennett 2020; Levin et al. 2021; Lyon 2020; Lyon et al. 2021). Basal cognition extends the standard subject of cognitive science and neuroscience to include the study of organisms with a limited or no nervous system. In what follows I look specifically at the studies focused on signalling across bacteria, plants, and developmental systems. Within the framework, signalling is suggested as one of the basic organizing principles underpinning cognition—and biological information processing more broadly (e.g., Lyon 2020)—with the most obvious example being neural signalling.[6]

5. At the time of writing this article, the change in the US NIH administration led to a move away from animal models. In a news release (NIH 2025a; published later in NIH 2025b), NIH announced that it intends to prioritize "human-based" technologies, listing "organoids, tissue chips, and other in vitro systems", "computational models" and "real-world data [of] health outcomes in humans at community and population levels." The news release cites "translational limitations" as the motivation of the move away from animal models, and couches the decision in the language of "innovation" and "cutting-edge technologies"—as clear from the selection of examples of proposed alternative research models. Nevertheless, at the time of writing, the decision has not been implemented directly in any policies and has resulted in several expressions of concerns, including from the Federation of American Societies for Experimental Biology (Garvy 2025).

6. Despite these far-reaching statements of the proponents of basal cognition framework, philosophical attention to the notion of signalling and communication, beyond animal behaviour, has been scarce. This topic is explored at length in Rorot (in preparation).

Table 1: Dietrich et al. 2020 analyze explicit methodological discussions in papers, as well as implicit choices made in the lab (based on field research of the authors) to derive a list of twenty criteria that guide the selection of a particular research organism, grouped into five more coarse-grained categories. These criteria are highly diverse, and encompass institutional, pragmatic, epistemic considerations, among others. The table presents the criteria briefly, as I draw on them in the analysis of case studies—full account can be found in Dietrich et al. 2020.

Cluster	Criteria
Access	Ease of supply; Phenomenal access; Ethical considerations
Tractability	Standardization; Viability and durability; Responsiveness; Availability of methods and techniques; Researcher risks
Resourcing	Previous use; Epistemic resources; Training resources; Informational resources
Economies	Institutional support; Financial considerations; Community support; Affective and cultural attributes
Promise	Applications; Comparative potential; Translational potential; Novelty

3.1 *Bacteria*

In 2003, the Nobel Prize in Chemistry has been awarded to Peter Agre and Roderick MacKinnon for "discoveries concerning channels in cell membranes" (Nobel Prize Outreach, nd[b]). MacKinnon, in particular, was awarded for "structural and mechanistic studies of ion channels."[7] MacKinnon's work has relied on analysis of bacterial potassium channels. His central achievement, which was the direct motivation for the Nobel prize, was uncovering the molecular basis of potassium conduction and the selectivity of ion channels in bacterium *Streptomyces lividans* (Doyle et al. 1998; see also MacKinnon 2004). However, the function of ion channels for bacteria has been uncovered only in 2015, in the work from Gürol M. Süel and his lab (Prindle et al. 2015). Süel's lab uses *Bacillus subtilis*, a widely accepted and extensively studied model organism (Barák 2021). For the undomesticated strain NISB3610 used in the experiments discussed here (Prindle et al. 2015), the complete genome sequence is available (Nye et al. 2017). The experiments of Süel and colleagues consisted of imaging the potassium signalling in growing biofilms using voltage indicator dyes. The experimental intervention focused on the availability of nutrients. Further, they recorded voltage directly with patch clamps, and compared the results with genetically modified bacteria, where the expression of the ion channel proteins was suppressed. Finally, they used mathematical modelling to establish whether the observed patterns of electrical activity can be attributed to the proposed potassium channel mechanism. Their results point out that ion channels in the biofilms conduct long-range electrical signals. These signals coordinate the metabolic states among cells of the biofilm, using a mechanism of positive feedback loop. Quite

7. The profile on the Nobel Prize website (Nobel Prize Outreach, nd[a]) cites this as the motivation for the prize and notes that "In 1998, using x-ray crystallography (that is, mapping molecule structures using the diffraction patterns that occur when x-rays pass through crystals), Roderick MacKinnon succeeded in demonstrating what a potassium ion channel looks like."

surprisingly, this positive feedback loop seems largely similar to the activity of ion channels in nerve cells (in fact, the relation between bacteria and brains is made explicitly on the Süel Lab website[8]).

The selection of bacteria for this study seems to depend on a number of factors (following the categorization in Table 1), from available resources and institutional reasons (the well-established role of bacteria in the study of ion channels), through their responsiveness, to the comparative and translational potential (established in previous work, and ultimately cemented with the Nobel Prize award to MacKinnon).

The authors begin key construction with a mapping already established in previous research. That key links the general mechanism of ion channels and the particular molecular make-up of potassium channels in bacteria to distinct ion channels expressed in various cells—most importantly in neurons—of other organisms. This is a functional identity key, which maps the same functions of ion channels (e.g., voltage gating) across organisms, regardless of different mechanistic underpinnings (different proteins used).

Uniquely, the extension of the key seems to be constructed in the opposite direction, at least as it applies to higher-level function, the role of biofilm-wide signalling. The inference is drawn from target to model, as an inverse key of sorts. Ion channels in nervous systems have long been understood to be involved in electrical signalling. Hence, Prindle and colleagues draw on this view of channel function, assuming that the functional identity of the underpinning mechanisms allows for the functional identity at a higher level of organization, i.e., that the channels in biofilms also enable long-distance information exchange. In doing so, they make a heuristic inference, following the heuristic of the localization of function [Wimsatt (2006); see also below in section 5]. If we assume structure-function correspondence, identifying analogous structures motivates the search for an analogous function–in this case, between the structure of ion channels in unicellular organisms and in neurons. Indeed, this extension of the key allows them to connect the results of their study to open issues in neuroscience:

> For example, the connection between neuronal signalling and metabolic activity (neurometabolism) is an active area of research. Furthermore, depletion of glutamate, the most common excitatory neurotransmitter, also forms the initial trigger for these collective metabolic oscillations synchronized by potassium. Therefore, it is intriguing to think not only about the structural similarities between bacterial and human potassium ion channels, but also their possible functional similarities with respect to long-range electrical communication. (Prindle et al. 2015, references removed)

3.2 *Plants*

At the beginning of the twenty-first century, a group of researchers began to call for the development of the field of "plant neurobiology" (Brenner et al. 2006). The point these authors underscore is the presence of systems for long-distance electrical signalling, of vesicle-mediated transport of auxin, a plant-growth hormone, in specialized vascular tissues (analogous to neurotransmitter transport), and production of chemicals "known

8. They state: "Our discoveries are revealing an unexpected functional link between microbiology and neuroscience," see https://suellab.github.io/research/.

to be neuronal in animals" (Brenner et al. 2006). This proposal was met with significant scepticism (Alpi et al. 2007; Kingsland and Taiz 2025; Mallatt et al. 2021), but persisted and later joined forces with the broader basal cognition research programme (e.g., Baluška and Levin 2016; Baluška and Mancuso 2021; see also Calvo, Raja, and Segundo-Ortin 2025).

One of the key points in the development of plant neurobiology have been the studies from František Baluška and his lab, which have argued that the vesicle-mediated transport of auxin in *Arabidopsis* and maize root apices (two standard MOs) bears important structural similarities to how neurotransmitters are transported in nervous systems (Schlicht et al. 2006; Mettbach et al. 2017). The studies reported in Schlicht et al. (2006) developed novel immunolocalization and visualization techniques (based on a novel antibody specific to a single hormone from the auxin class, indole-3-acetic acid), which allowed for discovering accumulation of auxin at the end-poles of root apex cells. They interpreted these results as indicating the limitations of a standard, chemiosmotic theory of auxin transport and support for the view that auxin is transported in a manner structurally similar to the neurotransmitters in the brain, and that the cellular end-poles can be conceptualized as "plant synapses" (Schlicht et al. 2006). Functionally, they take auxin vesicles to be involved in rapid (for plants) signalling, coordinating plant movements and tropisms, and integrating plant bodies (Mettbach et al. 2017; Baluška and Mancuso 2021)

The inference in this case follows similar patterns as in the case of bacterial biofilms discussed above, with the goal of establishing the link to neurobiology. Similarly to the case of bacteria, the inference begins with the structural similarities between the auxin-transport system in *Arabidopsis* root apices and the neurotransmitter vesicles in the nervous system. Notably, the neurotransmitters are well-studied and their dynamical and functional properties are established. Hence, the authors construct a tentative interpretation function (in the sense of DEKI), what I'll call an interpretation-sketch, based on those structural similarities, again following an inverse form of reasoning. The putative vesicle-mediated transport of auxin (note the criticism in Alpi et al. 2007, among others) is thus taken to follow the same dynamics as neurotransmitter vesicles do. This includes rapid export and uptake of auxin between cells. Based on these activity patterns, they are ascribed an analogous function to neurotransmitters in cell-to-cell communication. The interpretation function maps the dynamics between the different cellular systems. While not a functional identity per se, the interpretation connects some coarser-grained properties across the different organisms, analogously to how functional identity keys work. This step essentially proceeds from target to model, and concludes in establishing the *Arabidopsis* as a model of cell-to-cell communication, and eventually of information processing (which is the domain of interest for plant neurobiology and basal cognition alike).

Once *Arabidopsis* as an information processing-model is established, it is used in two ways. First, Baluška underscores that the presence of signalling mechanisms, and their structuring analogous to the ones in neural organisms, motivates applying a "cognitive lens" to plants (specifically, flowering plants, Baluška and Mancuso 2021). Hence, the fact that the model exemplifies some features of information processing is taken (through a realistic lens) as a novel piece of information about the model organism, and the group that is the standard target of that MO (flowering plants). Second, in the context of

neuroscience, the information processing domain is well-established. There is a number of different biological and artificial systems that are used as information processing-models of the nervous system. Effectively, showing that features of this domain can be exemplified by evolutionarily distant organisms (compared to standard models) has important consequences for other inferences drawn about nervous systems on the basis of information processing-models. Notably, in neuroscience these inferences use some standard functional identity (or similarity) keys, that are applied to various silicon-based or biological systems. For *Arabidopsis*, the evolutionary distance allows for identifying a basic, theoretical structure of the mechanisms of biological information processing, abstracting away from any peculiarities that may have arisen in the animal part of the tree of life, a feat of crucial importance to astrobiology, for example. Effectively, plants offer the most salient example of a system which allows for the direct study of patterns of difference across putatively cognitive systems. In a sense, "plant neurobiology" furnishes a novel set of boundary cases for neuroscience, in a way similar to how optimality modelling (e.g., Rice 2015), broadly used in mainstream neuroscience, does.

3.3 *Developmental systems*

Michael Levin and his lab, one of the hotbeds of basal cognition, study a variety of model organisms. Their work is highly rooted in developmental biology, and as such they use many systems derived from that field, primarily the frog *Xenopus laevis* and *Planaria* (see the Levin lab website[9]). Their perspective is based on the view of "morphogenetic systems as cognitive agents" (see the lab website[10]). This notion is embedded in the framework of "cognition all the way down" (Levin and Dennett 2020), which views biological systems as made up of agentic and cognitive parts—a notion that Levin has broadly explored (e.g., Levin 2019, 2022, 2023). Here I wish to focus on a particular set of experiments on *Planaria* (in particular, Oviedo et al. 2010; which uses the species *Dugesia japonica*, see also the review in Levin 2022).

Planarian flatworms are an important model organism for the study of development (with history stretching back to the research of Thomas Hunt Morgan). They exhibit astonishing regenerative capacities, as they can regenerate a whole body even from a thin slice (which fulfils the responsiveness criterion from Table 1, the reliability of responses to experimental manipulation). Genomes of several planarian species have been sequenced, and a variety of tools is available for working with them (fulfilling the criteria from the resources group, see Table 1). Levin lab experiments specifically target the understanding of morphogenesis, the process and mechanisms underlying the acquisition of shape. In experiments reported by Oviedo et al. (2010), the worms undergo an amputation where the tail, along with a portion of the body, is removed. They are then transiently submerged in a mixture of water with a gap junction blocker (octanol), and left to regenerate in normal water. During the regeneration, some animals are further submitted to a surgical procedure to disrupt ventral nerve cords. This treatment impacts the regular regeneration, and the worm achieves a significantly altered body plan, in many cases regenerating a second (or even a third) head, either protruding

9. https://drmichaellevin.org/resources/#question4
10. https://drmichaellevin.org/research/

from the side, or replacing the tail. These results indicate that morphogenesis does not rely directly on a genetically encoded body plan, but rather requires bioelectrical communication between the cells (altered by the gap junction blocker) and the inputs from the nervous system (in the presence of head post-amputation, signals through the ventral nerve cords can suppress the growth of an additional head, but the surgical procedure in the experiment further disrupts the anterior/posterior axis in regeneration). Further experiments (e.g., Durant et al. 2017) confirmed these results, and explored in greater detail the role of bioelectric signalling between the cells and its role for morphogenesis. Crucially the studies conducted by Levin and colleagues indicate that the modification of the body plan persists across multiple rounds of regeneration, without any further chemical intervention. They interpret these results as indicating that the body plan is at least partially stored by the pattern of bioelectric signalling which persists over a longer period.

These studies are used in two research contexts. More directly, they are embedded in the set of questions from developmental biology. In this context, the aim is to capture an important biological mechanism for the control of shape during development (morphogenesis). More importantly for current purposes, Levin explicitly connects this work also to the set of questions that guide basal cognition research. His research aims to illustrate the view of "cognition all the way down" by studying the behaviour of individual cells in an organism undergoing morphogenesis, and modelling them through "cognitive lens". In this context, similarly to the two case studies already discussed, individual cells in a developing (or regenerating) organism are interpreted as exemplifying information processing-properties. Levin's lab however, proceeds slightly differently than in the two cases already discussed. The interpretation in terms of information processing is justified on the basis of a direct intervention into a known mechanism. The existence of bioelectrical communication between cells has long been known, similarly to the fact that it's involved in developmental processes. What this research aims to highlight is the specific functional role of such cells, as well as its sensitivity to the specialized electrical communication circuit, i.e., the nervous system. The intervention highlights the extent of control that bioelectrical signals have. Standard conceptualizations of developmental processes consider the target morphology of the organism to be encoded or stored by individual cells (in their genetic code). This motivates an ascription of more complex information processing capacities to cells and the processes of bioelectrical signalling (potentially ascribing them some computational capacities, see Rorot 2022).

Such an interpretation allows, as in the case of plants, interpreting the developmental system as a model for basic principles of biological information processing, abstracting them from specializations likely to evolve along the different branches of the tree of life. But even more generally, this allows Levin and his collaborators to search for mechanisms underlying all flexible and adaptive behaviour. In doing so they construct an interesting tentative key, a key-sketch as I will call it, which identifies relevant units of analysis through their agentic behaviours, independently of the scale of organization at which they exhibit those behaviours. Once this identification is made (partially through stipulation, partially motivated by the experimental intervention), the relevant agentic entities are mapped onto one another. For instance, the activity of individual cells are mapped onto the activities of the organism as a whole. This allows for certain functional or organizational properties to be imputed between the different biological systems.

For instance, decentralized processing and storage of information is one such property, identified in the experiments on developmental systems, and then imputed to other biological systems, for instance memory (e.g., Colaço 2023; Colaço and Najenson 2024). As in the case of plant signalling, while these are not strictly functional ascriptions, they follow a similar pattern to Sartori's functional identity keys, in that the key maps coarser-grained properties that can be realized by different mechanisms across the model and target organisms.

4 MODELS, IDEALIZATIONS, AND ERRORS

The presence of heuristics and idealizations in scientific modelling has long been underscored in philosophical accounts of model use (Potochnik 2017; Weisberg 2007; Weisberg 2013; Wimsatt 2007; see also Cartwright 1983). MOs are no different in this regard. In the case of idealizations, this is recognized in the literature (e.g., Levy and Currie 2015; Sartori 2023), though these authors use this term more broadly than is currently accepted, essentially conflating idealizations with standardizations.[11] Nevertheless, MO-based inferences do involve introducing literal falsehoods and distortions, qualifying as genuine idealizations (e.g., Weisberg 2007). This can be seen quite explicitly in the case of *Drosophila melanogaster* as a model of neurodegenerative disease (e.g., Feany and Bender 2000). While *Drosophila* doesn't exhibit neurodegenerative disease in the wild, the symptoms can be induced by genetic tools intervening on analogous and homologous pathways to those hypothesized to be involved in the development of disease such as Parkinson's. This artificial insertion of symptoms is closely tied with important limitations of the model, such as the short lifespan of the fly which limits the development of the symptoms to early stages of neurodegeneration (see the overview in Vos and Klein 2021). Together, these limitations distort how the model exhibits the target phenomenon. Properly constructed keys take these distortions into account.[12]

Heuristic reasoning, on the other hand, has not been explicitly recognized as playing a role in MO-based research. Quite the opposite, a large chunk of philosophical study of MOs—including the work within the DEKI framework—has focused on the justifications of the inferences from MOs to targets. While this is an important issue for established MOs, the adoption of novel species in a given domain involves much "looser" inference schemas, as illustrated in the case studies.

Heuristics are cost-effective substitutions for truth-preserving algorithms, which do not guarantee correct outcomes. Compared to such exact inference schemas, heuristics offer significant improvements in complexity by transforming a problem into a "nonequivalent but intuitively related" one (Wimsatt 2007, p. 77). Crucially, the errors that heuristics introduce are not random, but systematically biased, and as such they can be scrutinized and (ideally) corrected, with their limitations and conditions of failure being predictable.

11. I owe this point to Guido Prieto, who pushed me to be clearer on this matter. See also footnote 1 on my view of the relation between idealization and standardization.

12. Note that this view would be more difficult to defend within the account of MOs that Prieto and Fábregas-Tejeda (2025) put forward, as they would simply consider the distortions as properties of the model carrier which fall outside the model itself. This move is blocked in the Ankeny, Leonelli, and Sartori interpretation which considers the whole organism as a model.

For model organisms, heuristics enable a construction of the key while the exact relation between model and target is not established, and the extent of distortions in the model is not known. In the case studies analysed here, the reductionist heuristic of localization plays (Wimsatt 2007, p. 82), embedded within the broader molecularization of life sciences (see Chadarevian and Kamminga 2003), plays the primary role. This heuristic assumes that an identified function is implemented by a localized structure or mechanism. In the case of biofilms and developmental systems, electrical signals are localized to activities of ion channels, and in the case of plants—chemical cellular communication to the vesicular containment of auxin. Crucially, in all three cases, it is difficult to justify the ascription of the function directly to the model organism. The structure, however, is known (except for the plant case, where structure is speculative too) and shared between model and target, justifying the inverse inference from target—where the functional ascriptions are commonly accepted—to model. This heuristic enables the construction of both interpretation function into the domain of information processing, and a key-sketch for imputing the properties of exemplified by the model to systems recognized as cognitive.

Importantly, viewing these reasoning schemas as heuristic enables tracing the (possible) errors and misrepresentations these models introduce. Wimsatt notes two particular risks of the localization heuristic: ignoring pleiotropy (multiple functions of a single structure) and division of labour ("missing other parts' roles in the hypothesized function because they are a part of the constant context, so they are always there to provide it," Wimsatt (2006), p. 470). Both of those limitations are visible in the case studies analysed above:

1. In terms of pleiotropy, in all cases the signalling or information transfer activity is regarded as separate from metabolism, despite their close functional coupling, especially in the bacterial biofilm case. This tracks the standard views of the nervous system. Tellingly, this metabolism-information processing discontinuity is considered as a key feature in the evolution of cognition by some theoreticians (e.g., the view of cognition as "meta-metabolic activity", see Godfrey-Smith 2016; Moreno, Umerez, and Ibañez 1997; Moreno and Etxeberria 2005; van Duijn, Keijzer, and Franken 2006). Nevertheless, there's a growing body of research which posits that information processing activity of neurons cannot be decoupled or analysed separately from their metabolism (e.g., Jacob, Ford, and Deacon 2023), especially in the case of cognitive impairment or neuropsychiatric disorders (see the review in Morella, Brambilla, and Morè 2022).[13]
2. In terms of division of labour, all three examples focus in the construction of a key-sketch on a subset of neural interactions—spiking activity of the neurons. While this is in line with the dominant view of the nervous system, the keys are constructed to the exclusion of a number of different elements that are increasingly recognized as contributing to nervous system's implementation of cognition, such as dendritic computations (London and Häusser 2005), ephaptic coupling (Anastassiou et al. 2011; Han et al. 2018), or neuron-glia interactions (Rangel-Gomez et al. 2024).

13. Bipolar personality disorder is particularly interesting in this regard (see Kasahara et al. 2006; Mertens et al. 2015) and relatedly impacts circadian rhythms (see McCarthy et al. 2016; McCarthy et al. 2022).

Despite its revolutionary potential, in its focus on reasoning motivated by the localization heuristic, basal cognition (at least in the three examples analysed here) follows the received (and relatively conservative) view of what kinds of mechanisms can process information. Indeed, localization is widespread in traditional neuroscience, where cognitive functions are commonly attributed to well-delineated structures (either anatomical or dynamically connected) in the brain. But already in this traditional context it's facing increased scrutiny (e.g., Noble et al. 2024; Westlin et al. 2023). While the flavour of localization in the basal context differs significantly, focusing primarily on a molecular (rather than anatomic) scale, it is still susceptible to the anti-reductionist arguments raised in that debate (e.g., Pessoa 2022). And regardless of one's views on the matter, it is important to keep track of the errors associated with structure-function localizations.

Importantly, the suggested heuristic perspective on the use of model organisms is not in conflict with the stricter character of justification that Sartori (2023) argues for (or that Levy and Currie consider, though differently, 2015). In classical parlance, the distinction between the two accounts can be cast in terms of the distinction between the context of discovery and the context of justification (traditionally associated with Reichenbach 1938; used here with all the now-standard caveats, see Melogno 2019). While Sartori highlights how scientists go about justifying the conclusions drawn from established research organism, within a stricter inferential framework, my suggestion here applies to the early stages of this research, when the organisms are first selected for a particular purpose. However, even in the context of justification, some heuristics remain at play, codified in the form of the local key that emerges from that initial, heuristic key-sketch.[14]

5 INTERPRETATION-SKETCHES AND KEY-SKETCHES

The DEKI is primarily geared towards capturing scientific representation, and aims to capture how we can reason about target phenomena on the basis of their models. In this sense the historical process of model development goes beyond the intended scope of the DEKI. Nevertheless, as I showed above, the framework offers tools for capturing the many epistemic operations involved in the development of novel models, though it requires some extensions.

The examples analysed here highlight that the development of novel models for a phenomenon often involves a number of heuristic steps. These steps are particularly relevant for establishing the relevant domain for the model, and for connecting it to the target. For clarity, I propose to distinguish interpretation-sketches and key-sketches from the interpretation function and key that are the central components of DEKI. In DEKI, the interpretation function composed with the key establishes the connection between model and target and allows to justify the correctness of the model.[15] Instead, the sketches are initial versions of the two mappings which do not justify model inferences.

14. This is true especially if one accepts some form of perspectival realism, see Massimi (2022); or, more radically, a view which emphasizes the indeterminate character of the world and notes how phenomena, scientific or otherwise, are co-constructed in the process of measurement, see Barad (2007); and Nemati (2024).

15. Note the distinction between "factual" and "derivational" correctness discussed in footnote 2. As I focus on local keys here, derivational correctness is of primary interest.

They are grounded in various heuristics that guide the development of the model and establish an initial relation to the target which allows for the model to be used as such.

This notion of "sketches" draws on the concept of a mechanism-sketch proposed by the neo-mechanist account of scientific explanation (Darden 2002; for mechanistic view of explanation, especially in the context of neuro- and cognitive science see Bechtel and Abrahamsen 2005; Craver 2007; Craver, Tabery, and Illari 2024; Machamer, Darden, and Craver 2000; Miłkowski 2013). Mechanism-sketches are incomplete representations of the target mechanism that specify only some of its features. Nevertheless, sketches already can provide some understanding of the target and constrain significantly further research.

The same applies to interpretation- and key-sketches suggested here. They are incomplete, possibly arbitrary mappings that lack sufficient empirical backing, and may contain some placeholders or be outright incorrect. Nevertheless, they serve an important role by allowing the construction, evaluation, and further tuning of the model. As visible in the examples discussed here, they can take forms analogous to complete keys, and if the model is accepted, they are filled in and eventually transformed into proper keys.

To flesh out the proposal, consider the interpretation- and key-sketches constructed in the three case studies considered. In the case of plants (section 3.2) and of developmental systems (section 3.3), there is an interpretation-sketch being developed. According to that sketch, the mechanistic and structural properties of the model organisms being introduced exemplify the properties of cell-to-cell communication (plants) and information processing (developmental systems). The mapping at this stage is relatively imprecise and heavily draws on analogical reasoning. In the case of the putative vesicular transfer of auxin, the structural properties of the vesicle are mapped to the features of neurotransmitter containers, and the dynamics are heuristically generalized based on the structure. The interpretation function in this case is relatively precise (compared to the next one), as the individual vesicle and the hormone molecule it transports are interpreted as an individual signal, with clearly delineated point of sending and reception, even though no clear function or meaning for these signals is suggested.[16]

In the case of planarian development, the mapping is partially based on experimental evidence, but the experimental intervention is interpreted as involving a change in the informational state of the cells undergoing morphogenesis. This informational interpretation itself is underdetermined by empirical data. Instead, it follows from a sort of "informational stance" (in the sense of Dennett (1998); see also Levin and Dennett (2020)). The mapping is much less precise than in the case of plants, as no clear information processing mechanisms are distinguished, the information is not quantified in any way, etc. Nevertheless, the suggestion that information about body plan is stored in the pattern of bioelectrical activity of the cells of regenerating organism is used as a basis for extending the parallel to neural processes, as discussed in the case study.

Finally, in the case of bacterial biofilms (section 3.1), the interpretation is already established and bacteria are commonly accepted as ion channel-models. Similarly, there is a standard key, mapping the structural properties and activities of individual ion

16. There is emerging evidence that even such low level biological signals are commonly ascribed semantic content by researchers, though in a significantly different way compared to more complex signals, such as involved in animal communication—see Rorot (in preparation).

channels, regardless of their exact biological makeup (e.g., the proteins their built of, what ions they transport). Yet, in the course of their study, Prindle and colleagues extend the existing key and propose a novel key-sketch. This considers the dynamical and functional properties of electrical interaction of multiple cells, mediated through the activities of their ion channels. The depolarization wave and the active propagation of the potassium signal observed in the experiments is mapped onto functionally analogous processes in the nervous system, and the role these processes play is equated. This key-sketch is perhaps the most complete one among the case studies analyzed, yet again—its construction occurs heuristically, as the analogies are identified based on the heuristic structure-function pairing. Further, this case can be seen as already providing some evaluation for the proposed sketch. In result, it is developed towards a proper key. The thorough experimental design, together with simulations, provides important justificatory foundations for the biofilm as a model of the nervous system.

All in all, the interpretation- and key-sketches differ from actual interpretation functions and keys primarily due to their incompleteness. They are constructed as mappings, but often involve significant handwaving and heuristic justifications, which are unable to ground models' (derivational) correctness as proper interpretations and keys do. Instead, they offer some initial epistemic purchase that can guide empirical research. Then, eventually, sketches are filled in or modified, and eventually can be regarded as proper interpretations and keys.

6 CONCLUSIONS

In the paper, I attempted to account for the epistemic operations involved in adopting a novel model organism in a field of research, focusing on the emerging research tradition of basal cognition. To this purpose, I have drawn from the DEKI account of scientific representation, which has been usefully applied to model organisms before. While DEKI is focused on established models, the framework it offers highlights the steps required for the introduction of a novel model.

In the case of model organisms, the introduction of novel models involves a number of heuristics, which justify the adoption of novel, tentative interpretation- and key-sketches. These sketches are incomplete but structurally resemble the full mappings from the model to the domain and from the domain to the target, which figure as main components of the DEKI account, and are necessary for establishing the correctness of the models.

The concept of interpretation- and key-sketches allows for a better understanding of the relation between the research conducted within the field of basal cognition and in neuroscience more broadly. While the basal cognition explicitly tries to expand the scope of neuroscientific research, one of the most serious criticisms it faces is its inability (so far) to produce results that are directly informative for neuroscientists.

While there is little philosophical analysis of the role of model organisms in neuroscience (the important exceptions are: Kaplan 2017; Nelson 2013, 2018), the field relies heavily on a very small subset of organisms, primarily mice (*Mus musculus*) and

rats (*Rattus norvegicus*)—and research carried out directly on humans (*Homo sapiens*).[17] This limits neuroscientific evidence base in important regards (see Keifer and Summers (2016)).

In this context, I propose to view the research carried out in basal cognition as providing novel model organisms for neuroscience, extending the diversity of available data, and eventually strengthening the methodologies of the neuroscientific use of model organisms (in the way argued for by Cisek and Hayden 2022). This introduces clear criteria for the adequacy and informativeness of MOs considered in basal cognition, and specifies how researchers working in other areas of neuroscience can directly benefit from the research carried out in that novel field. In that respect the debates over the proper definition of cognition, which tend to dominate the field, are not immediately relevant. The parallels between the models and targets can be constructed artificially, and the features may overlap only partially, while still providing important insights into the phenomena of interest. This is clearly visible, e.g., in the case of the use of *D. melanogaster* as a model for Parkinson's disease.

It is so in the three case studies analysed here. The reasoning patterns embedded in the interpretation- and key-sketches proposed by researchers enable us to see how the study of these simple model organisms can enhance our understanding of neuroscience, whether or not we are inclined to consider bacteria, plants, or individual metazoan cells as cognitive.

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17. Manger (2008) estimates up to 75% of research in neuroscience focuses on rats, mice or humans. That bibliographical study was significantly flawed, as it included any mention of the three species. Using these criteria, a search run on the PubMed database for the purpose of this article confirms the results: among the 2,369,514 articles returned by the search for "brain", 782,310 (ca. 33%) discuss rat and mouse brains (summed results of the searches for "rat AND brain" and "mouse AND brain"), and 1,418,842 (ca. 60%) discuss human brains (search for "human AND brain"), which suggests that the tendency Manger was pointing towards holds up since that article was published. The search was conducted on April 5, 2024.

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