

# Mathematical Modelling and Teleology in Biology

**Conference Paper****Author(s):**

Pérez-Escobar, José Antonio

**Publication date:**

2020

**Permanent link:**

<https://doi.org/10.3929/ethz-b-000387114>

**Rights / license:**

[In Copyright - Non-Commercial Use Permitted](#)

**Originally published in:**

Proceedings of the Canadian Society for History and Philosophy of Mathematics/ Société canadienne d'histoire et de philosophie des mathématiques, [https://doi.org/10.1007/978-3-030-31298-5\\_4](https://doi.org/10.1007/978-3-030-31298-5_4)

# Mathematical Modelling and Teleology in Biology

1  
2

José Antonio Pérez-Escobar

3

**Abstract** Mathematical modelling is a group of techniques which have been making their way into diverse biological fields. The incipient roles of these techniques in biology are transforming the scientific practice, and it is believed that the mathematization of biology is progressively putting it in line with the standards of rigor of the physical sciences. While the first statement is true, the second does not necessarily follow from it. In this paper, I will challenge the idea that mathematics brings biology closer to the standards of physics by showing how teleological notions, common in biology but not in today's physics, coexist and interact with modelling techniques in a very idiosyncratic scientific practice. To this end, I will explore modelling techniques of the so-called brain's internal compass, a component of the "brain GPS system," in computational neuroscience.

4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14

## 1 Introduction

15

Teleology (telos : end, goal, purpose ; logos : reason, explanation) is an explanatory strategy that appeals to the purpose of the object of study rather than its mechanical causes. Biology has traditionally incorporated not only mechanical explanations, but also teleological explanations. Yet, even modern biology, far away from vitalism (the metaphysical consideration that living beings are driven to purposes by an inner vital force) and intelligent design (teleology as the extension of God's intentions), still includes teleological notions in its explanations either as metaphysical propositions or at least as a heuristic strategy, acting "as if" biological phenomena were subjected to design or had purposes (Ratzsch 2010). It is because of these non-mechanical components in the explanations of biology that it has been proposed to be irreducible to strictly mechanistic sciences such as physics (Ayala 1968, 1999).

16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26

AQ1

---

J. A. Pérez-Escobar (✉)

Department of Humanities, Social and Political Sciences, ETH Zürich, Zürich, Switzerland  
e-mail: [Jose.perez@gess.ethz.ch](mailto:Jose.perez@gess.ethz.ch)

© Springer Nature Switzerland AG 2019

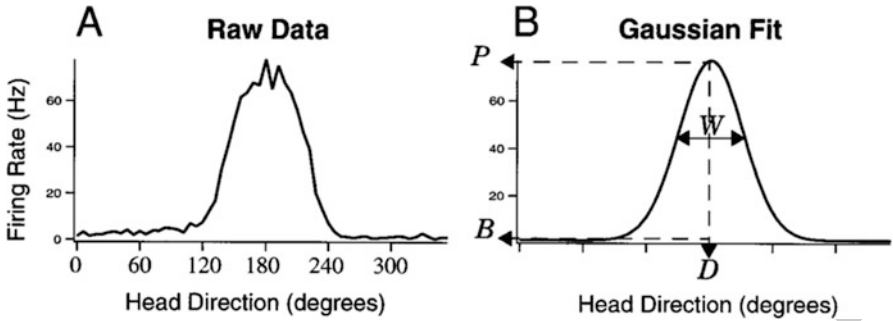
M. Zack, D. Schlimm (eds.), *Research in History and Philosophy of Mathematics*,  
Proceedings of the Canadian Society for History and Philosophy of Mathematics/  
Société canadienne d'histoire et de philosophie des mathématiques,  
[https://doi.org/10.1007/978-3-030-31298-5\\_4](https://doi.org/10.1007/978-3-030-31298-5_4)

It has been argued that the teleological component of biological explanations cannot be eliminated without loss of information and explanatory power (Ayala 1999). Therefore, it is not justified to do without it in order to render biology a strictly mechanical science. However, this has not deterred reductionist efforts. Yourgrau and Mandelstam (1955) claim that teleology is reflected in natural language, not in mathematical formulas. Indeed, formulas can describe the motion of the rock, but not its purpose. A popular idea among scientists and philosophers is that the more mathematical a science is, the more mature and rigorous it is (Storer 1967). Enquist and Stark (2007) fully endorse the development of a “quantitative, mechanistic and predictive biology” so that it becomes a “capital-S Science.” And indeed, biology has received mathematical methods with open arms in the last few decades. In this paper, I argue that the inclusion of mathematical methods in biology does not render it free from teleology. On the contrary, mathematical modelling interacts with teleological notions in the scientific practice and may even assist in anchoring teleological notions to physical phenomena. This, in turn, calls into question the role of mathematics as a central pillar for a project for the unification of the sciences.

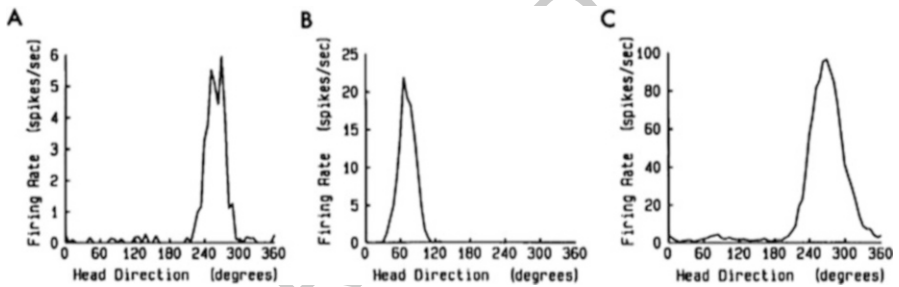
I will first offer a short overview of the so-called brain’s inner compass and its involvement in spatial computation and cognition. After that, I will discuss the research program around it and the roles of biophysical modelling, mathematical modelling and simulations, dedicating a section for each one. I will present the sections in that order, establishing a canonicity between them, and discussing how teleological notions are present at all points and lead the research process. Finally, I will discuss how the harmonical coexistence of different modalities of representation in the scientific practice may account for the preservation of teleological content in the later stages of the research program, its unproblematic conjunction with mechanical content, and the success of this hybrid strategy.

## 2 The Brain’s “Inner Compass”

The so-called inner compass is a key component of the “GPS system” of the brain, a system that has gathered massive attention from neuroscientists in the last few decades. The inner compass is comprised by cells which encode the angular direction that the organism faces. These cells, called “head-direction cells,” present a very characteristic pattern of activity : each of these cells has a “preferred direction,” so that when the organism faces that direction, the activity of the cell reaches its peak firing rate. The cell still responds to the direction faced by the organism when the angular distance from the former direction and the cell’s preferred direction is not bigger than  $45^\circ$ . Beyond an angular distance of  $45^\circ$ , the activity of the cell diffuses and becomes sparse. Moreover, the tuning of head-direction cells typically adjusts to a Gaussian distribution over their  $\sim 90^\circ$  response field (Fig. 1). The variability which head-direction cells (even samples of “representative” cells) express in this regard is illustrated in Fig. 2.



**Fig. 1** Parameters of the directional tuning function. (a) The tuning curve of a head-direction cell represents the cell's firing rate (Y-axis) as a function of a rat's directional heading in a horizontal plane (X-axis). The directional heading is plotted on a scale of 0–360. (b) To compute the parameters of the directional tuning function, a Gaussian function is fitted to the curve in (a). The mean of the Gaussian gives the cell's preferred firing direction,  $D$ ; the standard deviation of the Gaussian is equal to half of the cell's directional tuning width,  $W$ ; the peak height of the Gaussian gives the cell's peak directional firing rate,  $P$ ; the baseline of the Gaussian gives the cell's background firing rate,  $B$ . Taken from Blair et al. (1997)



**Fig. 2** Firing rate as a function of head direction for 3 representative cells from 3 different animals. Each plot is based on 8 min of recording, and head direction was analyzed with a 6° bin width. Note that the preferred direction and peak firing rate are different for each cell. (a) low-peak firing rate cell. (b) medium-peak firing rate cell. (c) high-peak firing rate cell. Taken from Taube et al. (1990a)

And, in spite of such variability, there is a well-defined concept of the “ideal” 68  
 head-direction cell against which all empirical observations are measured. But 69  
 where does this concept come from? What is a head-direction cell exactly then? 70  
 The discovery/creation dichotomy of objects of study is very controversial. Here, 71  
 several cells with similar electrophysiological characteristics are considered to 72  
 belong to a category, namely “head-direction cell,” represented by an object with 73  
 ideal characteristics. Such object, of course, is fictitious, but is appealed to in 74  
 order to classify neurons as “head-direction cell” or “not a head-direction cell.” 75  
 This is a relevant consideration in all forms of knowledge, but it is especially 76  
 important in electrophysiological studies, for two reasons. First, because the 77  
 recording of electrophysiological activity is a very indirect cell observation method 78

and classification procedures vary depending on the criteria of researchers and goals of studies. Normally, in order to be considered a head-direction cell, a given electrophysiological unit has to come “clean enough” out of the measuring procedure chosen, and provided that, then it has to meet more or less conservative criteria determining whether the activity of the unit resembles well enough that expected of an ideal head-direction cell. And second, because the construction of objects of study in biology often involves a second idealization in the form of a teleological judgment : a biological object is not just an ideal exemplar, but an ideal exemplar that serves an ideal purpose. In this sense, the “creation” of the biological object precedes actual observations, which operate under a lens of physical and teleological idealizations, and conditions further research.

Upon their “discovery” in 1990 (Taube et al. 1990a, b) and a previous short report in 1984 (Ranck 1984), the phenomenology of the electrophysiological characteristics of these cells and its correlation with the organism’s facing direction led to the consideration that they provide a sense of direction to the organism.<sup>1</sup> Such sense of direction would be a key element for spatial navigation, a critical ability of organisms for environmental adaptation. The early assignation of a role, function, or purpose to a biological object based on phenomenological characteristics and correlations is a common practice in the biological sciences, which guides and constrains critical aspects of the research process (for instance, what to look for and how to interpret whatever is found).

Just a year after the discovery of head-direction cells, McNaughton et al. (1991) considered a spatial navigation problem that animals typically encounter, and proposed different computational approaches that may lead to its resolution. The “geometrical solution,” although able to solve the spatial navigation problem, was promptly discarded in favor of the “compass solution,” among other reasons, due to its economy of storage : “it is the economy of storage that is one primary argument in favor of the compass solution, assuming such a mechanism is available” (McNaughton et al. 1991). Another reason why the “compass solution” was preferred was the existence of a candidate cell type which could be responsible for the computation. The mechanism underlying compass computation would, of course, be based on the head-direction cells—the neurobiological substrate for a sense of direction—discovered just one year before. Here has begun the teleologically-guided research process, where purpose precedes mechanism,<sup>2</sup> and where one finds

---

<sup>1</sup>In the neuroscience of cognition, the ascription of teleological content to the biological object is less straightforward than in other biological areas due to the abstract character of information processing and cognition, and therefore the process relies even more heavily on intuition. Usually, the teleological judgment is based on observations of physiological activity at the single-cell or network level, and on the behavior of the organism.

<sup>2</sup>This is not to say that the scientist explicitly commits to the metaphysical stance that the physical realization of the system is directed by purposiveness (although this may implicitly be the case), but that teleological intuitions in biological research guide the research process, including what is

explicit references to and inspiration from a *deliberately designed* artifact with a conferred purpose (a compass). 113  
114

### 3 Biophysical Modelling 115

In theoretical neuroscience, models usually have two aspects : a biophysical structure and a logico-mathematical representation. While the former represents the physical properties of the modelled system, the latter represents its abstract properties (such as information processing, Hebbian learning rules, or synaptic weights). 116  
117  
118  
119  
120

However, as I will show in an upcoming example, biophysical models may sacrifice physical likelihood in order to achieve a compromise between the representation of mechanical properties and accepted teleological notions. 121  
122  
123

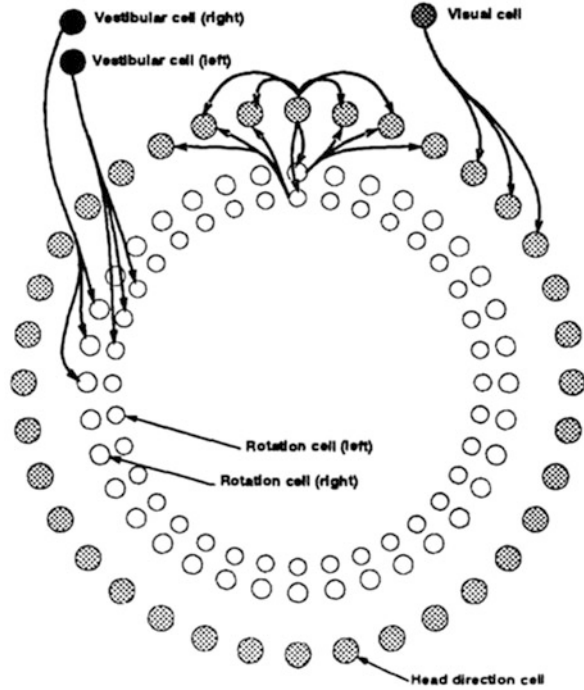
In 1995, Skaggs et al. (1995) put forward an influential biophysical model of the head-direction system based on the considerations of McNaughton et al. (Fig. 3). First, they arrange head-direction cells in a compass fashion as an illustration of their purpose (encoding facing direction), in a way that the position of a given cell in the ring matches its preferred angular direction. Second, if head-direction cells are performing spatial computations relative to angular direction, then these cells likely need information inputs from the visual and vestibular systems. The biophysical model in Skaggs et al. does just that integrating potential mechanisms of visual and vestibular inputs to the ring attractor arrangement of head-direction cells. 124  
125  
126  
127  
128  
129  
130  
131  
132

Note how the neuron at the top, the one whose preferred angular direction is being faced by the organism, is in turn exciting neighboring neurons, thus accounting for the observed activity of head-direction cells (responding at up to a 45° angular distance from their preferred direction). This is a mechanism proposed for their electrophysiological characteristics. However, visual and vestibular synaptic inputs, as well as clockwise and anti-clockwise rotation cells, are mechanisms proposed not only for their observed electrophysiological characteristics, but also for their assumed purpose : if such purpose was another, the proposed physical realization of the system could be very different. In addition, the ring attractor arrangement is also a compromise between the particular teleological notions with which the scientists work, and the unexhaustive physical characteristics known about the system. The model adapts to the physical and teleological characteristics of the cells, via a teleomechanical compromise : both the teleological notions and the mechanical information available constrain the possibilities of the model. 133  
134  
135  
136  
137  
138  
139  
140  
141  
142  
143  
144  
145  
146

---

simplicitly referred to as “to look for the mechanism.” The “mechanical commitment” of the neurosciences described by Kaplan (2011), thus depicts only part of the picture.

Fig. 3 Taken from Skaggs et al. (1995)



$$\tau \frac{dh_i^{HD}(t)}{dt} = -h_i^{HD}(t) + \frac{\phi_0}{C^{HD}} \sum_j (w_{ij}^{RC} - w^{INH}) r_j^{HD}(t) + I_i^V + \frac{\phi_1}{C^{HD \times ROT}} \sum_{jk} w_{ijk}^{ROT} r_j^{HD} r_k^{ROT},$$

Fig. 4 Taken from Stringer et al. (2002)

### 4 Mathematical Modelling

147

Inspired by the model proposed by Skaggs et al., Stringer et al. (2002) developed a mathematical model of the head-direction system. The model is as follows (Fig. 4)

The left-hand side of the equation represents the continuous activity of head-direction cell  $i$ . On the right-hand side of the equation, the first component is a decay term, the second describes the effects of the recurrent connections in the network,<sup>3</sup> the third stands for visual input to cell  $i$ , and the fourth represents connections

<sup>3</sup>  $\phi_0/C^{HD}$  stands for the overall strength of the recurrent inputs, so that  $C^{HD}$  is the number of inputs to one head-direction cell from other head-direction cells and  $\phi_0$  is a constant,  $w_{ij}^{RC}$  represents the excitatory synaptic weight from a given head-direction cell  $j$  to head-direction cell  $i$ ,  $w^{INH}$  is a constant which accounts for a global inhibitory effect of interneurons, and  $r_j^{HD}$  is the firing rate of head-direction cell  $j$ .

conveying idiothetic information (vestibular and proprioceptive information derived from motion that provides a sense of rotation) that accounts for rotations of the head-direction signal.<sup>4</sup> In the case of visual input amounting to 0, for example, in darkness, the idiothetic input can still account for the activation of the right head-direction cells when the organism changes its facing direction.

This model yields several general predictions. However, due to the limiting nature of the techniques available back then (mostly based on electrophysiological recordings and histological examination) and even still today (after adding techniques like optogenetics and advances in viral neuronal tracing and calcium imaging), an exhaustive quantitative and mechanical assessment of the model is unfeasible. What the mathematical model allows for, unlike the biophysical model, is to perform simulations, which can in fact be assessed quantitatively. Biophysical simulations cannot be performed due to technical limitations (it would require the synthesis of an artificial brain system). Mathematical models, on the other hand, provide a convenient solution by discarding the material aspect and preserving abstract relational structures of the systems. They can be used to perform quantitative simulations, although they cannot be assessed in terms of physical structure (not to mention the multiple realizability argument for computations). Second, such simulations can be contrasted quantitatively against the phenomenology of the original system (provided that an account of quantification of that phenomenology exists, like in the case of head-direction cell tuning). In this sense, the physical realization of the system takes a step back in importance.

The biophysical model is an iconic representation : the items and structure it depicts are intended to bear physical resemblance to the system it models. The mathematical model, on the other hand, is a symbolic representation : it bears no physical resemblance to the system it models, and its pairing to objects is supported by convention, or relies importantly on descriptions in natural language.<sup>5</sup> But no representation is exclusively iconic or symbolic (Goodman 1968 ; Klein 2003 ; Grosholz 2007), and the mathematical model is not completely emancipated from the iconicity of the biophysical model that precedes it. After all, the mathematical model is based on the biophysical model. It mathematically represents the same types of cells, the arrangement of inputs, and electrophysiological activity and implicitly assumes the same teleomechanical compromises. For instance, concerning inputs  $j$  to  $i$ , natural language is employed to clarify that “neurons that represent similar states of the agent in the physical world have strong connections.” That is, neurons that are situated nearby in the compass arrangement—which represent facing directions separated by small angular distances—are connected strongly. In addition, the ring structure is implicitly assumed by the introduction of rotation cells, and more evidently described in natural language, by specifying that these cells can be either “clockwise rotation cells” or “anti-clockwise rotation cells.” Moreover, the natural language surrounding the model in Stringer et al. shows teleological notions

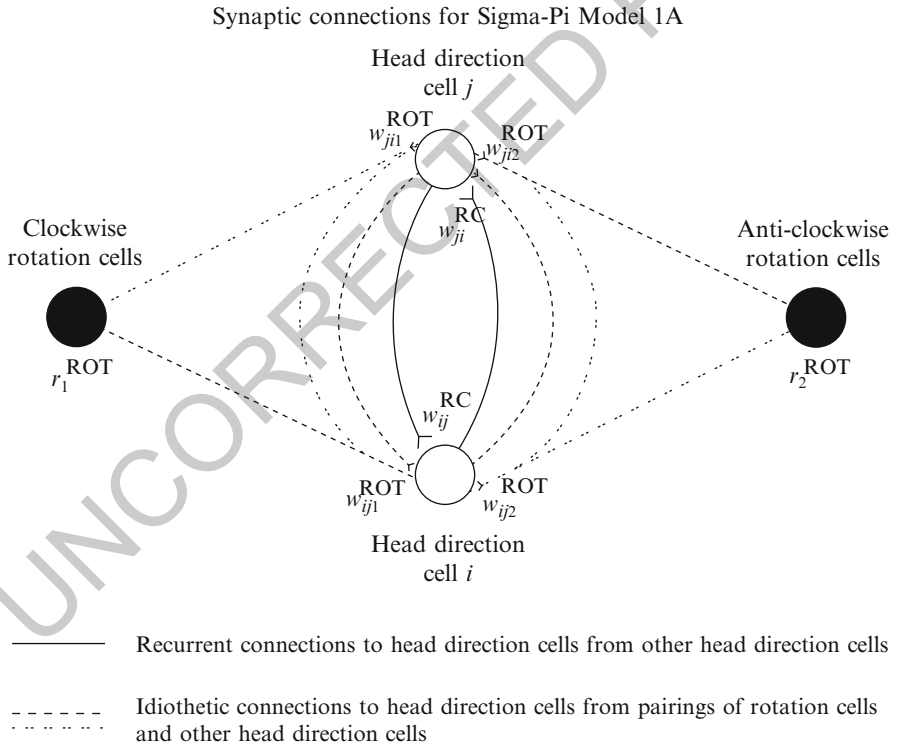
<sup>4</sup> $r_k^{\text{ROT}}$  is the firing rate of rotation cell  $k$  and  $w_{ijk}^{\text{ROT}}$  is the overall effective connection to head-direction cell  $i$ .

<sup>5</sup>This contrast of iconic representations against symbolic representations is due to Peirce (1885).



similar to those of Skaggs et al. : “Some neurons encode information about the orientation or position of an animal ( . . . ),” “A key challenge in these CANN models is how the bubble of neuronal firing representing one location in the continuous state space can be updated based on non-visual, idiothetic, cues to represent a new location in state space,” “These networks maintain a localized packet of neuronal activity representing the current state of the animal. We show how the synaptic connections in a one-dimensional continuous attractor network (of for example head direction cells) could be self organized ( . . . ).”

As we see, the mathematical model is partially emancipated from the biophysical model. Due to its symbolic character, it is emancipated enough to allow for simulations and quantitative predictions. However, it is due to its iconicity that it preserves many of the traits of the biophysical model, and therefore, the teleological precedence is still present at this stage of the research process. The process of emancipation is, however, continuous, and a middle step of the process is illustrated in Fig. 5, where both the iconic (cells, synapses) and symbolic (mathematical terms, natural language) are explicitly manifest.



**Fig. 5** Recurrent and idiothetic synaptic connections to head-direction cells in the sigma-pi model 1A. In this figure there is a single clockwise rotation cell with firing rate  $r_1^{ROT}$  and a single anti-clockwise rotation cell with firing rate  $r_2^{ROT}$ . In addition, the idiothetic synaptic weights from the clockwise and anti-clockwise rotation cells are denoted by  $w_{ij1}^{ROT}$  and  $w_{ij2}^{ROT}$ , respectively. Taken from Stringer et al. 2002

## 5 Simulations

212

We have seen before that the partial emancipation of the mathematical model 213 allows for simulations that can be assessed quantitatively. And indeed, this model 214 has been used to perform simulations, showing that several phenomena of head- 215 direction cells can be approximated quantitatively : subjecting an artificial agent 216 to clockwise and anti-clockwise rotations under these parameters, or having it 217 face different directions while stationary, yields an activity packet of the artificial 218 network similar to that observed in the brain's head-direction system. 219

How is this interpreted ? The quantitative assessment of the simulation indicates 220 that the proposed mechanism could account for a sense of angular direction. 221 This interpretation, however, relies on the initial teleological notion that such is 222 the purpose of head-direction cells, which directed the research process from the 223 beginning : the interpretation and quantification of the phenomenology of cells when 224 first discovered, the proposition of specific computational solutions to problems, the 225 arrangement of feasible physical implementations of such computations, and finally, 226 the elaboration of mathematical formulas and simulations that match quantitative 227 aspects of the phenomenology. Therefore, to the extent that mathematical models 228 and simulations turn out to be convincing, the initial teleological notions gain further 229 support in the later stages of research. 230

## 6 Mediation Between Modalities of Representation

231

So far, it has been shown how teleological content is present at all stages 232 of the research program, be it in form of intuition, or of models influenced by 233 such intuition. But how do teleological notions implicitly end up in a symbolic 234 representation like a mathematical model ? And how can teleological, material, and 235 formal content coexist in a single representation without turbulence, under control ? 236 A way to answer these questions is to analyze the relations between the different 237 modalities of representation at stake. 238

The first representations of teleological notions occur in natural language. 239 Natural language is particularly useful for explicit descriptions of teleological 240 content. For instance, after early observations of the phenomenology of a certain 241 type of cell, "the purpose of the head-direction cell system is to provide a sense of 242 angular direction" is a straightforward, early representation of a teleological notion 243 in natural language. 244

Later, we have iconic representations, which represent, among other types of 245 content, teleological content. But the iconic modality of representation is less 246 explicit and straightforward than the natural language representation, partly because 247 it represents several types of content, not only teleological. The amalgamation of 248 different types of content in a single representation is not necessarily a limitation of 249 the iconic modality, but rather, a useful aspect of it : it is the integration of different 250

content and the representative ambiguity that may account for part of the success of 251  
science and mathematics (Grosholz 2007, Chaps. 2–5). This applies to the way that 252  
molecules are iconically represented in chemistry (icons representing, and making 253  
compromises in the representation of, different types of content such as kinds and 254  
number of atoms, structure, particularity but also generality). The icon of a molecule 255  
must compromise explicitness and physical resemblance to accommodate all this 256  
information. For example, hydrogen atoms are not depicted but presupposed, and 257  
the physical structure of the icon must sacrifice physical faithfulness to be able to 258  
present somewhat clearly the components of the molecule (so that the translation of 259  
the icon to a formal representation, the Berzelian formula, is not too bothersome). 260  
Likewise, the iconic representation of the head-direction system is not completely 261  
faithful to its physical properties, since it has to accommodate more content than 262  
just that : Besides bearing certain physical resemblance, it facilitates the translation 263  
to a formal system (so it places emphasis on what are considered relevant aspects 264  
such as cells and synapses) and integrates teleological notions earlier represented 265  
by natural language (depiction of a ring attractor network reminiscent of compass- 266  
like circularity, hypothetical synapses conveying information critical for the role 267  
that head-direction cells are supposed to play, and a rotatory component), all at the 268  
expense of physical faithfulness. 269

In addition, the model does not substitute representations in natural language, 270  
but instead is presented together with natural language, which assists in the 271  
interpretation and includes clarifications on how the content of the iconic re- 272  
presentation (material, abstract relational, and teleological) is to be understood. 273  
This becomes evident just by looking at the presentation of the models discussed 274  
in this paper. However, the multifaceted and ambiguous character of the iconic 275  
representation demands more than just its coexistence with representations in 276  
natural language, which is not enough to control representative ambiguity. A certain 277  
tacit knowledge implicit in the scientific tradition and practices, and provided by 278  
apprenticeship and membership, is required. For instance, what is depicted in the 279  
iconic representation as a rotation cell is a compromise between physical structure 280  
(either as a proper cell or groups of cells and axons . . . ) and necessary function 281  
(the cognitive sense of direction must be subjected to angular rotations), and 282  
its interpretation varies depending on specific contexts and activities within the 283  
scientific practice : Neuroanatomical analyses focus on the physical facet (but do 284  
not completely disregard functional intuitions), while behavioral analyses prioritize 285  
cognitive functions (but the analysis is constrained to some degree by what is known 286  
about the physical). The translation of the iconic representation into a symbolic 287  
representation itself is another component of the scientific practice that is dependent 288  
on tacit knowledge. Even if presented amalgamated, different types of content from 289  
the iconic representation and natural language are carefully but unproblematically 290  
selected, rearranged, and transformed. Let us consider the rotation element again. 291  
Its mathematization in conjunction with the rest of elements in the equation is the 292  
result of a new, value-oriented integration of the physical, relational, and functional 293  
aspects : It is constrained by both notions of physical feasibility, like what kind of 294  
electrical activity is reasonable and what relations with other elements are likely, 295

and teleological notions, such as how the rotation element should modify the firing 296  
rate values of head-direction cells so that it contributes to the overall purpose of the 297  
head-direction system. 298

Finally, there are the symbolic/formal representations. According to Grosholz 299  
(2007, Chap. 3, p. 79), the symbolic modality of representation is more tolerant 300  
than the iconic modality regarding the kind of content it can represent. This is, in 301  
part, because the symbolic modality is not as constrained by physical resemblance 302  
(although it is not completely detached from it). And while the iconic modality is 303  
better at representing physical structure, the symbolic modality is more suitable 304  
for the representation of abstract relational structure. For this reason, symbolic 305  
representations can further sacrifice physical structure and make other content 306  
more explicit (relations between components) and, as we have already seen, enable 307  
important techniques (simulations), while at the same time preserving teleological 308  
notions in the form of necessary elements to account for the purpose ascribed 309  
to head-direction cells (idiothetic and visual input and a rotatory component that 310  
together modify the firing rate values of head-direction cells, account for compass- 311  
like dynamics and explain changes in the cognition of angular directionality). 312  
And while accomplishing those feats, inklings of the physical structure are still 313  
represented (the rotatory component preserves the compass-like circularity of the 314  
ring attractor arrangement, while synapses are represented in terms of abstract 315  
relations, forming a relational structure). The mathematical model is not only about 316  
quantities, but is part of the context of a scientific practice, a bigger picture where it 317  
acquires meaning from, and confers meaning to, other elements of the practice (for 318  
example, but not only, other representations). Yet again, and even if sometimes the 319  
mathematical model is regarded as a self-sufficient object, it does not substitute 320  
iconic representations or natural language, which help interpret the meaning of 321  
parameters and numerical values. And just like in the case of iconic representations, 322  
tacit knowledge must come into play to further control the ambiguity at issue. 323  
The mathematical model, even if conceived as an end product or the pinnacle of a 324  
research program, is a practice-embedded representation that enables techniques and 325  
unifies quantities and abstract relations with important intuitions of the scientists, in 326  
this particular case, structure and purpose. The symbolic representation is enacted 327  
by its ancillary iconicity and verbality and becomes defunct when regarded in 328  
isolation from its practical contingencies. 329

We have a scenario where natural language, iconic representations, and symbolic 330  
representations coexist not only in broad contexts like scientific practices, but also 331  
confined, simplified spaces like research papers. These representations, far from 332  
possessing univalent and straightforward meanings, include very different kinds of 333  
content, each important in its own way. Because they do not explicitly convey all the 334  
features of the phenomena they represent, but capture them only partially, they are 335  
ambiguous. Furthermore, the different representations in the practice are entangled 336  
with each other and cannot be dissolved without affecting their meanings and 337  
applications. Representational ambiguity, when controlled, is not faulty, but can help 338  
tackle the different aspects of heterogeneous and complex practices, like scientific 339  
practices. The harmonical coexistence of the different representations embedded 340

in the practice facilitated by the modulation of tacit knowledge and convention 341  
 keeps ambiguity under control. The representations involved in the case here 342  
 discussed, each of them multifaceted in their own way, enable the operativization 343  
 of multiple kinds of content (teleological intuitions, physical structure, abstract 344  
 relations, quantities). Under this practical harmony, the various representations 345  
 involved work their magic, gracefully wrapping up in the same package as diverse 346  
 and seemingly incompatible content as teleology and mechanisms. 347

## 7 Conclusion 348

Through the discussion of the brain's "inner compass" and the models here 349  
 presented, we have seen how the teleological notions that typically guide biological 350  
 research are present even when mathematical techniques are introduced. Instead 351  
 of merely depicting a plausible mechanism, the models hold on to the very same 352  
 teleological content to which researchers committed early in the research program. 353  
 Even more, mathematical modelling and computer simulations may further endorse 354  
 the use of teleological content as it becomes canonical in the research program.<sup>6</sup> 355

In the biological scientific practice, it is common to observe reality through a 356  
 teleological lens, which influences the process of constructing objects of study. 357  
 In the example discussed in this paper, we have seen how teleological notions 358  
 are present in all stages of the research program and precede new developments 359  
 in the chain of progress. This includes the stages where mathematical modelling 360  
 takes place. Mathematics is, therefore, compatible with teleology-based biological 361  
 scientific practice and is not a resource that will necessarily make biology a non- 362  
 teleological science. Its representative and justifying potential, often ambiguous, 363  
 multifaceted, and in interaction with iconicity and natural language, is far from 364  
 being limited to mechanisms, statistics, or abstract objects. And while mathematics 365  
 is ontologically tolerant in principle, it becomes ontologically insistent when 366  
 embedded in practices and surrounded by other representations. However, it remains 367  
 to be seen how much this ontological tolerance of mathematics can be stretched, as 368  
 it is currently under debate whether there are certain kinds of biologically relevant 369  
 content (such as historicity, organization, variation, and certain conceptions of 370  
 possibility and novelty) that current mathematics is unable to represent (see, for 371  
 example, Longo 2018 ; Montévil 2018 ; Montévil et al. 2016). 372

---

<sup>6</sup>Typically, in a research program, there is a teleological notion about a given biological phenomenon that stands dominant among alternatives, if there are alternatives. For example, regarding grid cells, it has been proposed that their function might be single-cell computation (and the feasibility of this has been backed by mathematical models as well) (Kropff and Treves 2008), but the canonical teleological notion is that they form a system that computes as a whole. In fact, "how the grid cell system processes spatial information" has been a source of inspiration for "actually designed" information processing neural networks (Banino et al. 2018), further blurring the line between "as if designed" and "actually designed."

## References

- Ayala, F. J. (1968). Biology as an autonomous science. *American Scientist*, 56(3), 207-221. 374
- Ayala, F. J. (1999). Adaptation and novelty : Teleological explanations in evolutionary biology. *History and Philosophy of the Life Sciences*, 21(1), 3-33. 375  
376
- Banino, A., Barry, C., Uria, B., Blundell, C., Lillicrap, T., Mirowski, P., . . . & Wayne, G. (2018). Vector-based navigation using grid-like representations in artificial agents. *Nature*, 557(7705), 429-433. 377  
378  
379
- Blair, H. T., Lipscomb, B. W., & Sharp, P. E. (1997). Anticipatory time intervals of head-direction cells in the anterior thalamus of the rat : Implications for path integration in the head-direction circuit. *Journal of Neurophysiology*, 78(1), 145-159. 380  
381  
382
- Enquist, B. J., & Stark, S. C. (2007). Follow Thompson's map to turn biology from a science into a Science. *Nature*, 446(7136), 611. 383  
384
- Goodman, N. (1968). *Languages of art : An approach to a theory of symbols*. Indianapolis, IN : Hackett publishing. 385  
386
- Grosholz, E. R. (2007). *Representation and productive ambiguity in mathematics and the sciences*. Oxford, UK : Oxford University Press. 387  
388
- Kaplan, D. M. (2011). Explanation and description in computational neuroscience. *Synthese*, 183(3), 339-373. 389  
390
- Klein, U. (2003). *Experiments, models, paper tools : Cultures of organic chemistry in the nineteenth century*. Palo Alto, CA : Stanford University Press. 391  
392
- Kropff, E., & Treves, A. (2008). The emergence of grid cells : Intelligent design or just adaptation ? *Hippocampus*, 18(12), 1256-1269. 393  
394
- Longo, G. (2018). How future depends on past and rare events in systems of life. *Foundations of Science*, 23(3), 443-474. 395  
396
- McNaughton, B. L., Chen, L. L., & Markus, E. J. (1991). "Dead reckoning," landmark learning, and the sense of direction : A neurophysiological and computational hypothesis. *Journal of Cognitive Neuroscience*, 3(2), 190-202. 397  
398  
399
- Montévil, M. (2018). A primer on mathematical modeling in the study of organisms and their parts. In M. Bizzarri (Ed.), *Conceptual and methodological challenges in systems biology* (pp. 41-55). New York, NY : Humana Press. 400  
401  
402
- Montévil, M., Mossio, M., Pocheville, A., & Longo, G. (2016). Theoretical principles for biology : Variation. *Progress in Biophysics and Molecular Biology*, 122(1), 36-50. 403  
404
- Peirce, C. S. (1885). On the algebra of logic : A contribution to the philosophy of notation. *American Journal of Mathematics*, 7(2), 180-196. 405  
406
- Ranck, J. B. (1984). Head direction cells in the deep layer of dorsal presubiculum in freely moving rats. *Society of Neuroscience Abstracts*, 10, 599. 407  
408
- Ratzsch, D. (2010). There is a place for intelligent design in the philosophy of biology : Intelligent design in (philosophy of) biology : Some legitimate roles. In F.J. Ayala & R. Arp (Eds.), *Contemporary debates in philosophy of biology* (pp. 343-363). Malden, MA : Wiley-Blackwell. 409  
410  
411
- Skaggs, W. E., Knierim, J. J., Kudrimoti, H. S., & McNaughton, B. L. (1995). A model of the neural basis of the rat's sense of direction. In G. Tesauro, D. S. Touretzky & T. K. Leen (Eds.), *Advances in neural information processing systems 7 : Proceedings of the 1994 conference* (pp. 173-180). Boston, MA : MIT Press. 412  
413  
414  
415
- Stringer, S. M., Trappenberg, T. P., Rolls, E. T., & Araujo, I. (2002). Self-organizing continuous attractor networks and path integration : One-dimensional models of head direction cells. *Network : Computation in Neural Systems*, 13(2), 217-242. 416  
417  
418
- Storer, N. W. (1967). The hard sciences and the soft : Some sociological observations. *Bulletin of the Medical Library Association*, 55(1), 75-84. 419  
420
- Taube, J. S., Muller, R. U., & Ranck, J. B. (1990a). Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *Journal of Neuroscience*, 10(2), 420-435. 421  
422  
423

- Taube, J. S., Muller, R. U., & Ranck, J. B. (1990b). Head-direction cells recorded from the 424  
postsubiculum in freely moving rats. II. Effects of environmental manipulations. *Journal of* 425  
*Neuroscience*, 10(2), 436-447. 426
- Yourgrau, W., & Mandelstam, S. (1955). *Variational principles in dynamics and quantum theory*. 427  
London, UK : Sir Isaac Pitman & Sons. 428

UNCORRECTED PROOF

## AUTHOR QUERIES

- AQ1. Please check and confirm if the affiliation is presented correctly.
- AQ2. Please check if edit made to Foonote 3 text “ $\varphi_0/C^{\text{HD}}$  stands for the overall strength of the recurrent inputs...” is fine.

UNCORRECTED PROOF