Mathematical Modelling and Teleology in Biology

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José Antonio Pérez-Escobar

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.

1 Introduction

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).

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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°. Beyond an angular distance of 45°, the activity of the cell diffuses and becomes sparse. Moreover, the tuning of head-direction cells typically adjusts to a Gaussian distribution over their ∼90° response field (Fig. 1). The variability which head-direction cells (even samples of "representative" cells) express in this regard is illustrated in Fig. 2.
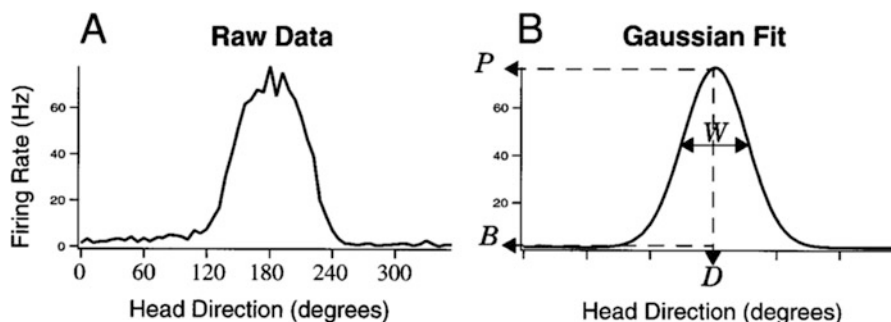
Fig. 1 Parameters of the directional tuning function. (**a**) The tuning curve of a head-direction cell represents the cell's firing rate (Y-axis) as a function of a rat's directional heading in a horizontal plane (X-axis). The directional heading is plotted on a scale of 0–360. (**b**) To compute the 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)
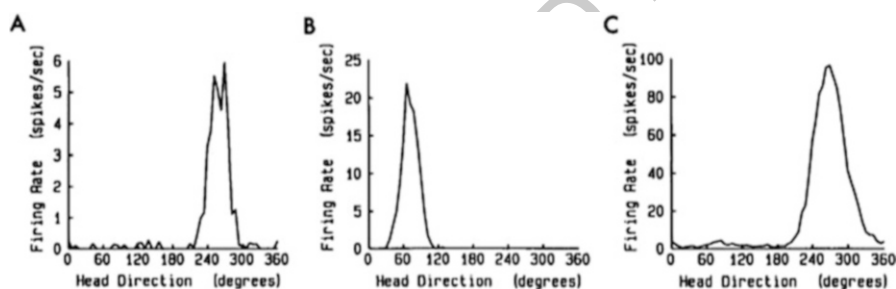

Fig. 2 Firing rate as a function of head direction for 3 representative cells from 3 different animals. Each plot is based on 8 min of recording, and head direction was analyzed with a 6" bin width. Note that the preferred direction and peak firing rate are different for each cell. (**a**) low-peak firing 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" head-direction cell against which all empirical observations are measured. But where does this concept come from? What is a head-direction cell exactly then? The discovery/creation dichotomy of objects of study is very controversial. Here, several cells with similar electrophysiological characteristics are considered to belong to a category, namely "head-direction cell," represented by an object with ideal characteristics. Such object, of course, is fictitious, but is appealed to in order to classify neurons as "head-direction cell" or "not a head-direction cell." This is a relevant consideration in all forms of knowledge, but it is especially important in electrophysiological studies, for two reasons. First, because the recording of electrophysiological activity is a very indirect cell observation method

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.[1] 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,[2] and where one finds

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[1]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.

[2]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
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3 Biophysical Modelling

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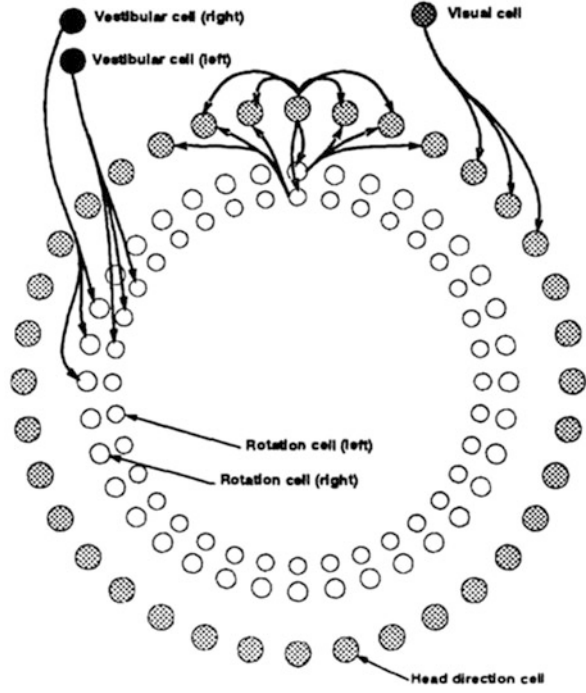
$$\tau \frac{dh_i^{HD}(t)}{dt} = -h_i^{HD}(t) + \frac{\phi_0}{C^{HD}} \sum_j (w_{ij}^{RC} - w^{INH}) r_j^{HD}(t) + I_i^V + \frac{\phi_1}{C^{HD \times ROT}} \sum_{jk} w_{ijk}^{ROT} r_j^{HD} r_k^{ROT},$$

Fig. 4 Taken from Stringer et al. ([2002](#))

4 Mathematical Modelling

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,[3] the third stands for visual input to cell i, and the fourth represents connections

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[3] φ_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 φ_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.[4] 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.[5] 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

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[4] $r_k{}^{ROT}$ is the firing rate of rotation cell k and $w_{ijk}{}^{ROT}$ is the overall effective connection to head-direction cell i.

[5] 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.
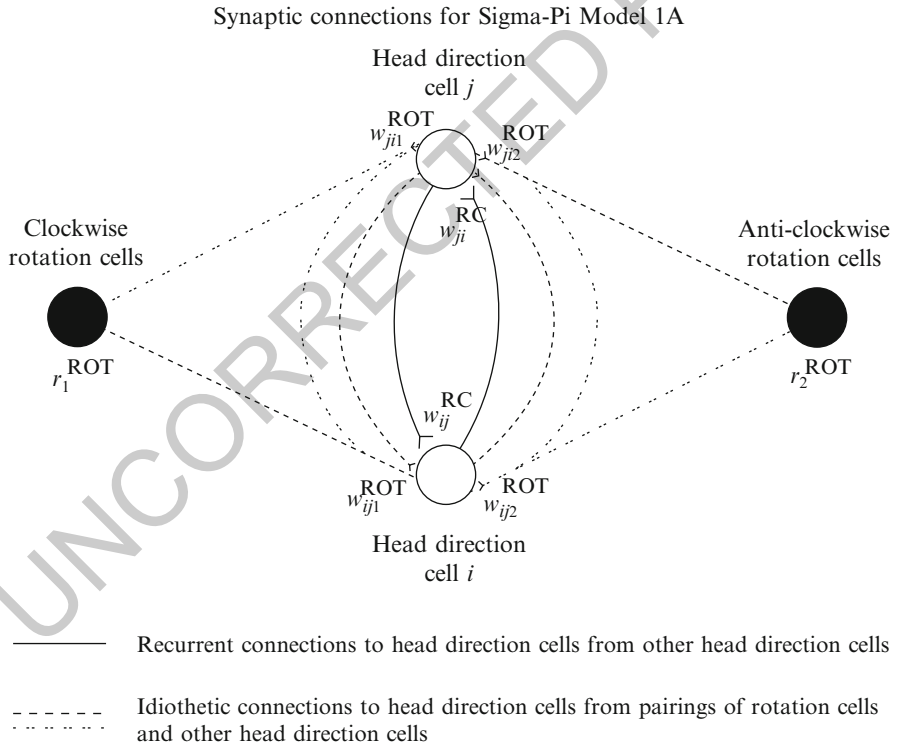
Fig. 5 Recurrent and idiothetic synaptic connections to head-direction cells in the sigma–pi model
1A. In this figure there is a single clockwise rotation cell with firing rate r_1^{ROT} and a single anti-
clockwise rotation cell with firing rate r_2^{ROT}. In addition, the idiothetic synaptic weights 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

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

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

6 Mediation Between Modalities of Representation

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

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

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

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

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

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

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

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

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.[6] 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

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[6]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."

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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.