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MAP THINKING ACROSS THE LIFE SCIENCES

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> The encyclopedic arrangement of our knowledge [...] is a kind of world map which is to show the principal countries, their position and their mutual dependence, the road that leads directly from one to the other.
>
> *Jean le Rond d'Alembert, 'Preliminary Discourse' (1751)*

This chapter supplements existing geospatial ontologies from the perspective of mapping practices of other disciplines. I draw on what I elsewhere call *map thinking*, namely,

> philosophical reflection concerning what standard geographic maps are and how they are made and used. The purpose of such contemplation is to explore the promises and limits of representations – cartographic and beyond. [...] Map thinking massages the imagination; excavates hidden assumptions; challenges and synthesizes dualisms; and invites us to reflect on space and time – including the future.
>
> *(Winther, 2020: 4–5)*

Map thinking is rich in rewards. The power and pervasiveness of traditional maps – of cartographic and GIS representations – will be familiar to readers of this volume. But map thinking in the natural sciences may not be, although it is highly prevalent across the life sciences.

The sciences are suffused with the rich traditions and practices of mapping and cartography (Robinson and Petchenik, 1976; Wood, 1992; Harley, 2001; Jacob, 2006; Brotton, 2018; Edney, 2019). Let us consider one form of map thinking: map analogizing. Maps and mapping have served as significant analogies for knowledge and representation at least since the eighteenth century in the Western tradition (see epigraph). The basic form of the map analogy is 'a scientific theory is a map of the world' (Winther, 2020: 35). This thesis is revelatory: imagining modeling and theorizing across the sciences as mapping projects illuminates some obscured but key features of scientific representation – its plurality, context-dependence, and purposiveness.

In order to fully capture the power of map analogizing, we must be more concrete. The charge of this chapter will be to first identify three map types, which I call *literal*, *causal*, and *extreme-scale*. While actual cartographic objects – that is, maps in the familiar sense – serve as the core inspiration for map thinking and the basic map analogy, I expand the meaning of

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maps and mapping considerably. Mapping in science also includes the making of various representations, sometimes dynamic, of processual networks or causal connections identified via statistics or experiments, and of the world after scaling it down or up in an extreme manner.

It is this panorama of map types, and the spaces that they chart, that I turn to in this chapter. For me, 'mapping is a communal and personal representational effort to imagine and control the different kinds of space of distinct map types' (Winther, 2020: 40). The three map types help shed light on representational processes in three life science projects that I have not previously explored: the evolution of Darwin's finches according to Peter and Rosemary Grant, Kurt Kohn's biochemical causal maps, and the extreme-scale gene expression maps of the Allen Human Brain Atlas. Map thinking these influential scientific research programs provides insight into their methods and purposes. It also helps us look differently at the cartographic object – the traditional map – itself.

Literal maps of Darwin's finches

Darwin's finches are an iconic case of evolution in action. The fifteen or so species differ in beak size and shape, and in feeding habits.[1] Islands are the ecological, evolutionary, and geospatial context. The cactus finch (*Geospiza scandens*), for instance, is a ground finch typically living in areas with the Galápagos 'prickly pear' cactus *Opuntia*, from which it feeds (flowers, fruits, and insects living on the cactus). In contrast, the woodpecker finch (*Camarhynchus pallidus*) amazingly uses a stick or cactus spine to pry out grubs and worms from trees. These species are adapted to unique lifestyles (cf. Lack, 1947: 146; Grant, 1981, 1986; Grant and Grant, 1989, 2002, 2008).

These birds take centre stage in David Lack's classic of evolutionary ecology, *Darwin's Finches*. This work notably established the birds' adaptive radiation, including a model of allopatric speciation (geographical separation). Of 27 figures in Lack's book, 13 (48%) are, or contain, what I will call *literal maps*. A literal map is a visual rendition with geospatial objects at geographic scales. Literal maps become scientific literal maps when they are used as a scientific representation and thereby assist in the scientific work of explanation, prediction, understanding, data organization, and so on. For example, a topographic map becomes a scientific literal map when deployed in a scientific project, such as an ecological or geological one (Winther, 2020: 38). In the biological sciences, literal scientific maps can include maps of ecosystems or of the distribution of particular species.

Lack's book starts with two maps of the Galápagos. The first situates the archipelago in the Pacific Ocean, labels Ecuador and Panama on the South American mainland, and outlines the 1,000-fathom line. The second, larger-scale map, names 13 of the islands both in English and Spanish. These maps ground Lack's discussions of the distribution, variability, and phylogeny of Darwin's finches, and of the evolutionary processes of their specialization, speciation, and adaptive radiation.[2] These scientific literal maps provide a pragmatic context for Lack's evolutionary theorizing. They are the means with which narratives of evolutionary speciation are told.

Literal maps themselves can also serve as abstract theoretical models. Here again Darwin's finches are a useful case study. For instance, literal maps play an especially central role in Peter Grant's efforts to articulate a model of allopatric speciation.[3] Grant's theory or model of allopatric speciation consists of the following five steps (Grant, 1986: 264–265; cf. a similar four-step model in Grant, 1981: 654–655):

1 *Founding.* Speciation starts with a founder population from the mainland colonizing an island (e.g., San Cristóbal);

2 *Cross-Island Migration*. New populations migrate repeatedly across various islands; populations change due to natural selection, and individuals become adapted to local conditions on each island;
3 *Sympatric Reproductive Isolation and Full Speciation*. Eventually a transmuted population meets the original founder population, with which it does not generally interbreed; speciation occurs fully as reproductive isolation and ecological differentiation of the transmuted and original populations are fine-tuned in sympatry;
4 *Further Migration*. Populations of the new species undergo analogous specialization and adaptation through repeated dispersal (analogous to 2);
5 *Further Speciation*. New species that had evolved in (2)–(3) meet after (4), and the same process of reproductive isolation and ecological differentiation promotes further speciation and multi-species adaptive radiation (analogous to 3).

A map of the Galápagos (Figure 45.1) represents the circular, cross-island movement starting with founding (step 1), by a small immigrant population, on the island of San Cristóbal. Subsequently, there were three cross-island migrations (step 2) from San Cristóbal to, successively, Española, Floreana, and Santa Cruz. A small number of individuals from the derived

Figure 45.1 Galápagos map embedding the first three steps of the five-step theory or model of allopatric speciation, printed in different permutations in Grant (1981, 1986, 2008), Grant and Grant (2002) (e.g., speciating finches get smaller in 2002 and bigger in 2008). Redrawn for clarity and geospatial precision by Mats Wedin. (Republished with permission of Princeton University Press, from *Ecology and Evolution of Darwin's Finches* (Princeton Science Library Edition), Grant, PR. (p. 264), figure 74 (2017; originally published in 1986); permission conveyed through Copyright Clearance Center Inc.)

populations on Santa Cruz then migrated back to San Cristóbal in step 3. Regarding the last two stages, Grant contends: 'The cycle of events was repeated many times, each involving an allopatric phase (step 4) and a secondary contact phase (step 5), and resulting in the formation of 13 species, possibly more' (Grant, 1986/2017: 264). Grant's map-based model of adaptive radiation via allopatric speciation depicts an evolutionary machine for churning out new finch species.

The literal map of Figure 45.1 and its attendant model also comprise a *causal* map, which illustrates the evolutionary and ecological processes of migration, local adaptation, and competitive exclusion among nearly related varieties or species. The basic five-step model shown for four islands could even be extended via, for instance, the branching and iterative colonization of distinct sets of islands and the associated multiplication of speciation cycles.

In their impressive book from 2008, Peter and Rosemary Grant reprinted a more visually compelling version of the literal and causal map from 1986 (Grant and Grant, 2002: 134, figure 4), representing the theory of allopatric speciation 'as a model, which is an abstraction designed to capture the essence of speciation from a mass of particulars' (Grant and Grant, 2008: 28). The map model plays an epistemic role in the three 'stages' of adaptive radiation that they classify. Here Darwin's finches are only at the first stage, and the third stage is radiation leading to differences among major branches of the tree of life (Grant and Grant, 2008: 153–160). For instance, the evolution of genetic incompatibilities occurs 'in sympatry at step 3 of the map model' (Grant, 2015: pers. comm). Although only five of 89 figures and colour plates in Grant and Grant's (2008) book are maps (i.e., figures 1.1, 2.2, 3.1, 5.3, and 11.2), geospatial information is contained in many of the non-map figures.

Ecology texts are still replete with species maps serving as literal maps, sometimes doubling as causal maps, even if other representations such as mathematical graphs and data charts are more common today than in the mid-twentieth century. Just a cursory glance at one standard ecology textbook, (i.e., Begon *et al.*, 2006), indicates the ongoing liberal use of maps. In this example, of the 21 figures in Chapter 1, nine (43%) are geographic (or near-geographic) literal maps, or contain such maps in them. Future qualitative and quantitative study could track the variety of purposes to which the cartographic object is put in ecology by exploring its varied uses in ecological textbooks, professional books, and articles. A historical perspective would track changes in the relative frequency of species or ecosystem maps over time, compared to other visual representations.

Geospatial imagination and visualization practices suffuse ecological and evolutionary theories and visualizations. Considering how and why this occurs could clarify the purposes of cartographic practices themselves, including the explicit representation of dynamic, causal processes.

Causal maps of biochemistry

Biochemistry is important to emergent interdisciplinary fields such as biomedicine, systems biology, and synthetic biology. Causal maps of biochemical reactions are typically 'topologically accurate in the same sense as the London Underground map is' (Winther, 2020: 39). Space is highly abstracted, with key objects (molecular agents) represented via symbols and spatial organization. According to Kurt Kohn of the National Cancer Institute in Bethesda, Maryland, USA, the plane of graphical space is a convenient organizer of reaction sets into functional classes (e.g., replication, transcription, or cell cycle control).[4]

Consider also the 'biochemical pathway maps' adorning the walls of many labs, which were first produced by the Swiss pharmaceutical company Roche in 1965.[5] These graphics render key biochemical reactions among molecular agents on a large causal map. Reactants such as the

sugar glycogen or the lipid cholesterol are represented with nodes. Arrows denote various types of reaction, including covalent modification, non-covalent binding, and enzymatic stimulation.

Although the graphical plane of such biochemical causal maps often contains some elements of extreme-scale maps (e.g., the cell membrane), it is much more concerned with the topology and temporality of causal relations – representing which reactants, catalysts, and so forth give rise to which products, under which conditions. Such graphical depictions of causal networks are valuable for experimenting and modeling in the molecular life sciences.

Specialist biochemical research relies heavily upon map thinking for understanding biological processes. In characterizing gene regulatory networks, for instance, Douglas Erwin and Eric Davidson examine the complexities involved in genes taking input from and regulating one another, concluding that 'the total map of their interactions has the form of a network' (Erwin and Davidson, 2009: 142). Or consider some relevant articles titles: 'toward a protein-protein interaction map of the budding yeast' (Ito *et al.*, 2000); 'detailed map of a cis-regulatory input function' (Setty *et al.*, 2003); 'a map of the interactome network of the metazoan *C. elegans*' (Li *et al.*, 2004); and others (Collins and Barker, 2007; Cui *et al.*, 2007; Zhao *et al.*, 202

Biochemistry maps are more concerned with representing causal influence than physical structure. Proximity on these maps thus tends to represent causation, at least when an arrow or some other causal indicator is present. As with all other abstractions, *the (causal) map is not the reality*. The threat of pernicious reification looms in concretizing abstractions (Winther, 2020: 90–94).

Molecular interaction maps (MIMs)

Consider molecular interaction map (MIM) methodology, a visualization tool for representing molecular interactions among proteins developed by Kurt Kohn and collaborators (e.g., Kohn, 1998, 1999, 2001; Kohn *et al.*, 2004, 2006). MIMs have achieved some market penetration in systems and synthetic biology.[6] Let us consider three broad classes of pragmatic features of Kohn's MIM visualization tool: (i) *desiderata*, (ii) *purposes*, and (iii) *conventions*.

Desiderata (or desired features) of MIMs include (i) a unique, singular, and unambiguous depiction of each molecular kind (Kohn, 1998: 1065–1066, 1999: 2704; Kohn *et al.*, 2006: 11); (ii) a clear network topology (Kohn, 1998: 1066); (iii) extensible notation for multimolecular complexes (Kohn, 1999: 2704, 2001: 86); (iv) reliable map coordinates (visual MIM or interaction number (electronic MIM) for location and identification purposes (Kohn, 2001: 84; Kohn *et al.*, 2006: 10–11); and (v) general and abstract single diagrams capturing cellular and molecular types and states (Kohn, 2001: 84; Kohn *et al.*, 2006: 10–11). MIMs should be as explicit as possible.

Purposes or outcomes of MIMs include (i) translating MIM diagrams 'into an input file for computer simulation' (Kohn *et al.*, 2006: 10, citing Kohn, 1998, 2001; Kohn *et al.*, 2004); (ii) suggesting novel experimental questions or empirical interpretations (Kohn, 1998: 1066, 1999: 2703, 2001: 84, 88); (iii) 'impos[ing] a discipline of logic and critique' (Kohn, 1999: 2703); and (iv) understanding how 'biological effects' emerge from 'molecular interactions' (Kohn, 1999: 2707).

MIMs require visual conventions. Basic *objects* such as 'elementary molecular species' – including proteins, protein domains, or DNA promoter sites – are depicted in call boxes (Kohn *et al.*, 2006: 3, figure 2). Basic *processes* such as covalent modification or inhibition are represented with various kinds of arrows (Kohn, 2001: 85, figure 1; Kohn *et al.*, 2006: 3–4, figures 3 and 4). Bertin's map, discussed below, also differentiates objects (e.g., French departments) from processes (e.g., migration).

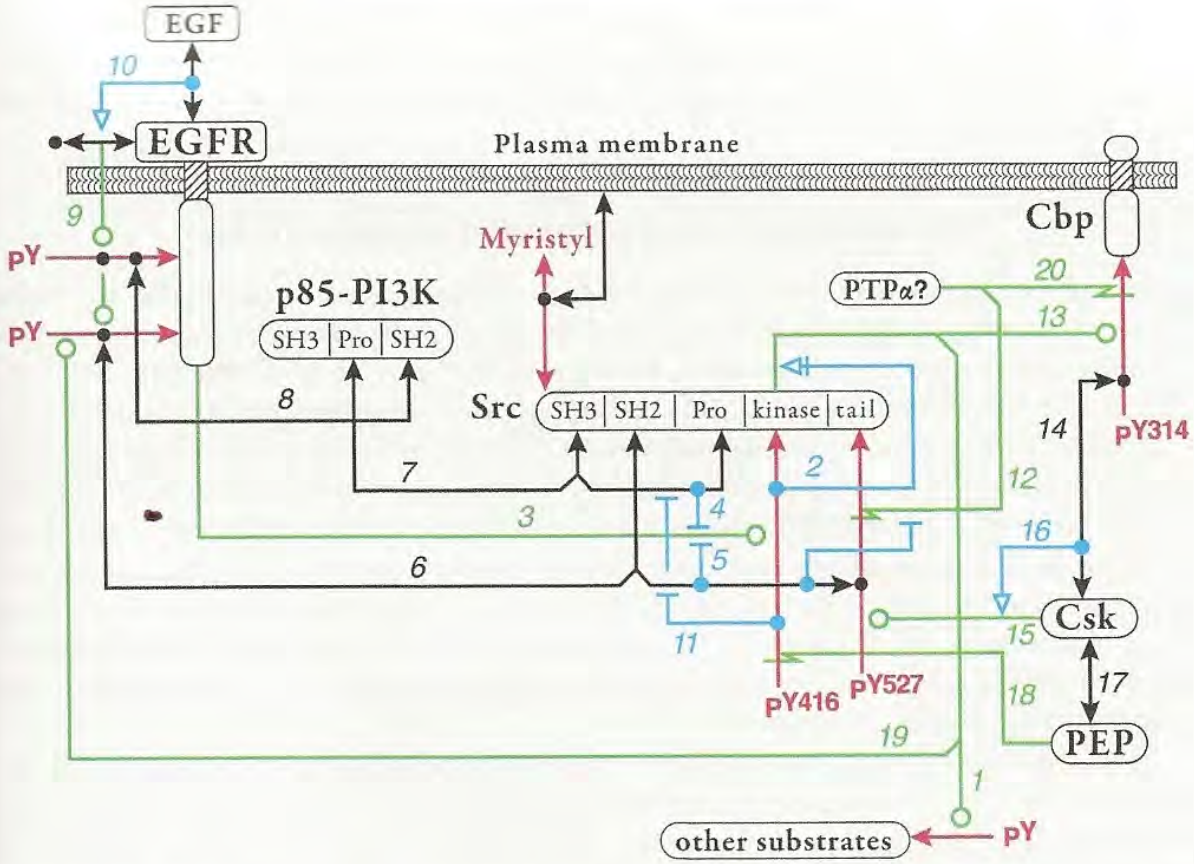

Figure 45.2 The Src enzyme regulates and triggers many biochemical signalling pathways involved in cell division, survival, motility, and adhesion (Sen and Johnson, 2011; Cirotti *et al.*, 2020). In an unregulated, activated state, Src is often implicated in cancer progression, making the *SRC* gene an oncogene (Stehelin *et al.*, 1976); J. Michael Bishop and Harold E. Varmus won a Nobel Prize in 1989 for discovering the gene. Kohn's MIM here shows different domains of Src, and details both intra- and intermolecular interactions. It thus helps us tell a story about what causes Src to open up (its active state) or close (its inactive state). Roughly put: Src amino acid location Y416 (a tyrosine) must be phosphorylated for Src protein activation (#2; 'a bar behind the arrowhead signifies necessity', 'the [blue] node represents the phosphorylated species', Kohn, 2001: 85). The binding of EGF to the transmembrane protein EGFR (#10) triggers Src activation (#3; the open circle indicates 'enzymatic stimulation of a reaction' Kohn, 2001: 85). An active Src can phosphorylate other protein substrates (#1). But the Y416 phosphorylation is inhibited by intramolecular binding which closes Src (#4 and #5). (See Kohn, 2001: 85, 89–91 for further explication.). Partial map key: 'black for binding interactions [...]; red for covalent modifications and gene transcription; green for enzyme actions; blue for stimulation and inhibition' (Kohn, 2001: 90). (Reproduced from Kohn, 2001: 90, figure 8, with the permission of AIP Publishing; permission conveyed through Copyright Clearance Center Inc.)

In Figure 45.2, note how Src and EGFR function as objects, while the different types of arrows denote various kinds of temporal processes. Conventions, together with desiderata and purposes, permit explicit and useful graphical renditions of complex biochemical pathways, whereby basic objects and processes are identified in a manner that can be automated and understood logically.

MIMs grant a synoptic view of the biochemical landscape, focusing on causal, topological relations rather than (tiny; inverse scale) geospatial features. And they are only one visualization technique deploying the map analogy in making causal maps.[7] Even so, Kohn writes, 'a molecular interaction map can be used in much the same way as a road map or electronic

circuit diagram' (Kohn, 1999: 2703; cf. Kohn, 1999: 2704–2707, 2001: 84; Kohn *et al.*, 2006: 10–11). Furthermore, 'a coordinate grid and an alphabetical list of molecules' permits finding single molecules in a manner 'analogous to the way towns are found on a roadmap' (Kohn *et al.*, 2006: 10–11).

Maps of French interdepartmental migration (1954)

Deep similarities between causal and literal maps can be gleaned by turning to migration maps (cf. Winther, 2020: 180–187). Following the spatial map analogy, we can connect biochemical causal maps, as represented in Figure 45.2, to Figure 45.3 (cf. Winther, 2020: 36, figure 2.2). Recall the three pragmatic assumption kinds identified for MIMs: desiderata, purposes, and conventions. Overlapping desiderata between Kohn's methodology and Bertin's map include unique depiction of each object kind (e.g., molecule; department capital), a clear network topology, and reliable map coordinates. Second, both abstractions share purposes such as summarizing data, suggesting novel interpretations, clarifying patterns and processes, and understanding how general features can emerge from lower-level processes (e.g., biochemical; basic migration). Finally, both maps contain basic objects and processes. Rich empirical, causal, and temporal information is summarized in both representations via resonant diagrammatic conventions.

The maps are of course not the same. For instance, arrows imply reactions in MIMs whereas they capture geographic movement in Bertin's map. Interestingly, Bertin's map takes very large patterns and puts them in a smaller, digestible graphic form while Kohn's map does the inverse. Analogies are always partial.

Extreme-scale maps of gene expression in brains

Some recent Big Science projects aim to produce atlases or simulations of the brains of humans, rats, and other animals (see http://www.brain-map.org/; https://blogs.cuit.columbia.edu/rmy5/bam/; https://braininitiative.nih.gov/; http://bluebrain.epfl.ch/; Markram *et al.*, 2015). I shall focus on the gene expression maps surveyed, abstracted, and visualized by the Allen Human Brain Atlas (Hawrylycz *et al.*, 2012; Shen *et al.*, 2012).

Knowing the chromosomal location of genes does not tell us their function. Focusing on differential gene activation among tissue types, or organ regions, is essential to understanding a fundamental biological question: how do sameness and homogeneity become difference and heterogeneity, at the genetic, cellular, and tissue levels? Gene expression must be understood – and mapped – in the context of localized intra- and intercellular space. Resulting gene expression maps may either reduce space (such maps are at the very large or high end of standard geospatial scale) or *amplify* space (i.e., inverse scale, Winther, 2020: 71–73), depending on whether they represent, respectively, an object larger than the map, such as a brain, or microscopic objects and processes such as genes and cellular location.

The Allen Human Brain Atlas aims to construct a 'comprehensive map of transcript usage across the entire adult brain' (Hawrylycz *et al.*, 2012: 391). Surveying approximately 20,000 genes across roughly 170 brain structures, the atlas maps the brain's transcriptome architecture (Hawrylycz *et al.*, 2012: 392–394),[8] with an eye towards future studies of the function and dynamics of distinct brain regions, down to the neuronal level.[9]

Deploying high-throughput experimental practices and significant computational power, three kinds of maps were constructed. Recall first that genes together with biochemical machinery produce corresponding messenger RNA during transcription. The presence of

Figure 45.3 This is figure 3 of Bertin's composite map of 'Interdepartmental migrations in France' (1954), which grants a synoptic view of the migration landscape in mid-1950s metropolitan France. Two maps are superimposed here: one showing all migration among all French metropolitan departments (administrative regions), except for Paris (Bertin, 1983: 350, figure 1); and another depicting all migration between Paris and all other departments (Bertin, 1983: 350, figure 2). Each target or source 'empty space' represents the capital, or rough centre, of one of approximately ninety departments. Migration quantities of more than 2% of original department population/year are represented with black arrows or triangles. White arrows or triangles indicate migration of less than 2% per year of the department's population, but more than 10,000 migrants. For both black and white symbols, area is proportional to absolute migration quantity. In figure 1, regular black arrows or a few non-Paris-pointing black triangles, capture all significant interdepartmental migration in all pairwise combinations (e.g., note multiple thick arrows pointing to Lyon). All migration vis-à-vis Paris is represented in figure 2 with triangles, whether black (to Paris) or white (from Paris). This composite map was created by Serge Bonin, laboratoire de Cartographie, École Pratique des Hautes Études, Bertin (1983: 350), figure caption: 351. Redrawn for clarity by Mats Wedin. (Republished with permission from Jacques Bertin, *Semiologie graphique. Les diagrammes, les reseaux, les cartes*, 2005: 350, (c) Ed. de l'EHESS, Paris.)

a particular transcriptional RNA product in a cell or tissue area thus signifies the presence of an active gene. These extreme-scale maps embody gene expression spatial information:

i *Global microarray maps* are produced via an 'all genes, all structures' strategy relying on microarray technology to produce approximately 10 million microarray expression

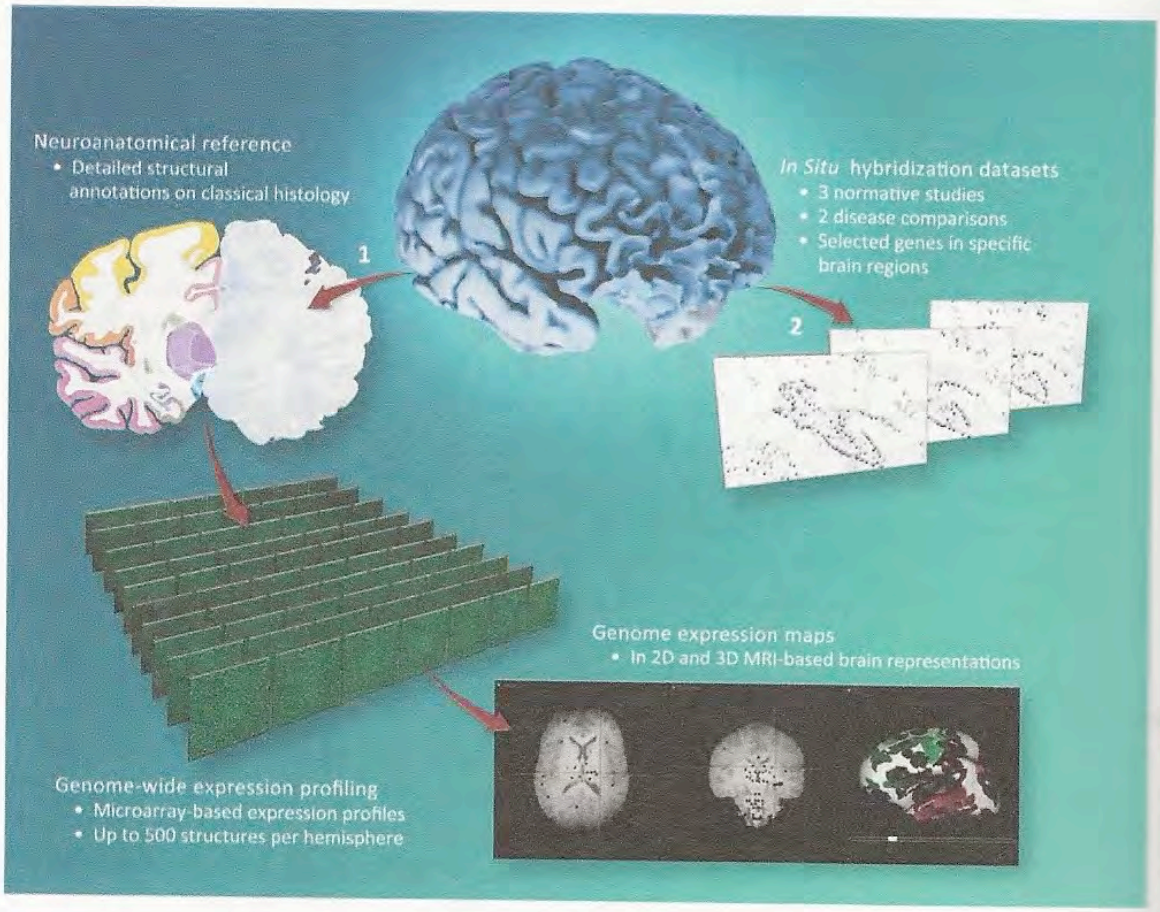

Figure 45.4 Two basic experimental strategies for producing gene expression maps of human brains. (Reproduced from Shen *et al.*, 2012: 712, figure 1, Copyright (2012), with permission from Elsevier.)

datapoints per brain (11,414 differentially expressed genes × 900 neuroanatomical sites) (Hawrylycz *et al.*, 2012: 391, 394; Shen *et al.*, 2012: 711). These datapoints can be represented in zoomable 2D and 3D brain maps (Figure 45.4, bottom).

ii *Heat maps* display in tabular form gene set expression overlap among pair-wise brain structures. These are also generated from microarray data (see, e.g., 'the genetic geography of the brain': http://casestudies.brain-map.org/ggb).

iii *Histological maps* employ in situ hybridization maps to permit local visualization, in particular tissues or cells, of the transcript products of genes (Figure 45.4, top).[10]

Global microarray, heat microarray, and histological gene expression maps permit data mining and visual inference about potential causal mechanisms, helping identify the causal structure of development, and furthering the exploration and discovery of the genetic geography of human brains.[11] For instance, Allen Atlas maps may be used 'to identify molecular networks that underlie brain structure and function and which are often targets of disease; and to characterize cell types and circuitry that drive behavior and thought' (Shen *et al.*, 2012: 714).

Rethinking geospatial ontologies through the life sciences

The life sciences explore processes at many scales, from the vast continents and epochs of ecology and evolution to the miniscule magnitudes of biochemistry and genetics. Literal

maps are particularly instructive for examining Darwin's finches, but we must also amplify space with extreme-scale maps if we wish to represent microscopic objects and processes. Bringing multiple levels into focus helps provide a fuller picture of life.

There is a strong drive in the philosophy of science to analyse explanation in terms of causation (e.g., Cartwright, 1989, 2007; Craver, 2007; Glennan, 2017): to explain a phenomenon is to model the processes causing it, thereby allowing for understanding and prediction. Thus, to understand or predict the evolution of beak size or shape, the production of certain molecular objects or agents in biochemical reactions, or the path from genotype to phenotype, we must produce causal models of these phenomena.[12] Literal or extreme-scale maps can be understood as causal maps when they serve as heuristics, inspiration, or even actual models in scientific causal projects. Analogously, geospatial maps can serve as causal maps insofar as they help us explain, understand, or predict phenomena in the social or behavioural sciences, such as human migration or voting patterns.

Finally, time has received increasing attention in the geospatial sciences in recent years (e.g., Yuan, 2008; Andrews, 2021; Kraak and Ormeling, 2021: chapter 8). Here geographers, cartographers, and GIS specialists might benefit from a detour through philosophy of science, especially discussions of temporal dimensions and dynamics in different sciences (e.g., van Fraassen, 1989, 2008; Winther, 2006, 2020: chapters 6–8). Causes occur in time, making temporal ontologies worth investigating.

Conclusion

Examining map thinking in the life sciences can help us rethink geospatial ontologies and practices. Map thinking is highly general. Map analogizing may yet end up working in both directions: not only does science rely on the cartographic map, but the cartographic map may yet be floodlit, transformed, and fractured by attention to map thinking in science.

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Notes

1 Grant and Grant (2008: 3) write '14 or 15'; Lamichhaney *et al.* (2015) have closer to 18 or so species in their genetic, phylogenetic, and morphological analyses.
2 Lack (1947) offers a succinct three-page summary of his book's 16 chapters on pages 160–163; for state-of-the-art phylogenetic inferences on Darwin's finches, see Lamichhaney *et al.* (2015, 2018).
3 In his first extended book on Darwin's finches, one of Peter Grant's main interlocutors was David Lack. Grant and Grant (2008: xvii) also dedicate a book to Lack's memory.
4 See, e.g., the large figure 6 of Kohn (1999: 2708–2711), with map key on page 2705, figure 1.
5 See, e.g., http://biochemical-pathways.com/#/map/1.
6 See, e.g., http://discover.nci.nih.gov/mim/index.jsp, and citations listed in Kohn *et al.* (2006: 11).
7 See, e.g., iPath http://pathways.embl.de/; KEGG Pathway Maps: http://www.genome.jp/kegg/kegg3a.html.
8 Hawrylycz and colleagues surveyed the total genome (roughly 30,000 genes, according to this study: Hawrylycz *et al.*, 2012: 393). Since differences in phenotypic structure and function must be correlated with differences in gene expression patterns, they focused on genes not expressed uniformly across the brain.

9 Importantly, gene expression patterns across individuals seem to be highly – but not perfectly – correlated, with over 90% overlap (Hawrylycz *et al.*, 2012: Supplementary Figure 2).

10 A seminal article notes: 'The hybridization of [experimentally produced] RNA to the [cell's own] DNA in a cytological preparation should exhibit a high degree of spatial localization, since each RNA species hybridizes only with sequences to which it is complementary' (Gall and Pardue, 1969: 378). Gilbert (2007: 362) reviews in-situ hybridization.

11 Further kinds of gene expression maps were also produced, and the principal components correlated highly with spatial brain structure (Hawrylycz *et al.*, 2012: 398, figure 6). Moreover, human embryo brain studies complement this one (Miller *et al.* 2014); on mouse brains, see Ko *et al.* (2013).

12 Another tradition in the philosophy of science, influenced by theoretical physics, views explanation, understanding, and prediction more in terms of formal mathematics (e.g., Friedman, 1983; van Fraassen, 1989, 2008). Indeed, in physics – and even in the biological and social sciences – formal *state-space maps* showing the abstract topography of, and voyages in, mathematical phase spaces are crucial (e.g., Nolte, 2010; Winther, 2020, chapters 6 and 8; see Grant and Grant, 2002: 137–139 for state-space maps of the evolution and ecology of Darwin's finches).

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