Explaining the Brain

Mechanisms and the Mosaic Unity of Neuroscience

Carl F. Craver

CLARENDON PRESS · OXFORD

OXFORD
UNIVERSITY PRESS

Great Clarendon Street, Oxford OX2 6DP

Oxford University Press is a department of the University of Oxford.
It furthers the University's objective of excellence in research, scholarship,
and education by publishing worldwide in

Oxford New York

Auckland Cape Town Dar es Salaam Hong Kong Karachi
Kuala Lumpur Madrid Melbourne Mexico City Nairobi
New Delhi Shanghai Taipei Toronto

With offices in

Argentina Austria Brazil Chile Czech Republic France Greece
Guatemala Hungary Italy Japan Poland Portugal Singapore
South Korea Switzerland Thailand Turkey Ukraine Vietnam

Published in the United States
by Oxford University Press Inc., New York

First published 2007

British Library Cataloguing in Publication Data

Data available

Library of Congress Cataloging in Publication Data

Craver, Carl F.
Explaining the brain : mechanisms and the mosaic unity of neuroscience / Carl F. Craver.
p. ; cm.
Includes bibliographical references and index.
ISBN–13: 978–0–19–929931–7 (alk. paper)
ISBN–10: 0–19–929931–5 (alk. paper)
1. Neurosciences—Philosophy. 2. Brain—Philosophy. I. Title.
[DNLM: 1. Neurosciences. 2. Philosophy. WL 100 C898e 2007]
QP356.C73 2007
612.8—dc22 2006103230

Typeset by Laserwords Private Limited, Chennai, India
Printed in Great Britain
on acid-free paper by
Biddles Ltd., King's Lynn, Norfolk

ISBN 978–0–19–9299317

10 9 8 7 6 5 4 3 2 1

Detailed Contents

5

A Field-Guide to Levels

Summary

Explanations in neuroscience typically span multiple levels. The term level, however, is multiply ambiguous. I develop a taxonomy of different kinds of levels, and I show why one must be careful to keep these different kinds distinct. Using an example from contemporary neuroscience—the multilevel mechanisms of spatial memory—I argue that "levels of mechanisms" captures the central explanatory sense in which explanations in neuroscience (and elsewhere in the special sciences) span multiple levels. The multilevel structure of neuroscientific explanations is a consequence of the mechanistic structure of neuroscientific explanations. I emphasize the importance of levels of mechanisms by showing how other common notions of levels (such as levels of science, levels of theories, levels of control, levels of entities, levels of aggregativity, and mereological levels) fail to describe the explanatory levels appearing in the explanation for spatial memory.

1. Introduction

The descriptive fact that explanations in neuroscience typically span multiple levels gives rise to scientific disputes about the relative significance of different levels and to philosophical disputes about the existence and explanatory relevance of nonfundamental levels. Yet the term "level" is multiply ambiguous. Its application requires only a set of items and a way of ordering them as higher or lower. Not surprisingly, then, the term "level" has several common uses in contemporary neuroscience.[1] To

[1] Machamer (personal communication), Churchland and Sejnowski (1992), and Hardcastle (1998) called my attention to this fact.

name a few, there are levels of abstraction, analysis, behavior, complexity, description, explanation, function, generality, organization, science, and theory. Consequently, scientific and philosophical disputes about levels cannot be addressed, let alone resolved, without first sorting out which of the various senses of "level" is under discussion.

In this chapter, I develop a taxonomy of ways to think and talk about levels. My taxonomic approach contrasts with Wimsatt's (1976a, 1994) prototype of levels, which characterizes levels in terms of a cluster of rankable features. Wimsatt's classic treatment of levels is the appropriate starting place for any scientifically informed discussion of that topic. In his view, levels are distinguished in part by the *sizes* of objects. Objects at different levels also stand in *composition* relations. Objects at the same level are governed by the same *laws* and exhibit *forces* of similar magnitudes. Objects at the same level also have *regular* and *predictable* relations with one another and are *reliable detectors* of one another. *Theories* are found at levels because that is where the regularities are. Finally, everything at a given level is investigated with the same set of *techniques* and according to similar *disciplinary perspectives*. Wimsatt's reason for offering a prototype of levels, as opposed to a definition, is that some examples of levels lack one or more of these central features. Because the levels metaphor is ambiguous, however, the prototype account obscures the distinctions among different senses of "level." My taxonomic approach highlights the similarities and differences among different senses of level.

Because I am primarily interested in the multilevel structure of explanations in neuroscience, I begin in Section 2 with an uncontroversial example of such: the mechanisms of spatial memory. Charles Stevens praises this explanation as approaching the "dream of neurobiology ... to understand all aspects of interesting and important cognitive phenomena—like memory—from the underlying molecular mechanisms through behavior" (Stevens 1996: 1147). Squire and Kandel claim that "Memory promises to be the first mental faculty to be understandable in a language that makes a bridge from molecules to mind, that is, from molecules to cells, to brain systems, and to behavior" (2000: 3). My goal is to ask which of the different senses of level best describes the levels in this example of multilevel explanation. I develop the taxonomy of levels in Section 3. Finally, in Section 4, I introduce *levels of mechanisms* as the sense most relevant to understanding the spatial memory example and similar multilevel explanations. I show that this way of thinking about levels is consistent with many presumed features of levels (for example, that things at lower levels are smaller than things at higher levels and are studied with different techniques) but inconsistent with others (for example, that levels are monolithic strata in nature; that things at different levels interact causally; and that levels, fields, and theories correspond to one another).

I leave one significant sense of "level" out of my taxonomy for now: "levels of being," or, as I will call them, *levels of realization* (cf. the sense of "orders" in Kim 1998[2]). This is perhaps the dominant notion of "level" under discussion in metaphysics and the philosophy of mind. In levels of realization, a property or activity at a higher level is *realized by* a property or activity at a lower level of realization. The item at a lower level of realization is not part of the item at a higher level; the realized and realizing properties are properties of one and the same thing. Marr's levels of analysis (computational, algorithmic, and hardware/implementation levels) are levels of realization. Levels of mechanisms, in contrast, are a variety of part–whole relation. The property or activity at a higher level of mechanisms is the behavior of the mechanism as a whole (the *explanandum phenomenon*); the parts of the mechanism and their activities are at a lower level. I do not include levels of realization in the present discussion because any attempt to locate them within the taxonomy would be contentious. I discuss the causal relevance of realized variables in Chapter 6.

2. Levels of Spatial Memory

The explanation of spatial memory (henceforth LM), as represented schematically in Figure 5.1, is commonly said to have roughly four levels.[3] The topping-off point in this hierarchy is the spatial memory phenomenon. Call this the *level of spatial memory*.[4] This level is typically associated with scientific fields, such as experimental psychology and ethology, and with different techniques, such as mazes, for assaying different forms of spatial

[2] Kim (1998) describes levels of realization as "orders," and he talks about higher- and lower-order properties.

[3] I take no stand on whether this example of explanation is ultimately the right explanation. What matters is not the specific details, but rather the overall explanatory pattern of fitting items into a multilevel structure.

[4] There are many different spatial memory phenomena, but for now I gloss over that matter.

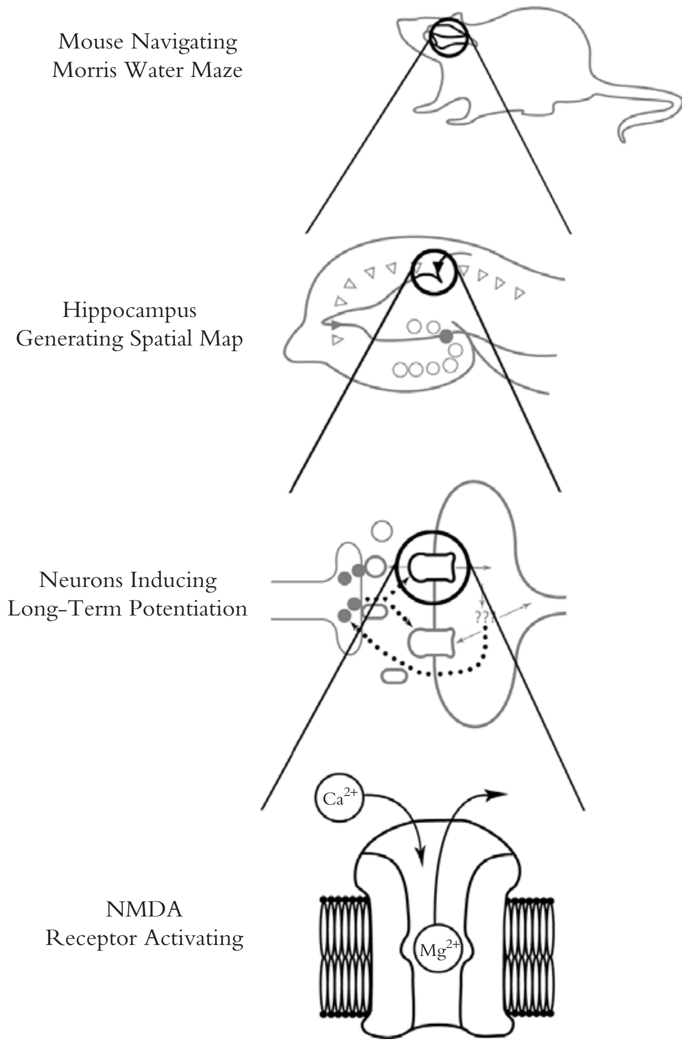

Figure 5.1. Levels of spatial memory

memory. Spatial memory is tested in radial arm mazes, sunburst mazes, three-table problems, and the Morris water maze. The last of these is a circular pool filled with an opaque liquid covering a hidden platform. Rats are trained to use various cues from the pool's environment to find the platform and escape the water. The liquid environment in the pool allows researchers to mask the olfactory cues, which is a problem with standard box mazes. In order to test different aspects of spatial memory, researchers can vary where they put the rat in the maze, features of the environment, and other cues pointing to the location of the platform. Researchers monitor the time that it takes the rat to find the platform and, in some cases, the trajectory of the rat through the pool. Experiments of this sort are used to define the phenomenon of spatial memory.

At a lower level—the level of *spatial map formation*—are the computational properties of neural systems, including brain regions such as the hippocampus and other areas in the temporal and frontal cortex. Considerable evidence suggests that the hippocampus, a structure in the medial temporal lobe, is necessary for forming spatial memories. A transverse slice of the hippocampus, with its characteristic tri-synaptic loop, is shown in Figure 5.2a. This loop runs from the perforant path fibers coming from the entorhinal cortex, through the granule cells (○) of the dentate gyrus, and from there to the pyramidal cells △ of the cornu Ammonis region (labeled CA1 and CA3). Rats with bilateral lesions to the hippocampus exhibit profound deficits in maze learning and other tasks. Similar results can be obtained by using pharmacological agents to block the activities of crucial neurotransmitters in the hippocampus, or to prevent protein synthesis in hippocampal neurons. The results of such interference experiments have also been supported by activation experiments. If one records from single cells in the hippocampus as the rat navigates a familiar space, one will find that specific cells in the hippocampus (now known as "place cells") fire preferentially when the rat enters a given location in the maze in a particular orientation (O'Keefe and Dostrovsky 1971; Wilson and McNaughton 1993). For this reason, researchers hypothesize that the hippocampus functions as a spatial map.

How does the hippocampus generate spatial maps or contribute to the storage of spatial memories? The answer is still controversial, but answers typically appeal to phenomena at the *cellular-electrophysiological level*. The dominant hypothesis since the 1970s has been that spatial maps are formed through LTP in hippocampal synapses. This hypothesis is supported by evidence that interventions to inhibit LTP prevent spatial learning, that interventions to strengthen LTP can prime learning, and that synapses undergo LTP during learning and memory tasks.

In Figure 5.2b (top), LTP is represented as a lasting enhancement of the post-synaptic response to the same pre-synaptic electrical signal following

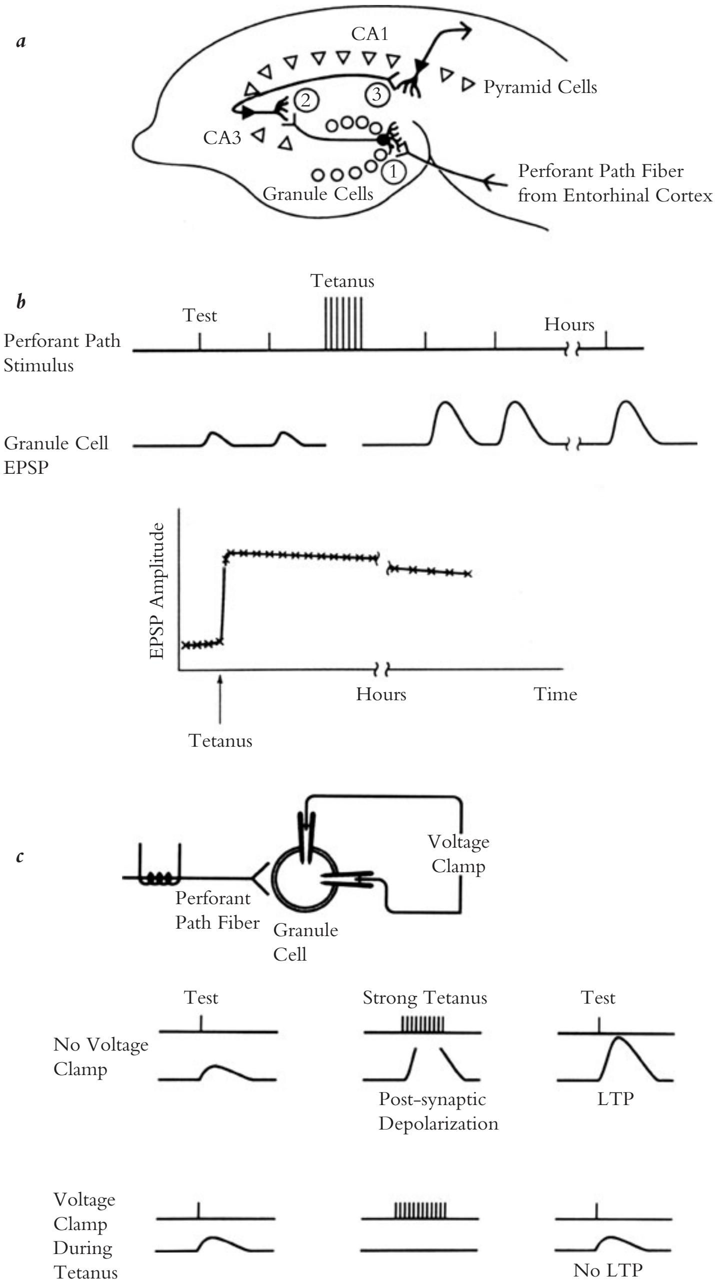

Figure 5.2. A textbook depiction of LTP

Source: Reprinted with permission from Levitan and Kaczmarek (1991) a tetanus (rapid and repeated stimulation). The top line represents stimuli delivered to the pre-synaptic cell. The bottom line records the post-synaptic response. As shown in the first third of the diagram, a test stimulus to the pre-synaptic cell produces a regular depolarization of the post-synaptic cell (that is, an excitatory post-synaptic potential, or EPSP). The experimental intervention (in the middle third) involves applying a tetanus to the pre-synaptic cell. Following this intervention (in the last third), the same test stimulus produces a much greater EPSP than before. This facilitation lasts for hours, days, or weeks, as shown in Figure 5.2b (bottom). Figure 5.2c illustrates that LTP requires the simultaneous activation of both pre- and post-synaptic neurons. The top record is the same as in Figure 5.2b. In the bottom record, the post-synaptic cell is voltage clamped during the tetanus (in the middle), that is, an external source of current counters any voltage changes in the post-synaptic neuron. LTP is not induced in the absence of post-synaptic depolarization (in the last third). The idea is that spatial maps are created or stored by adjusting the strengths of synapses in the hippocampus.

The bottom of this hierarchy—the *molecular level*—consists of the molecular mechanisms that make the chemical and electrical activities of nerve cells possible. These molecular mechanisms are studied with molecular tools such as gene knockouts and with pharmacological agonists and antagonists that excite and inhibit different biochemical pathways. As I discuss in Chapter 3, if the post-synaptic cell remains polarized (as in Figure 5.2d), the channel through the NMDA receptor remains blocked by large, positively charged Mg^{2+} ions. But if the post-synaptic cell is depolarized, the Mg^{2+} ions are driven out of the channel, allowing Ca^{2+} ions to diffuse into the cell. The Mg^{2+} blockade is a coincidence-detection device that ensures that LTP is induced only when both the pre- and post-synaptic cells are simultaneously active. Interfering with this coincidence-detection device by, for example, removing the NMDA receptor or changing its conformation has effects that ramify throughout this hierarchy, producing deficits in LTP, spatial map formation, and performance in the Morris water maze (see Tsien et al. 1996a, 1996b; McHugh et al. 1996, which I discuss in greater detail in Chapter 7).

My decision to break this explanation into four levels is surely an oversimplification. There might be more levels. One might choose to identify networks of cells in the hippocampus, or cascades of molecules beneath a properly electrophysiological level. The hierarchy could also be expanded upward and downward. Upward, one can consider memory systems in the context of other cognitive and physiological mechanisms (such as emotion and sleep) or in the context of social groups and cultures. Downward, one can consider the protein folding mechanisms that give NMDA receptors their characteristic shapes and activities.

Even without these amendments, this explanatory sketch exhibits the kind of hierarchical structure found elsewhere in the neurosciences and beyond. The mechanisms of osmoregulation discussed in Chapter 1 span from behaviors (such as drinking and urination) to molecules (such as aquapores and oxytocin). The mechanism of the action potential discussed in Chapters 2 and 4 exhibits a similar telescoping structure from the behavior of whole cells and patches of membrane to the fine-grained conformation changes in voltage-gated ion channels. In investigating the visual system, one can focus on the visual system as a whole, on the contributions of distinct brain regions, on neural networks such as optical dominance columns, and on the chemical reactions in the retina. This kind of hierarchical structure is also used to relate Alzheimer's disease and Creutzfeldt-Jacob disease to physiological and molecular mechanisms, to link phenotypes to genotypes, and to tie polymer structure to atomic structure. LM levels are representative of multilevel explanations across the sciences, and so they are a good test case for identifying an explanatorily interesting sense of level.

3. A Field-Guide to Levels

My view is that the levels in this multilevel explanation are best understood as levels of mechanisms. Lower levels in this hierarchy are the components in mechanisms for the phenomena at higher levels. Components at lower levels are organized to make up the behaviors at higher levels, and lower- and higher-level items stand in relationships of mutual manipulability (as established with the interlevel experiments I discuss in Chapter 4). Thinking of levels in this way shows why the notion of "level" is so closely bound up with the notions of explanation and organization, and it allows one to integrate the notion of "level" with the view of explanation I have developed in the preceding chapters. In talking with other neuroscientists and philosophers, I find that most of them readily accept this view of levels.

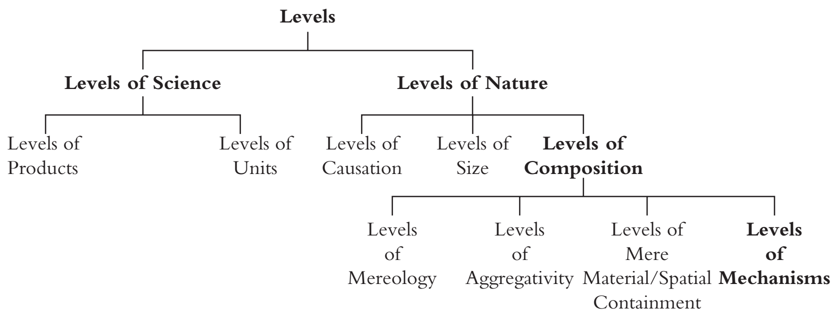

Figure 5.3. A taxonomy of levels

However, I also find that most of them confuse this view of levels with a host of unrelated and sometimes misleading associations. To guard against these misleading associations, I develop a taxonomy of levels (represented diagrammatically in Figure 5.3) to demarcate my notion of levels from its nearest neighbors. I distinguish the nodes in this taxonomy by examining three defining questions.

The first defining question is: what are the relata? That is, what kinds of things are sorted into levels? The top node of Figure 5.3, for example, marks a distinction between levels of science and levels of nature. The relata in levels of science might be either *products* of science or *units* of science (as shown one node down on the left). Products of science are epistemic constructs, such as analyses, descriptions, explanatory models, and theories. When one says that theories about molecules are at a lower level than theories about cells, or that brain regions and cells occupy different levels of description, one is talking about levels of products of science. Units of science include such groups as fields (Darden 1991), paradigms (Kuhn 1962), perspectives (Wimsatt 1994), and research programs (Lakatos 1977). When one says that nuclear physics (a field) is at a lower level than molecular biology (another field), one is talking about relationships among scientific units. One can also understand the term "levels" as describing levels of nature. These are represented on the right branch of Figure 5.3. Levels of nature relate items in the world, such as activities, entities, properties, and states. As I argue, the levels metaphor is not univocal across these different relata. Nor, I argue, do these notions of level correspond neatly to one another. To use the term level clearly, one must specify the relata (see Wimsatt 1976a: 215).

The second defining question is: what is the interlevel relation? That is, by virtue of what are two items at different levels? The three divisions under "levels of nature" in Figure 5.3 correspond to different kinds of relation: causality, size, and composition. The levels metaphor is frequently articulated as a size relationship: things at lower levels are smaller than things at higher levels (for example, Wimsatt 1976a; Kim 1998). Sometimes levels are spoken of as levels of "complexity," according to which things at higher levels are more organized than things at lower levels. Some say that things at different levels are causally related (for example, Campbell 1974). It is easy to slide from one sense of interlevel relation (for example, size) to another (for example, complexity) without noticing or acknowledging it.

The last defining question for a sense of levels is the placement question: by virtue of what are any two items at the same level? Different expositors of the levels metaphor appeal to different features in order to place items together at the same level. Some locate things at the same level if they are roughly the same size. Gould (1980) claims, in addition, that items at the same level are acted on by similar forces, are governed by the same laws, and interact (most often) with one another (see also Wimsatt 1994). I argue below that there may not be a uniquely correct answer to this question for all senses of levels. I argue, in fact, that there is no unique answer to the placement question for levels of mechanisms.

In the rest of Section 3, I move from left to right in Figure 5.3. I show that none of the notions of level, except for levels of mechanisms, adequately describes the notion of level implicit in the LM explanation. Moreover, I show that the different senses of level fail to correspond to one another, contrary to what the prototype model suggests. Once I have cleared this ground, I return to levels of mechanisms in Section 3.3.

3.1 Levels of science (units and products)

Philosophers frequently define levels by reference to divisions in science rather than by reference to divisions in the structure of the world. In this, they follow Oppenheim and Putnam's (1958) view in their "Unity of Science as a Working Hypothesis." For them, the unity of science comprises unity among either units of science (for example, fields, disciplines, and research programs) or among its products (for example, descriptions, explanations, and theories). Oppenheim and Putnam presume that units and products of science correspond to one another and that these, in turn, correspond to divisions in the structure of the world. In particular, they identify six "mereological" levels of nature: elementary particles, atoms, molecules, cells, organisms, and societies (1958: 9). Each level of nature, they suggest, also corresponds to a unique theoretical vocabulary (1958: 10) and a unique set of explanatory principles (that is, laws) that constitute a theory specific to that level (1958: 4). Each level-specific theory, in turn, corresponds to a different science, from particle physics at the bottom to the social sciences at the top. The unity of science is achieved by explaining the phenomena in the domain of one field of science with the theories of another field of science.

Oppenheim and Putnam intend this view of levels and the unity of science to be an accurate description of the science of their day. However, it is at best a caricature. The most obvious oversimplification is the six-level image of the world. Surely they did not intend these six levels to describe the world in all of its complexity, and surely they could acknowledge that science might add, delete, or modify any level in this hierarchy. Nonetheless, the descriptive shortcomings of this simplistic image help to show what would be required of a more adequate view of the multilevel structure found in many scientific explanations. First, their hierarchy has gaps. It does not include stable units formed of molecules (such as NMDA receptors), networks of cells (such as the CA1 region), organs (such as the hippocampus), or units of organization between organisms and societies (such as families or friendships). The hierarchy has no place for ecosystems, gases, planets, or solar systems. Are solar systems at a higher level than societies (because they are bigger) or are they at a lower level (because they are associated with physics)? Solar systems cannot be at a higher level than societies, because societies are not mereological parts of solar systems. Nor can they be at the same level as elementary particles, given that solar systems are composed of elementary particles. Wimsatt's branching diagram in Figure 5.4 is more accurate in these respects. There are more nodes, and the levels branch as they ascend. In this "reductive illustrative," as Wimsatt calls it, the world is structured in many different hierarchies that converge only at the lowest level. One hierarchy extends from atoms to solar objects. Another extends from atoms, through a "biopsychological thicket," to "individual thought and language." On this view, atoms are at a lower level than both plasma and organic molecules, although plasma and organic molecules are not in the same hierarchy. These changes transform

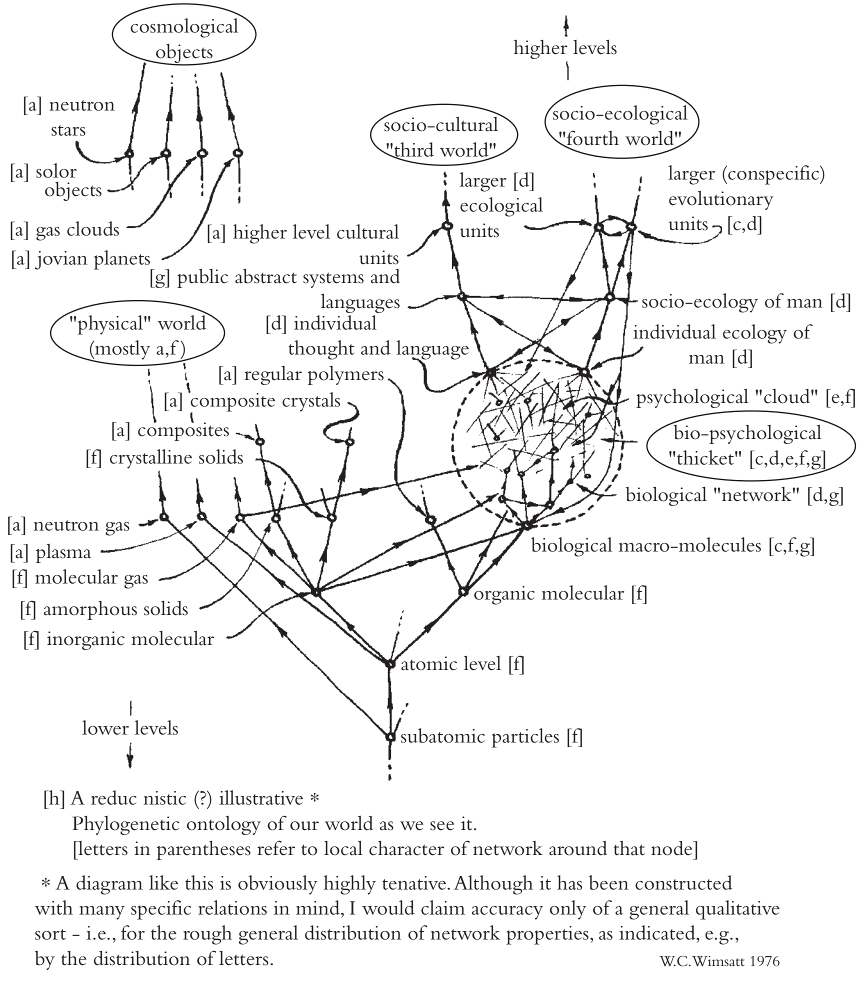

Figure 5.4. Wimsatt's branching diagram of levels
Source: Reprinted with permission from Wimsatt (1976: 253)

Oppenheim and Putnam's six levels into a much more accurate description of the hierarchies described by contemporary science.

My primary criticism, however, is not of the simplicity or descriptive inadequacy of this six-layered vision of the world. Oppenheim and Putnam could clearly grant that the world is not so tidy. Rather, I object to the supposed correspondence between levels of nature, levels of units, and levels of products of science. Oppenheim and Putnam do not seem to recognize any difficulty in moving freely between these different conceptions of levels. Consider the following passage as just one example:

> It has been contended that one manifestly cannot explain human behavior by reference to the laws of atomic physics. It would indeed be fantastic to suppose that the simplest regularity in the field of psychology could be explained directly—that is, "skipping" intervening branches of science—by employing subatomic theories. But one may believe in the attainability of unitary science without thereby committing oneself to this absurdity. (1958: 7)

In this passage, Oppenheim and Putnam shift without notice from describing structures of the world (human behavior), to describing products (explanations and theories), to describing fields of science (psychology and atomic physics).

In neuroscience, this tidy correspondence breaks down. Consider the above sketch of LM levels from the perspective of Oppenheim and Putnam's view of levels. The LM explanation constitutes a theory. It is not a deductively closed and interpreted axiomatic system, as Hempel characterizes theories, but it nonetheless satisfies a view of theories as models of systems (Craver 2002a; Giere 1999; Glennan 2005; Suppe 1989). These different items are integrated in a *single* theory not because they can all be described by theoretical predicates appropriate to a level of nature, but because they can be used together to describe, predict, explain, and test aspects of spatial memory. This theory is composed of items drawn from multiple Oppenheim and Putnam-style levels. The influx of Ca^{2+} ions (atoms) through the NMDA receptor (molecules) initiates the sequence of events leading to LTP (cells), which is part of the mechanism for forming a spatial map in the CA1 region (organs). Map formation is part of the explanation for how the mouse (whole organism) navigates through familiar environments (ecosystems) and among conspecifics and predators (societies). As Schaffner (1993a, 1993b) argues, most biological and biomedical theories span levels from molecules to physiological systems. The theories of neuroscience are no exception.

There can also be multiple theories at a single level of nature on any reasonable definition of a single level. If one orders levels by size, for example, then Wimsatt's diagram picks out a single level containing neutron gases, plasma, molecular gases, amorphous solids, crystalline solids, regular polymers, and biological macromolecules. These phenomena occupy different domains of investigation, they are characterized by different theories, and different kinds of scientists study them even though all the objects under investigation are the same size. Similarly, an electrophysiologist and a cellular anatomist might be interested in the structures and activities of cells in the hippocampus, and thus focus their attention at the same level (on many standard accounts of sameness of level). Nonetheless, they approach the same level with two distinct bodies of theory. Part of what Wimsatt intends to capture in his depiction of the "biopsychological thicket," I believe, is the fact that in such domains of science, there are multiple different theories, many of which are difficult to order neatly into levels, and most of which are reticulately connected to one another. Theories in neuroscience, in short, do not correspond to tidy levels of nature.

For similar reasons, there is no tidy correspondence between the distinct fields of neuroscience (units) and Oppenheim and Putnam-style levels of nature. Single fields increasingly reach across multiple levels of nature, and different fields often approach items at the same level of nature from different perspectives. The LM theory is the combined product of anatomy, biochemistry, computational neuroscience, electrophysiology, molecular biology, neuroanatomy, pharmacology, psychiatry, and experimental psychology. Cognitive neuroscience is, by its very nature, a field that encompasses psychological, physiological, cellular, and molecular items within its domain. In the experiment mentioned above, researchers intervene to knock out the NMDA receptor and then detect the deleterious effects of that manipulation on LTP, spatial maps, and performance in the Morris water maze (McHugh et al. 1996). In a similar experiment, researchers altered the structure of the NMDA receptor and noted enhanced LTP, sharper spatial maps, and improved learning curves (Tang et al. 1999). Experiments of this sort, which are increasingly the norm in neuroscience, require contributions from several different fields. In the interdisciplinary climate of contemporary neuroscience, individual researchers often acquire competence with techniques drawn from different fields and with techniques that target various levels of nature. Contemporary neuroscience thus does not fit Oppenheim and Putnam's hierarchical structure. Fields, journals, and scientific organizations are now organized around interfield collaboration to such an extent that it is no longer possible to resolve neuroscience into well-defined strata of research.

In the case of LM levels and other hierarchically organized explanations, theories, fields, and levels of nature (in Oppenheim and Putnam's sense) dissociate from one another. Researchers in single fields do research at multiple distinct levels of nature, and sometimes multiple fields bring their resources to bear on a single level. For these reasons, I confine my attention from this point on to levels of nature rather than to levels of science.

3.2 Levels of nature

I propose then that we start by thinking of levels as primarily features of the world rather than as features of the units or products of science.[5] As possible relata in levels of nature, I include entities, activities, properties, and mechanisms. I also distinguish among three interlevel relations: causation, size, and composition. In this section, I consider each of these different relations, along with a few permutations of different relata, to illustrate how ambiguities arise from failing to keep these different relations distinct.

3.2.1. Causal levels (processing and control) Sometimes the levels metaphor is used to describe causal relations. Two examples are levels of processing and levels of control.

In *levels of processing*, the relata are the stages of a task or an extended process. These stages are related to one another sequentially and causally (see Churchland and Sejnowski 1992: 23). Levels of processing are sometimes inscribed in the names of brain regions with such terms as "primary" and "secondary," as in "primary somatosensory cortex" and "secondary auditory cortex." For example, the flow of information through the visual system is commonly said to begin with the retina, passing through the lateral geniculate nucleus (LGN) and the primary visual cortex (V1) before being sent on to "higher-level" visual areas (such as V2, MT, or any of roughly twenty-five other major visual processing regions). The LGN is frequently said to be responsible for "lower-level" visual processing. V1 is responsible for higher-level processing, and MT (among others) processes information at a higher level still. Levels of processing are ranked relative to one another by their place in a causal (and derivatively, temporal) sequence. Processing in the retina occurs earlier than processing in the LGN, and the

[5] Levels of sciences and theories could then be seen as derivative upon, and at best approximations of, these ontic structures.

processing in the LGN occurs earlier than the processing in V1. Processing in the retina is causally required for, prepares the information for, or filters information into, later processing in the LGN, V1, and MT. For this reason, hydrodynamic metaphors are more appropriate for describing levels of processing than are stratigraphic metaphors: later stages are downstream in the flow of information from earlier stages.[6]

Levels of processing are relevant to understanding aspects of the LM mechanisms as well. The hippocampal trisynaptic loop shown in Figure 5.2a can be idealized into levels of processing. Perforant path fibers from the entorhinal cortex synapse on the granule cells of the dentate gyrus regions. Granule cells then project to the pyramidal cells in CA3, which, in turn, project to CA1. In this hippocampal circuit, CA1 is downstream from CA3, which is downstream from the dentate gyrus. Each region is at a higher level of processing than its predecessor.

However, the LM levels described in Section 2 are not levels of processing. The primary difference is that LM levels are relationships between a whole and its parts, while levels of processing are relationships between distinct items. LTP is part of forming spatial maps, and forming spatial maps is part of learning to navigate a novel environment. The retina is not part of the LGN. Furthermore, higher levels of processing are later in the flow of information than lower levels. They receive information that has been prepared by items at lower levels. They are "downstream" from earlier levels of processing, and items that are "upstream" causally influence them. Activities at lower LM levels, in contrast, are temporally contained within the activities at higher levels. The formation of spatial maps is not later than the induction of LTP; LTP is part of the process by which spatial maps are formed. LTP does not prepare information for consumption by the hippocampus; it is part of the consumption of information by the hippocampus. Finally, LM levels also lack the causal relations characteristic of levels of processing. This is because entities at lower levels are parts of

[6] The tidy division of processing units into "earlier and later" may break down in mechanisms with multiple parallel and feedback connections. Indeed, one might even suggest that it breaks down for the visual system as well, given the complex feedback from V1 to LGN to the retina. As the number of relevant causal relations in a mechanism increases, the clear temporal order among the component stages begins to break down. (See the discussion of complex mechanisms in Bechtel and Richardson 1993.) In such cases, speaking of stages as higher or lower in a hierarchy of information processing requires one to idealize away from the reticulate interconnections among components in order to see a predominant direction of causal influence.

entities at higher levels, and activities at lower levels are stages of activities at higher levels. To view LM levels as causally related, one must violate the common assumptions that causal relationships are contingent and that cause and effect must be wholly distinct. If one confuses levels of processing with LM levels, one might think of the interlevel relationship as a causal relationship despite these disanalogies.

A similar issue arises if one construes LM levels as *levels of control*. In levels of control, the relata are agents or actors (literally or metaphorically). They are related by subordination. Higher levels of control direct, dominate, or regulate activities at lower levels. Bosses and employees, generals and privates, teachers and students are all related by levels of control. The metaphor of control and subordination invites confusion when applied to nonintentional contexts, but often the metaphor is entirely appropriate. Genes are sometimes described as controlling development,[7] and the pre-frontal cortex and cingulate cortex are sometimes said to exhibit executive control over other brain regions and behavior (Fuster 1997; Smith and Jonides 1999; Posner and DiGirolamo 1998). More formally, the apparatus of control theory, with controllers, plants, and feedback connections, has been useful in many areas of biology and neuroscience (for a recent discussion, see Grush 2004). Very roughly, formal applications of this control metaphor describe controllers as receiving input from the output of the controlled system (that is, the plant), as comparing the output to a target output, and as then manipulating the plant in such a way as to bring it closer to producing the target output. Not all systems described with the language of control have these features. Sometimes the language of "control" is used merely to describe a predominant cause (as in the case of genes and the pre-frontal cortex). The important thing is that the controller and the plant are *distinct* parts of a larger system. Each part feeds input into and receives output from the other parts. Like a boss and subordinates, the pre-frontal cortex is said to monitor and regulate the behavior of *other* brain regions. This is unlike LM levels, in which objects are related as parts to wholes. The hippocampus is part of the mouse, and the synapses are parts of the hippocampus. An analogous understanding of the control system described above is to understand the whole system (including controller,

[7] Of course, this view is hotly debated. Genes are parts of complex mechanisms, and different perspectives lead people to privilege different components of the mechanism (or none at all) as being "in control."

plant, and feedback) as controlling the plant. This is the sort of situation envisioned by many advocates of "top-down causation." To describe LM levels in terms of levels of control is thus to import a strained understanding of the dependency relationship between levels.[8]

3.2.2. Levels of size It is perhaps most common to describe levels of nature as levels of size. In such levels, the relata are entities (for example, mice, hippocampi, and cells), and they are ranked by relative size. Churchland and Sejnowski (2000: 16), in the classic diagram of levels shown in Figure 5.5, rank entities from molecules measured in Angstrom units to organisms measured in meters. Size is also a core feature of Wimsatt's prototype of levels (shown in Figure 5.6). Wimsatt represents levels as local maxima

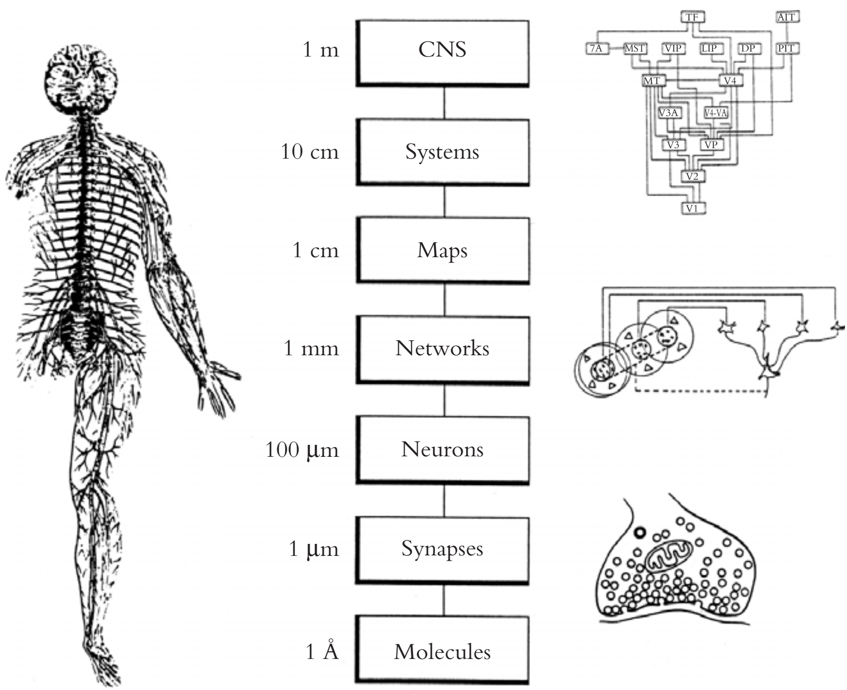

Figure 5.5. Churchland and Sejnowski's classic diagram of levels in neuroscience
Source: Reprinted with permission from Churchland and Sejnowski (1988)

[8] Those who suspect that the hierarchical world-view is associated with a male-centered and dominance-oriented hierarchy transparently confuse levels of the sort represented in LM levels with levels of control.

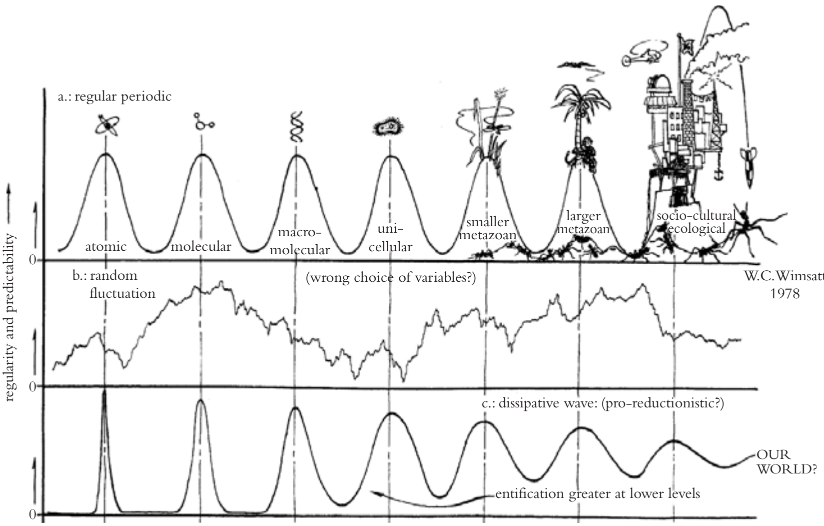

Figure 5.6. Levels as local maxima of regularity and predictability*

* Appearing over a roughly logarithmic size scale

Source: Reprinted with permission from Wimsatt (1976: 240)

of regularity and predictability in the phase space of possible ways of organizing matter. Levels appear as peaks of regularity and predictability when graphed against a ''roughly logarithmic'' size scale. An orderly world, with well-defined peaks of regularity and predictability at different size scales, is shown at the top. A world without levels, where regularity and predictability vary randomly with no well-defined peaks or valleys in any size range, is drawn beneath it. The bottom world (Wimsatt labels it ''Our World?'') shows a dissipating wave, with regularity and predictability diminishing and spreading out over broader size ranges as size increases.

Wimsatt's and Churchland's diagrams vividly illustrate the idea that levels correspond to sizes. They also illustrate an empirical hypothesis about the structure of the world, that is, that regularities tend to be found in certain size ranges and not in others. LM levels satisfy the first intuition: rats are larger than hippocampi, which are larger than cells, which are larger than molecules. The second hypothesis, concerning the clustering of regularities within size ranges, is more difficult to evaluate. One reading of this hypothesis is that those items that participate in regularities tend to be found at levels. This reading is trivial, however, because any putative between-level item for which there are robust regularities will, ipso facto, define a level. On a more substantive reading, Wimsatt's claim is that regularities hold more between items at the same level than between items at different levels. Wimsatt is led to this idea by his belief that objects tend to interact with other objects of roughly the same size (and so at the same level), and that things in the same size-range are acted on by the same forces (1976a: 237). When Wimsatt introduces Figure 5.6, he says, "Still supposing that levels are to be individuated solely on the basis of size factors, imagine a picture like that of Figure [5.6], in which regularity and predictability of *interactions* is graphed as a function of the size of the interacting entity" (1976a: 238; italics added). For Wimsatt, things at a level "interact most strongly and frequently" (1976a: 215) with things at the same level. This explains why he believes that regularities cluster within levels.

There are two problems that need to be kept separate. The first concerns causal interactions across size scales. There is a question (i) whether there can be causal interactions between things at different size scales, and a second question (ii) whether causal interactions between things at different size scales are less frequent than causal interactions between things at the same size scale. As to (i), Wimsatt and I agree that the answer is yes: large things (even arbitrarily large things) can interact with small things (even arbitrarily small things). Elephants squash fleas, planets attract molecules, and I breathe atoms. No one should disagree about any of this. However, if one recasts (i) as (i*), whether there can be causal interactions between things at different levels, the matter is more controversial. If one understands levels as involving a compositional relationship (as I am inclined to do, and as Wimsatt is sometimes inclined to do), then, as I have explained above, there is reason to be skeptical about interlevel causal claims. The skepticism arises from the fact that the ordinary concept of causation seems to carry with it a number of assumptions about the logical independence of causes and effects, the temporal precedence of causes and effects, and so on that are difficult, if not impossible, to square with the idea of interlevel (compositional) relations (see Chapter 4). The point is that the notion of levels of size carries very different implications for thinking about interlevel causes than does the notion of levels of composition. Wimsatt's prototype account makes this more confusing than it needs to be. As to (ii), I make no bets. It is an intriguing hypothesis.

The second problem to be sorted out concerns regularities. There are questions about (iii) whether there are regularities between things at different size levels, and (iv) whether regularities between things at different size scales are less common than regularities between things at the same size scale. As to (iii), the answer certainly seems to be yes again, using the same examples referenced above. As to (iv), I make no commitment. Suppose, however, that we ask the same questions about interlevel relationships and that we construe the interlevel relationship as involving a compositional relationship. Unlike the case of causation discussed in the preceding paragraph, this reconstrual makes no difference to the discussion of regularities. There are regularities between wholes and their parts. The most mundane examples are regularities of composition (for example, the fact that diamonds are composed of carbon atoms). More complex cases include the kinds of regularities revealed by interlevel experiments. The behavior of the whole is dependent on the behavior of the components in such a way that interventions to change the components can change the behavior of the whole and vice versa. While there are not interlevel causal relations in LM levels, there are many interlevel relations of dependency, and thereby interlevel relations of regularity and predictability. One can disrupt spatial memory by ablating the hippocampus or knocking out NMDA receptors. Building theories in sciences with multilevel domains involves discovering regularities that span levels and that allow prediction of how changes at one level influence changes at other levels. Regularities can be found both at and across levels.

The primary problem with understanding LM levels as levels of size is that size relations among LM levels are incidental by-products of a more fundamental *compositional* relationship among those levels. What matters is that navigating rats are partly composed of hippocampi generating spatial maps, not that navigating rats are larger than their hippocampi. These hippocampi are, in turn, composed of potentiating synapses and activating NMDA receptors. Wimsatt mentions composition as one of the features in his prototype of levels, but he is not committed to the idea that all things at different levels relative to one another also are compositionally related. This is evidenced first by his willingness to talk about the frequency of causal interaction among levels, as I discuss above. This lack of commitment to compositional relations in levels is also explicit in Figure 5.6. On the left are atoms, which are parts of molecules, which are parts of cells. On the right, however, are unicellular organisms, smaller metazoan organisms, and larger metazoan creatures. Except in very special circumstances (for example, mitochondria), these latter items are not related compositionally. The view of levels as local maxima of regularity within size ranges, while an interesting empirical hypothesis about the structure of the world, does not adequately describe the central feature of LM levels: composition.

3.2.3. Levels of composition LM levels exhibit a special kind of composition relation. In this section, I distinguish four kinds of composition: mereological, aggregative, spatial/material, and mechanistic composition. Mechanistic composition, I claim, is the crucial feature of LM levels.

3.2.3.1. Levels of mereology The mereological, or part–whole, relation is the most familiar variety of compositional relation appealed to in discussions of levels (see Oppenheim and Putnam 1958; Kim 1993: 337; Schaffner 1993a: 102). There are many accounts of the mereological relation, and it is not always clear which among them the authors intend to endorse. Many mereological systems contain features that are ill matched to the project of describing LM levels (Sanford 1993). Mereology, at least in many cases, ignores relations among the parts, treating every complex thing as an aggregate. This is not so much a shortcoming of mereology as a by-product of the fact that mereological systems are not designed to characterize levels in science. It might turn out that features of some formal mereological system are appropriate for describing certain aspects of levels in neuroscience. However, the best starting point for characterizing the containment relationship is to look at examples of neuroscientific explanations, and then to evaluate whether or not the formal apparatus adequately expresses that relationship. Starting with the formal apparatus of mereology requires too many assumptions, and some of these assumptions are misleading.

Consider first the *reflexivity theorem*: every object is part of itself. This theorem is in many classic formulations of mereology (including Tarski [1929] 1956; Woodger 1937), and it is a cornerstone of many proofs in formal mereology. However, the reflexivity theorem is unhelpful in describing LM levels. If the levels relationship is a part–whole relation, and every item in the LM hierarchy is a part of itself, then every item in the hierarchy is at a higher and lower level than itself. This result fits poorly with many of the functions that the levels metaphor is supposed to serve in neuroscience. First, it violates the assumption that LM levels are exclusive, that is, that each item appears at only one level in a given hierarchy. One central function of the levels metaphor is to sort items into different taxa; if the same item falls into different levels with respect to itself, that sorting function is void. Second, the levels in the LM hierarchy are closely tied to the notion of (ontic) explanation. The behavior of the hippocampus is part of the explanation for the ability of organisms to navigate their spatial environments, and LTP in hippocampal synapses is part of the explanation for how spatial maps are formed. The hippocampus, on the other hand, is not an explanation for itself. To avoid this problem, one could develop a mereology without the reflexivity axiom (as suggested by Rescher 1955). Another option is to develop an account of levels that places Y at a lower level than X only if Y is part of X according to the mereological relationship and, in addition, X is not identical with Y (that is, to specify that Y is a *proper part* of X). I have little doubt that formal mereological systems can be recast to accommodate the features of LM levels. My point, rather, is that in building an appropriate mereology for levels in neuroscience, one should begin with the sort of levels that appear in the LM hierarchy and ask what the mereology must be to adequately reflect the relevant features of those levels. One condition on an adequate mereology is that lower-level items are proper parts of higher-level items.

A second component of many formal accounts of mereology is the *extensionality theorem*: an object is completely determined by the set of its parts. A consequence of this theorem is that two objects are identical if and only if they share all their parts. This wording of the extensionality requirement rules out one of the central features of LM levels, namely, that the parts at a lower level are *organized* into the wholes that they compose (see Rescher 1955). Suppose that one took all of the cells in the hippocampus as shown in Figure 5.2a and rearranged them into an entirely different network of connections, say, a bust of Santiago Ramon y Cajal. According to the extensionality theorem, the hippocampus and the bust would be identical by virtue of the fact that they share all of their components. There is no reason to prevent people from talking this way, but it is not a useful way to talk about LM levels. LM-type levels are frequently spoken of as "levels of organization" to reflect the fact that it matters how the components are organized with respect to one another. In short: relations matter. Every complex is a mereological sum, but mechanisms are always literally more than the sum of their parts. Any account of the composition relation in LM levels must accommodate this fact.

Finally, formal accounts of mereology are sometimes formulated to apply equally to both abstract and concrete items. The NMDA receptor is, in some sense, part of the synapse. The holdings of Jones's Swiss bank account are part of his total wealth. Concepts are sometimes thought of as parts of propositions. But the part–whole relationship between Jones's holdings and his wealth is different from the part–whole relationship between the NMDA receptor and the synapse. The NMDA receptor is *materially* contained in the sense that the matter in the receptor is included in the matter that constitutes the cell, and it is *spatially* contained within the cell's boundaries. Again, there may be some common way of talking about parts and wholes that applies to both abstract and concrete objects, and this may be useful for some purposes. Starting with LM levels, however, one would not be led to this conclusion. Material and spatial containment are crucial features of LM levels.

3.2.3.2. Levels of aggregativity There are several varieties of material/spatial containment. Some refer to LM-type levels as *levels of aggregativity*. This choice of words misleadingly suggests that properties of things at higher levels are simple sums of the properties of things at lower levels. In levels of aggregates, the relata are properties of wholes and the properties of parts, and the relation between them is that higher-level properties are sums of lower-level properties. The mass of a pile of sand is an aggregate of the masses of the individual grains. When wholes are sums of their parts, the wholes change continuously with the addition and removal of parts. Intersubstitution of parts makes no difference to the property of the whole. The parts do not interact in ways that are relevant to the aggregate property (Wimsatt 1994). The pile gets heavier continuously as one adds new grains of sand, and moving them about has no effect on the weight. Replacing individual grains with equally weighted replicas has no effect on the weight of the pile, and the grains do not interact with one another in ways that influence the weight of the pile.

Aggregative properties are rarely interesting. The total alcohol content of the gin in a glass, for example, is an aggregate of the alcohol contents of its unit subvolumes. The volume of a glass of gin, on the other hand, is technically not a mere aggregate of the volumes of the component molecules;

rather, the total volume depends on the average kinetic energy of, and electromagnetic interactions among, the component molecules. Consider synaptic transmission in hippocampal neurons. As an action potential reaches the axon terminal of the pre-synaptic neuron, Ca^{2+} channels open and Ca^{2+} rushes into the cell. As a result, a vesicle containing neurotransmitters fuses to the neuronal membrane and releases its contents into the synaptic cleft. The neurotransmitters diffuse across the cleft and act upon receptors on the post-synaptic cell. The process relies crucially on near-aggregate phenomena. Action potentials are aggregate fluxes of ions across the cell membrane, Ca^{2+} concentrations are aggregates of Ca^{2+} ions, and concentrations of neurotransmitters are aggregates of individual neurotransmitter molecules. Each of these aggregates partially depends in part on the relative spatial location of the component parts, concentration being parts per volume. As these examples illustrate, it is much more common to find levels that violate the above-mentioned conditions on aggregativity; these levels come closer to the forms of mechanistic organization that I describe in Chapter 4.

3.2.3.3. Levels of mere material/spatial containment Before I examine this mechanistic sense of levels, I examine another variety of composition relation that falls short of characterizing LM-type levels.[9] While not exactly aggregates, these levels are properly thought of as *levels of mere material/spatial containment.* In levels of mere material/spatial containment, the relata are entities. One entity is at a lower level than another entity if the lower-level entity is within the spatial boundaries of the higher-level entity and makes up part of the matter in the higher-level whole. I know of no one who advocates this view of levels, but the contrast highlights crucial features of levels of mechanisms.

Levels of mere material/spatial containment are too permissive to characterize the nature of LM levels. In particular, thinking of levels in this way does not allow one to distinguish between mere *pieces* of a system and its *components*.[10] Dividing a system or mechanism into material/spatial pieces any which way will not break it into components. One might slice

[9] One might argue, on the grounds presented here, that containment should not be understood as a species of composition relation.

[10] I am grateful to Tom Polger for suggesting this distinction, which is something like that originally drawn by David Sanford (1993) in his effort to develop a common-sense mereology.

it, dice it, spiral cut it, or merely hack it to bits. Each of these methods of decomposition would produce pieces, but unless one is very lucky, none of those pieces would be components. Suppose that one were to divide a rat into 1 cm cubes (cf. Haugeland 1998). Some cubes would contain no components relevant to spatial memory, most cubes would contain parts that are irrelevant to spatial memory, and no cubes (taken as a whole) would be components of the spatial memory system. The cubes would be haphazard collections of stuff that, as a whole, make no identifiable contribution to anything rats do. You could not pluck many of them out without a systematic collapse; the cubes contain crucial stuff. However, the cubes are not themselves components. Components, in contrast, are pieces that make identifiable contributions to the behavior of a mechanism. Being *a piece of* S is nothing but a compositional relation. This kind of relation holds between a glass of gin and one of its unit subvolumes. Being *a component of* S involves, in addition, being relevant to the behavior of the whole.

This example illustrates that decomposition into lower-level parts—components rather than pieces—for the purposes of mechanistic explanation is always a decomposition relative to a behavior of the system. It is framed by an *explanandum phenomenon*. As Stuart Kauffman notes:

> A view of what the system is doing sets the explanandum and also supplies criteria by which to decide whether or not a proposed portion [that is, piece] of the system with some of its causal consequences is to count as a part and process of the system [that is, component]. Specifically, a proposed part will count as a part [component] of the system if it, together with some of its causal consequences, will fit together with the other proposed parts [components] and processes to cause the system to behave as described. (Kauffman 1971: 260)

The cubes fit together spatially, but unless one is very lucky, they cut across the relevant components in the mechanism. The idea of spatial decomposition is by itself too weak to rule out decomposition of a mechanism into cubes. Mechanistic decomposition cuts mechanisms at their joints.

3.3 Levels of mechanisms

The point of the foregoing considerations is that LM levels are levels of mechanisms. Levels of mechanisms are levels of composition, but the composition relation is not, at base, spatial or material. In levels of mechanisms, the relata are behaving mechanisms at higher levels and their components at lower levels. These relata are properly conceived neither as entities nor as activities; rather, they should be understood as acting entities. The interlevel relationship is as follows: X's ϕ-ing is at a lower mechanistic level than S's ψ-ing if and only if X's ϕ-ing is a component in the mechanism for S's ψ-ing. Lower-level components are *organized together* to form higher-level components. Levels of mechanisms are represented in Figure 5.7. At the top is a mechanism S engaged in behavior ψ. Below it are the ϕ-ings of Xs that are organized in S's ψ-ing. Below that are the ρ-ings (pronounced "rho-ings") of Ps (English pronunciation) that are organized in the ϕ-ing of Xs. By organization, I mean that the parts have spatial (location, size, shape, and motion), temporal (order, rate, and duration), and active (for example, feedback) relations with one another by which they work together to do something. Organization is the interlevel relation between a mechanism as a whole and its components. Lower-level components are made up into higher-level components by organizing them spatially, temporally, and actively into something greater than a mere sum of the parts.

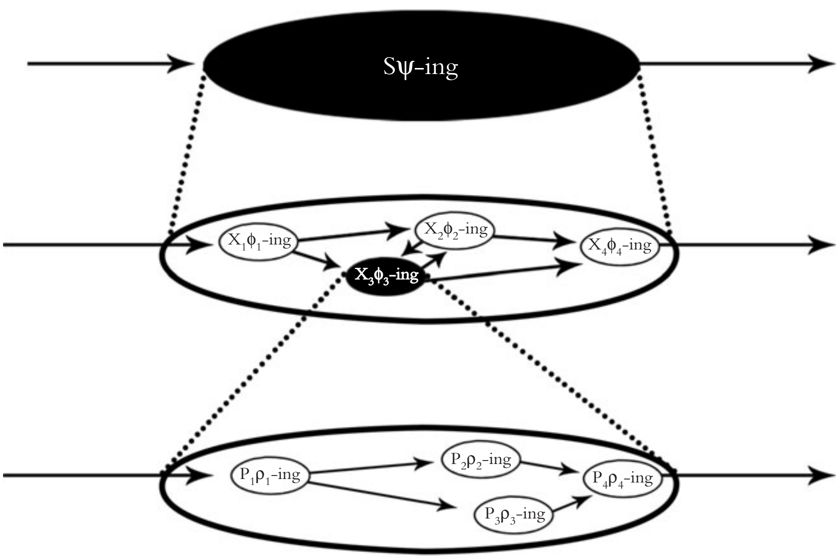

Figure 5.7. Three levels of mechanisms

Levels of mechanisms satisfy many of the central features of levels in Wimsatt's prototype. Levels of mechanisms are transparently componential, unlike mere size levels. Because components are inside the mechanism by definition, it follows that the entities in a mechanism are no larger, and are typically smaller, than the mechanism as a whole. This is consistent with the possibility that distributed components could be as large as the mechanism as a whole (for example, the circulatory system takes up most of the organism), but no component can be larger than the mechanism as a whole, in part because this would imply that the mechanism is larger than itself. Levels of mechanisms are also loci of stable generalizations, and consequently can be seen as local maxima of regularity and predictability. This is because parts of the mechanism that make an intelligible (that is, regular and predictable) contribution to the behavior of the mechanism as a whole are identified at levels. Levels of mechanisms thus satisfy many of the central features associated with levels in the first place.

However, levels of mechanisms fail to satisfy other widely held beliefs about levels. First, in contrast to the common way of speaking about levels, levels of mechanisms should not be conceived as levels of objects (for example, societies, organisms, cells, molecules, and atoms). They are levels of behaving components. In many cases, the components picked out in a mechanistic decomposition fail to correspond to paradigmatic entities with clear spatial boundaries. The synapse, for instance, is composed of part of a pre-synapatic cell (the axon terminal), part of a post-synaptic cell (the dendrite or bouton), and the gap between them. What unifies these items into a component is their organized behavior: the pre-synaptic cell releases transmitters that traverse the cleft and act on the post-synaptic cell. Synapses are not cells or parts of cells. Nor are they composed of cells alone. Rather, they are components unified by their organization in an activity.

Second, unlike Oppenheim and Putnam's six levels of nature, levels of mechanisms are not monolithic divisions in the structure of the world. The idea of monolithic levels is reinforced in Wimsatt's diagrams in Figure 5.4 and 5.6. Each size scale in Figure 5.4 contains identifiable strata across branching nodes at similar size scales. In Figure 5.6, the peaks of regularity and predictability span all atoms, all molecules, all unicellular organisms, and so on. It may turn out, as Wimsatt suggests, that the world exhibits such peaks of regularity and predictability. However, levels of mechanisms are far more local than the monolithic image suggests. They are defined only within a given compositional hierarchy. Different levels of mechanisms are found in the spatial memory system, the circulatory system, the osmoregulatory system, and the visual system. How many levels there are, and which levels are included, are questions to be answered on a case-by-case basis by discovering which components at which size scales are explanatorily relevant for a given phenomenon. They cannot be read off a menu of levels in advance.

To put the point differently, on my view of levels, it makes no sense to ask if my heart is at a different level of mechanisms than my car's water pump because there is no mechanism containing the two (except in bizarre science-fiction cases, in which case talk of levels might be appropriate). Similarly, it makes no sense to ask if ocular dominance columns are at a different level than kidneys because the two are not parts of the same mechanism. Likewise, the question of whether a given molecule and a given cell are at different mechanistic levels can be asked only in the presumed context of a given mechanism and a presumed decomposition of that mechanism. Similarities of size and functional role are not definitive of levels. My central point is that levels of mechanisms are defined componentially within a hierarchically organized mechanism, not by objective kinds identifiable independently of their organization in a mechanism.

The idea of monolithic levels of nature that I reject can be generated by abstracting from interlevel relations among particulars to interlevel relations among types. Compare the following three sentences:

(a) This pyramidal cell is at a lower level of mechanisms than this hippocampus.
(b) Pyramidal cells are at a lower level of mechanisms than hippocampi.
(c) Cells are at a lower level of mechanisms than organs.

Statement (a) has a clear mechanistic reading: a particular pyramidal cell is a component of a particular hippocampal mechanism. This statement is true if the cell is a component in a mechanism for a given task carried out by the hippocampus. For example, a given pyramidal cell can be a component in some hippocampal mechanisms but not others, and thereby be at a lower level in some hippocampal mechanisms but not others.

When Wimsatt speaks of the compositional relationship between levels, he asserts something like (b). He writes, "Intuitively, one thing is at a higher level than something else if things of the first type are composed of things of the second type'' (1976a: 215). However (b) is ambiguous. It might mean:

(b1) The pyramidal cells that compose hippocampi are at lower levels than hippocampi.

Or it might mean:

(b2) All pyramidal cells are at a lower level than all hippocampi.

Clearly (b1) is a generalization of (a), in which the compositional relationship is straightforward. This reading is unproblematic and is consistent with the view of levels of mechanisms that I recommend. However (b2) has exceptions. Pyramidal cells are found in many regions of the brain, and the pyramidal cells that are not part of a hippocampal mechanism are not at a lower level of mechanisms than hippocampi. As with my heart and the water pump, it makes no sense to ask if pyramidal cells are at a lower level than hippocampi *generally*. Some pyramidal cells are at a lower mechanistic level than hippocampi, and some are not.

Precisely the same ambiguity attends (c), the monolithic view of levels that Oppenheim and Putnam (1958) propose. It may be taken as asserting that cells are at lower levels than the organs that they specifically compose, or it might mean that all cells are at lower levels than all organs. The first option follows for levels of mechanisms; the second does not. Given that not all cells are components of organs, not all cells are at lower levels of mechanisms than organs.

One consequence of my mechanistic view of levels is that there can be no unique answer to the question of when two items are at the same level. I can provide only a partial answer: X and S are at the same level of mechanisms only if X and S are components in the same mechanism, X's ϕ-ing is not a component in S's ψ-ing, and S's ψ-ing is not a component in X's ϕ-ing.[11] To say that S's ψ-ing is at a higher level than X's ϕ-ing, is to say something of local significance in contrast to the monolithic

[11] This has struck some readers as circular because it appears to state that X and S are at the same level if they are not at different levels. Appearances to the contrary, this is not circular. I have defined ''same level'' in terms of the notion of ''different level,'' and the latter is defined in terms of componency relations. The appearance of circularity, I believe, results from the fact that most people assume that the notion of ''same level'' must be primitive in comparison with the notion of ''different level,'' and I have reversed that assumed order.

relationships expressed by (b) and (c). This point is visually illustrated by comparing Figures 5.7 and 5.8. Figure 5.7 depicts three mechanistic levels: a level for S's ψ-ing (the "topping-off" point for this model), a level for the ϕ-ings of Xs, and a level for ρ-ings of Ps (the "bottom-out" point for this model). Notice that this hierarchy, like the hierarchy that I sketch for the mechanisms of spatial memory, traces a single local strand: from the mechanism as a whole, to one of its components, and on to one of its components in turn. In contrast, in Figure 5.8, S's ψ-ing is decomposed into two sequential activities ($\phi 1$ and $\phi 2$) of two entities (X1 and X2). Beneath each are the mechanisms for those behaviors. These mechanisms are composed of the ρ-ing of Ps and the τ-ing (tau-ings) of Ts (English pronunciation). My claim that mechanistic levels are local entails that the τ-ing of Ts is not at a lower level than the $\phi 1$-ing of X1s. Mechanistic levels are levels of containment, and objects that are not related to one another as component to mechanism are not assigned to different levels.

This local view of levels provides a more solid foundation for understanding the unity of neuroscience than Oppenheim and Putnam's monolithic view of levels. Facts about cells-in-general are not explained in terms of facts about molecules-in-general. Rather, certain facts about cells are explicable in terms of some molecular items and not others. Different physiological systems have different levels of explanation and different kinds of components. Different fields of neuroscience are unified as their experimental tools, vocabularies, and conceptual structures are brought to bear upon similar problems framed by a top-most *explanandum phenomenon*. What each field contributes, and the relative importance of every contribution, however, varies from explanatory context to explanatory context. Some components appear in many different mechanistic hierarchies. Schaffner (1993a) introduces yet another sense of levels, *levels of generality*, to characterize this fact. Mechanisms of protein synthesis, for example, appear in several different neuroscientific explanations. The mechanism for the action potential also has wide application. Still, the wide scope of a privileged few components should not lead one to reintroduce the construct of monolithic levels of nature. Other parts and levels appear in only a few systems. Columnar organization, for example, appears in a few sensory systems such as the visual system and the barrel cortex, but it is not a general feature of all sensory systems, let alone all cortical systems. I develop an alternative vision of the unity of science in Chapter 7.

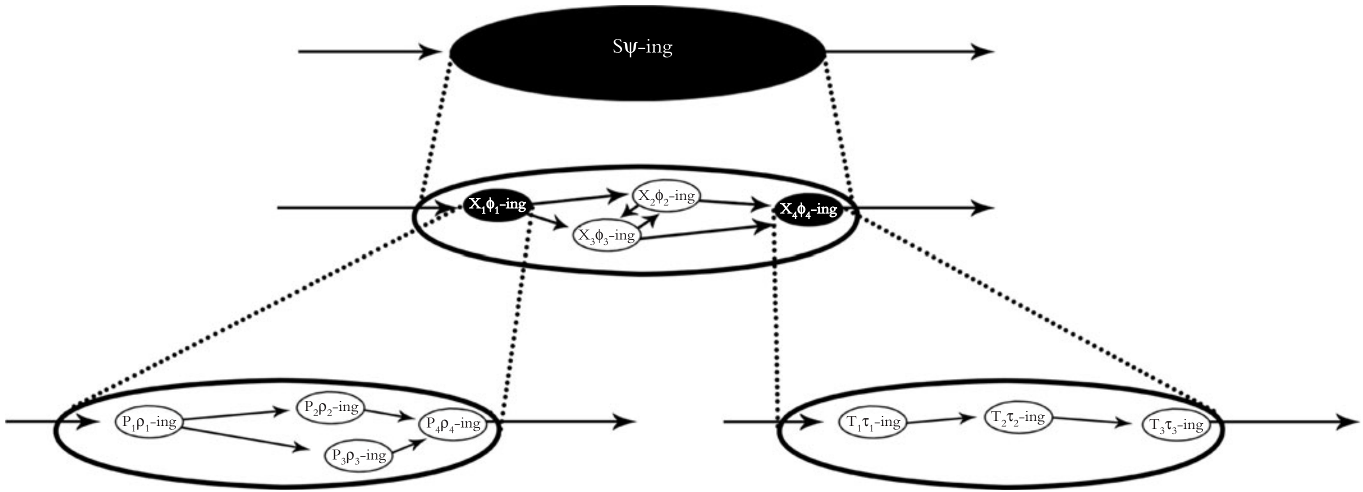

Figure 5.8. Levels are defined locally within decomposition hierarchies

The mechanistic view of levels helps to resolve some confusion about the nature of interlevel causation. First, one ought not to say that things at different levels causally interact with one another. If levels are levels of mechanisms, then there are very serious difficulties with the notion of interlevel causation. The lower-level components and their organization compose the higher level, meaning that "interlevel causation" is an interaction between the behavior of a mechanism as a whole and the parts of the mechanism. This idea is strained. On the other hand, in the case of levels of mechanisms, there is no difficulty concerning how things of one size scale can interact with things of another size scale. For example, elephants carry viruses and squash fleas. Any prejudice against these forms of causation, or prejudice in favor of rewriting them as interactions between items at similar size scales, reflects the influence of continued adherence to a monolithic view of levels (preserved as a vestige in Wimsatt's work). In the mechanistic view, what places two items at the same mechanistic level is that they are in the same mechanism, and neither is a component of the other. Two items at very different size scales can satisfy this relationship.

4. Conclusion

Talk of levels is multiply ambiguous. The levels metaphor is very flexible, and it is often used without specifying the sense of level under discussion. To prevent equivocation, I have developed a set of taxonomic principles for distinguishing different senses of levels and a taxonomy or field-guide for distinguishing different readings of the levels metaphor. This taxonomy also helps clarify a central interpretation of the levels metaphor: levels of mechanisms. The mechanistic interpretation is central because it fits core cases of neuroscientific explanation, such as LM levels. It also extends the view of mechanistic explanation I develop in the previous four chapters by showing what it means for mechanistic explanations to be multilevel. In Chapter 6, I defend the view that higher mechanistic levels are explanatorily relevant. I also show that realized phenomena (that is, phenomena at higher levels of realization) are often causally, and so explanatorily, relevant for many of the explanantia of interest to neuroscientists.