

Interpreting Neurodynamics: Concepts and Facts

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Abstract

The dynamics of neuronal systems, briefly neurodynamics, has developed into an attractive and influential research branch within neuroscience. In this paper, we discuss a number of conceptual issues in neurodynamics that are important for an appropriate interpretation and evaluation of its results. We demonstrate their relevance for selected topics of theoretical and empirical work. In particular, we refer to the notions of determinacy and stochasticity in neurodynamics across levels of microscopic, mesoscopic and macroscopic descriptions. The issue of correlations between neural, mental and behavioral states is also addressed in some detail. We propose an informed discussion of conceptual foundations with respect to neurobiological results as a viable step to a fruitful future philosophy of neuroscience.

1 Introduction

A major driving force behind the attention that neuroscience has received in recent decades is the deep mystery of how cognition, perception and behavior are related to brain activity. Many scientists have been fascinated by the wealth of empirical data for individual neurons, neural assemblies, brain areas, and related psychological and behavioral features, and by progressively powerful computational tools to simulate corresponding cortical networks. At the same time, the interested public has been attracted by fancy illustrations of brain activity (e.g., from imaging techniques) and by pretentious claims of neural solutions to basic philosophical problems (e.g., free will versus determinism) in popular magazines and newspapers.

However, heaps of data, extensive simulations, pretty pictures and bold statements cannot replace the insight that is inevitable to relate the available facts to one another in an intelligible manner. We are talking about the old-fashioned stance that understanding is the ultimate goal of scientific effort. In this respect, the need for a profound conceptual basis in the neurosciences begins to be recognized; the pioneering “Philosophical Foundations of Neuroscience” by Bennett & Hacker (2003) is an outstanding example, also in the sense that it is – still – a singular example.¹ It is uncontroversial that experimental and numerical work is and will remain mandatory for scientific progress. But it can only unfold its full value if it is embedded within a conceptually sound theoretical framework.

In this paper we intend to give an example of how this might look like for a specific field of neuroscience that was recently coined neurodynamics. This term characterizes the dynamics of the states and properties of neural systems.² It is obvious that the rich body of established knowledge in this regard can neither be exhaustively accounted for nor done full justice to on some ten pages. Therefore, we had to (somewhat arbitrarily) select topics which we think are particularly suited to indicate both potential pitfalls due to missing conceptual clarity and the insight that can emerge if detailed results are embedded in a profound conceptual framework.

¹Another recommended compendium of approaches in theoretical neuroscience, with historical scope, is the two-volume opus entitled *Neurocomputing* (Anderson & Rosenfeld, 1988; Anderson et al., 1990). It offers a substantial collection of seminal papers, each introduced with contextual background by the editors, emphasizing the evolution of ideas and mutual relations between individual articles.

²The notion of a neural system includes the brain, but of course it covers more. Although many of the issues addressed in the following will refer to the brain, there are additional features that exceed brain dynamics. For this reason we do, in general, refer to neurodynamics rather than brain dynamics.

There are some respects in which our work differs from Bennett & Hacker (2003). First, our scope is distinctly narrower than theirs. Second, our discussion is predominantly focused on neurobiological aspects, toward the end also on options to relate them to mind and behavior, but we tend to abstain from discussions of positions of so-called opinion leaders in the philosophy of mind or of cognitive science. Third, our way to entertain conceptual and philosophical issues uses mathematics, a tool that is almost entirely avoided by Bennett & Hacker (2003). The advantage is that conceptual terms can be precisely defined, and minute differences between similar terms can be clearly spelled out. For instance, the broad and often vaguely used notion of determinism, prominent in many debates in the neurosciences and neighboring fields, will be contrasted with refined variants such as determinacy and determinateness. Variability, variation, and error will be distinguished as different versions of stochasticity. Many kinds of causation or causality will be addressed and delineated from prediction and predictability.

Conceptual clarifications like this, and quite a few more, form the material presented in Section 2. We should add that a fundamental philosophical distinction, of basic significance for many other notions in this paper, is that of ontic and epistemic descriptions. This distinction emphasizes whether we understand the state of a system (and its dynamics) “as it is in itself” (ontic) or “as it turns out to be due to observation” (epistemic). As mentioned, a formal approach is chosen for the benefit of precision to define and refine the necessary terms. As a rule, each subsection is succeeded by “notes” which present background information, interpretive difficulties, or references to the neurobiological scenarios discussed subsequently in Section 3. The material of Sec. 2 is selected in such a way that as many as possible critical points of interpreting neurodynamics in Sec. 3 can be addressed on its basis.

Vice versa, the material presented in Sec. 3 contains notes that refer back to the conceptual discussion in Sec. 2, in order to facilitate cross-checks for the interested reader. The basic philosophy-of-science notions of Sec. 2 are related to the (sometimes rather differently used) technical terms in the neuroscience literature. Detailed theoretical and experimental results of neurodynamics will be presented to demonstrate where and how both the requirement and the power of conceptual clarity enters and becomes helpful. We will outline different kinds of neurodynamics covering the full range between purely stochastic and purely deterministic descriptions. It will be shown that the most suitable kind of description can change drastically across hierarchically understood levels. Finally the problematic issue of correlations between neural states on the one hand and mental or behavioral states on the other will be touched.

The final Section 4 provides some conclusions concerning typical fallacies to avoid and promising directions to go in interpreting neurodynamics.

2 Conceptual Clarifications: From Determinacy to Stochasticity

In this section we introduce some elementary notions that are crucial for an informed discussion of determinacy and stochasticity, but are often used with vague associations or badly defined specifications or both. We use the terms *determinateness* and *determinism* to distinguish between the determinacy of *states* of a system (or classes of such states) and its *dynamics* (or classes of its dynamics), respectively, in Secs. 2.1 and 2.2.³ By way of characterizing these terms we

³The terminology is adopted from Jammer’s discussion of Heisenberg’s usage of these terms (Jammer, 1974).

address closely related terms such as error and variation, causation and prediction, which serve important purposes particularly in the description of complex systems. In Sec. 2.3, we outline the notions of stochasticity, randomness, chance, and the role that probability plays in their context. Sec. 2.4 describes techniques of how to represent stochastic processes deterministically and *vice versa*.

An important further issue is the difference between *individual* and *statistical* descriptions of a system. It is tightly related to one of the most fundamental questions concerning the status of scientific theories: the distinction between epistemological and ontological statements.⁴ While ontology is a branch of metaphysics, epistemology comprises all kinds of issues related to the knowledge (or ignorance) of information gathering and using systems. The ways in which human beings process information (perceptually, cognitively, and otherwise), thus represent a set of central epistemological questions. By contrast, ontology refers to the nature and behavior of systems as they are, independent of any empirical access. For a proper account of these issues in physical systems, Scheibe (1973) proposed the notions of epistemic and ontic states of a system. The way in which the interplay between ontic and epistemic descriptions can be used to study relations between different levels of description is addressed in Sec. 2.5. At the same time, it will become necessary to define ontic and epistemic descriptions as *relative* to each other rather than absolute.

2.1 Determinateness, Error and Variation

States of a system to which *epistemic descriptions* refer are called *epistemic states*. The mathematical representation of such states encodes empirically obtainable knowledge about them. If the knowledge about states and their associated properties (also called observables) is expressed by probabilities in the sense of relative frequencies for a statistical ensemble of independently repeated experiments, we speak of a *statistical description* and of *statistical states*.

Insofar as epistemic descriptions refer to a state concept encoding knowledge, they depend on observation and measurement. Such kinds of empirical access necessarily introduce a context under which a system is investigated. Therefore, properties or observables associated with an epistemic state are *contextual*. General fundamental principles cannot be expected within epistemic descriptions.

States of a system to which *ontic descriptions* refer are called *ontic states*. They are designed as exhaustive representations of the mode of being of a system, i.e. an ontic state is “just the way it is”, without any reference to epistemic knowledge or ignorance. Ontic states in this sense are conceived as context-independent as possible (cf. Sec. 2.5). The properties (or observables) of the system are understood as *intrinsic*. As *individual states*, ontic states are the referents of *individual descriptions*.

If a system is represented in a state space Ω , its ontic state is represented by a point $x \in \Omega$. In an algebraic formulation the intrinsic observables associated with the ontic state of the system are represented by elements of a C^* -algebra \mathcal{A} (Yoshida, 1971). Since there is a one-to-one correspondence between the points $x \in \Omega$ and the pure state functionals on $\mathcal{A} \simeq \mathcal{C}_r(\otimes)$ (i.e., the extremal positive linear functionals on $C_0(\Omega)$), ontic states are represented by pure state

⁴In physics, for instance, the mathematical formalism required for an ontic and individual description is generally different from the formalism required for an epistemic and statistical description (Atmanspacher & Primas, 2003).

functionals. The ontic valuation $v : \mathcal{A} \rightarrow \mathbb{R}$ of any observable $B \in \mathcal{A}$ is dispersion-free, $v(B^2) = v(B)^2$, if \mathcal{A} is commutative; classical point mechanics is an example. We call a state of a system *determinate* if its observables are dispersion-free. Such states have a pointwise representation in Ω . This illustrates that an information theoretical characterization, with “finite” information, is not appropriate for ontic descriptions (of classical systems).

For an epistemic (statistical) description, one defines a Kolmogorov space (Ω, Σ) by specifying a σ -algebra Σ of subsets A in Ω . Since epistemic descriptions refer to empirical purposes, Σ is required to be the Boolean algebra of experimentally decidable alternatives. Any normalized measure μ on (Ω, Σ) is a probability measure characterizing an epistemic (statistical) state. Note that the definition of an epistemic state requires a Kolmogorov space (Ω, Σ) , not only a state space Ω . It refers to our knowledge as to whether an ontic (individual) state x is more likely to be in some subset A rather than in others. An ensemble (à la Gibbs) of ontic states is an example of a clearly statistical concept of an epistemic state.⁵

Equivalently, epistemic states can be represented by Radon–Nikodým derivatives $d\mu/d\nu$, where ν is a reference measure (typically the Lebesgue measure). They are positive and normalized elements of the Banach space $L^1(\Omega, \Sigma, \nu)$. The dual of this Banach space is the W^* -algebra \mathcal{B} of ν -essentially bounded Borel-measurable functions on Ω , the algebra of bounded observables. Such a representation of epistemic states (and their associated observables) generally requires a partition of Ω whose construction depends on the selected context (and its associated relevance criteria). If the support of the probability measure μ representing an epistemic state is not a singleton, μ represents the information about the localization of the ontic state in Ω .

To the same degree to which ontic descriptions are context-independent, they hide the richness and variety of empirical reality. This manifests itself in the fact that pattern detection and recognition devices determine what is considered as relevant or irrelevant. Patterns are detected and recognized by rejecting information which is selected as irrelevant in particular contexts (but may be relevant in others). Based on such contexts, *an epistemic state refers to the (generally incomplete) knowledge that can be obtained about an ontic state.*

Notes

The limited informational content of an epistemic state μ can be due to two basically distinct kinds of reasons. First, it can be due to “objective” influences such as uncontrollable perturbations originating from the system’s environment or intricate interdependencies among its internal constituents. Second, it can be due to “technical” reasons such as the imprecision of measurements or the fact that any decimal expansion of real numbers has to be truncated somewhere for computational purposes.

In the second case, the epistemic state encodes the reduced amount of knowledge about an individual ontic state that results from explicitly epistemic procedures. We use the notion of *error* to address this situation. Error characterizes the scatter of measured or rounded values of an observable with respect to an assumed “true” value in an ontic state. Variation, on the other hand, refers to a distribution of ontic states, each of which is characterized by a “true” value

⁵However, the corresponding probability distribution can also be viewed in an individual, ontic interpretation (in terms of a distribution “as a whole”), as in kinetic theory (à la Prigogine) or in classical continuum mechanics (à la Truesdell).

of one of its associated observables. This is the situation in the first case above.⁶ In complex systems, epistemic states and the corresponding distributions are generally “superpositions” of both error and variation.⁷

In addition to the technical notion of variance as the second moment of a distribution and the notion of variation as introduced above, there is the term *variability*. In scientific literature, variability is most often used as a generic characterization of change. For instance, both variance and variation can be kinds of variability, but also the feature of the dependence of the value of an observable on time is often denoted as variability. This applies in particular to neuronal signals whose variability simply refers to deviations from a constant value. Variability in the sense of time-dependence can be due to a deterministic dynamics or due to stochastic influences (see the following two subsections).

2.2 Determinism, Causation and Prediction

The temporal evolution of an ontic state $x \in \Omega$ as a function of time $t \in \mathbb{R}$ is a trajectory $t \mapsto x(t)$; the ontic state $x(t)$ determines the intrinsic observables that a system has at time t exhaustively. The temporal evolution of an epistemic state μ corresponds to the evolution of a bundle of trajectories $x(t)$ in Ω . The concept of an individual trajectory of an individual, ontic state is irrelevant within a purely epistemic description.

If the dynamics is reversible then $\mu(T^{-1}(A)) = \mu(T(A)) = \mu(A)$ for all $A \in \Sigma$, where $T : \Omega \rightarrow \Omega$ is an automorphism on the state space Ω . Time t can then be introduced via the a one-parameter group of the t -th powers of T . If T is a μ -preserving invertible transformation, the evolution of a corresponding system is both forward and backward *deterministic*. In such a case, there is no preferred direction of time. Fundamental physical laws (e.g. in Newton’s mechanics, Maxwell’s electrodynamics, relativity theory) are time-reversal invariant in this sense.⁸ (Note that fundamental physical laws are also time-translation invariant, such that no instance in time is distinguished and, thus, there is no *nowness* in physics.)

Phenomenological physical theories such as thermodynamics operate with a distinguished direction of time where the time-reversal symmetry of fundamental laws is broken. This leads to an irreversible dynamics given by a one-parameter semigroup of non-invertible transformations describing an evolution that is either forward or backward deterministic. (Note that, from a purely *mathematical* point of view, semigroups are more general than groups, since they do not require an inverse element. In this sense, a basic mathematical definition of *determinism* refers to one-parameter semigroups, where the parameter is physical time $t \in \mathbb{R}$ (Nickel, 2002).)

The breakdown of both time-translation invariance and time-reversal invariance is necessary to distinguish first a particular instance in time t (*nowness*) and then, relative to this instant, two temporal domains called past and future. In this way, a *tensed time* can be generated which differs fundamentally from the *tenseless parameter time* of physics. The concrete implementation

⁶From the perspective of statistical modeling, the two situations are known as fixed-effect modeling (with errors) versus random-effect modeling (with variation). Within a stochastic approach, the latter case is sometimes characterized as doubly stochastic (cf. Sec. 2.3).

⁷In quantum systems, the situation is even more subtle since ontic states are usually not dispersion-free. This must not be confused with fluctuations or statistical spreads, amounting to variations due to supposed valuations by point functions.

⁸For a discussion of time-reversal invariant equations of motion versus invariances of their solutions see Atmanspacher et al. (2006).

of this transition is altogether mysterious so far; an interesting speculative framework of how to achieve it was proposed by Primas (2003).

For a discussion of notions such as *causation* and *prediction*, concepts that are more specific than determinism alone, tenseless time is a sufficient prerequisite. Among several varieties of causation, this applies particularly to *efficient causation* in the sense of cause-effect relations that are conceived on the basis of a well-defined ordering relation between earlier and later events. This ordering is also significant for the notion of prediction (and retrodiction).

It is important to realize that any type of causation implies that the concerned events are correlated, but the converse does not hold. The observation of correlations (say between *A* and *B*) is a most basic cornerstone of all empirical science, but the assignment of a causal relation is *never* a result of empirical observations alone. Even experimental designs that investigate the effects of perturbed initial conditions or perturbed input variables cannot exclude the possibility of a (hidden) common cause for both *A* and *B* and render a direct causation from *A* to *B* spurious. In order to assign and specify causal relationships to a measured correlation, it is inevitable to embed the empirical material within a theoretical framework.

Let us now illustrate and delineate the three notions of determinism, causation, and prediction by three historical quotations from Laplace, Maxwell, and Poincaré. In a famous quotation in the preface to his “Essai philosophique sur les probabilités”, Laplace (1951) addressed a distinctively ontic type of determinism:

We ought to regard the present state of the universe as the effect of its antecedent state and as the cause of the state that is to follow. An intelligence knowing all the forces acting in nature at a given instant, as well as the momentary position of all things in the universe, would be able to comprehend in one single formula the motions of the largest bodies as well as the lightest atoms in the world, provided that its intellect were sufficiently powerful to subject all data to analysis; to it nothing would be uncertain, the future as well as the past would be present to its eyes.

The intelligence in question became known as Laplace’s demon; its capabilities reach beyond the epistemic realm of empirical observation and knowledge. Moreover, Laplace presumes a directed time when talking about cause and effect. Such a time concept is transcended in the last two lines of the quotation which refer to a type of determinism more general than causation.

More than half a century later, in 1873, Maxwell delivered an address at Cambridge University concerning the debate between determinism and free will in which he said (Campbell & Garnett, 1882):

It is a metaphysical doctrine that from the same antecedents follow the same consequences. No one can gainsay this. But it is not of much use in a world like this, in which the same antecedents never again concur, and nothing ever happens twice. ... The physical axiom which has a somewhat similar aspect is ‘that from like antecedents follow like consequences’. But here we have passed ... from absolute accuracy to a more or less rough approximation. There are certain classes of phenomena ... in which a small error in the data only introduces a small error in the result. ... There are other classes of phenomena which are more complicated, and in which cases of instability may occur ...

Maxwell clearly distinguishes ontic and epistemic descriptions as based on the notions of stability and uncertainty in this quote. His focus is on causation though – his argument is on antecedents

and consequences in the sense of causes and effects. If they are understood as ontic states at earlier and later times, the statement “from like antecedents follow like consequences” characterizes a strong version of causation which is, for instance, not applicable to chaotic systems exhibiting a sensitive dependence on initial conditions. Under such conditions, a weak version of causation is relevant. It does not contradict the “metaphysical” (ontological) statement that “from the same antecedents follow the same consequences”. In the framework of strong causation small changes in the initial conditions for a process can only result in small changes after any amount of time. Weak causation includes the possibility that small changes in the initial conditions are amplified as a function of time, such that “same consequences” can only be obtained by “same antecedents”.

Early in the last century, Maxwell’s formulation was refined by Poincaré (1908):

If we knew exactly the laws of nature and the situation of the universe at the initial moment, we could predict exactly the situation of that same universe at a succeeding moment. But, even if it were the case that the natural laws had no longer any secret for us, we could still only know the initial situation approximately. If that enabled us to predict the succeeding situation with the same approximation, that is all we require, and we should say that the phenomenon had been predicted, that it is governed by laws. But it is not always so; it may happen that small differences in the initial conditions produce very great ones in the final phenomena. A small error in the former will produce an enormous error in the latter. Prediction becomes impossible ...

Here, the issue of prediction is addressed explicitly. Its obviously epistemic meaning at the end of the quote appears to be somewhat confused with ontic arguments at its beginning. “If we knew exactly ...” alludes to Laplace’s demon with its ontic realm of relevance, but it is immediately mixed up with causation (“initial conditions”, “succeeding moment”) and epistemic predictability (“we could predict”).

Both Maxwell and Poincaré referred to what is today known as deterministic chaos. The behavior of chaotic systems in this sense is governed by deterministic equations, yet it is not predictable to arbitrarily high accuracy. In the theory of nonlinear dynamical systems, this behavior is characterized by a diverging Kolmogorov-Sinai entropy, $h_T \rightarrow \infty$, corresponding to a vanishing predictability horizon $\tau \approx 1/h_T \rightarrow 0$. A perfectly regular, deterministic system is characterized by $h_T = 0$. Chaotic systems with finite positive Kolmogorov-Sinai entropy, $0 < h_T < \infty$, fill the gap between perfectly predictable and perfectly unpredictable behavior and exhibit predictability horizons $\infty > \tau > 0$.

Notes

In contrast to efficient causation, the notion of *formal causation* is often used to refer to conditional logical propositions, so-called implications, rather than temporal cause-effect relations. In particular situations, logical reasons may be translatable into temporal causes, but in general this is not the case. If, for instance, a fundamental law is regarded to be the reason for the behavior of a system, this is clearly an atemporal statement.

Another variant of causation is *circular causation*, typically occurring in self-referential (e.g., recurrent or reentrant) systems where local outputs reappear as local inputs. This is a typical situation in complex systems, where the alleged fallaciousness of circular causation can easily be

avoided by considering time delays. In another context, the description of complex systems can often be improved by or even requires considering circular causation in terms of self-consistency criteria. For the mind-brain context see Freeman (1999).

Finally, the notion of *downward causation* is sometimes used to characterize the idea that, in a multilevel description of a system, higher-level properties “influence” lower-level properties. A good example is the emergence of convection rolls in Benard cells, where the convective motion governs the motion of individual molecules in the cell. For a discussion of downward causation for the mind-brain problem see Szentagothai (1984). A more appropriate term for such phenomena would be that of downward constraints (see Sec. 2.5).

A very popular fallacy, extending over virtually all fields of science, is the confusion of causation with correlation. As a prominent example, cognitive neuroscience is an extensive playground for fallacious ascriptions of causation. The standard mistake, clearly pointed out by Fell et al. (2004), can be illustrated by statements of the type “brain states cause mental states”. This typical flaw can be traced to an infelicitous blend of materialist and reductionist background assumptions addressed to some extent by Bennett & Hacker (2003). In general, any topic in which different levels of description are involved is vulnerable to the same confusion.

As another, more specific example, the economist Granger (1969) suggested a technique, today addressed as “Granger causality”, for determining whether one time series is useful in predicting another. This technique exploits correlations among segments of two time series A and B at different times. If earlier segments of A are useful in predicting later segments of B , A is said to “Granger-cause” B (or *vice versa*). Situations with a hidden common cause of A and B provide striking counterexamples as far as causation is concerned: Even though A allows predictions about B , a change of A does not entail a change of B . For the application of Granger causality to neuroscience see Ding et al. (2006) and Seth (2008).

A standard strategy in the study of temporal correlations between two different sources (e.g., action potentials of two neurons) is to analyze cross correlation functions. Typically, the result of such studies yields considerable signals at both positive and negative time lags. The significance of the negative time lags is not something like *backward causation*, but they reflect the recurrent structure of the network in which the neurons are immersed.

A fundamental kind of conceptual difficulty arises if both ontic and epistemic perspectives need to be taken into account together. This is the case in deterministic chaos, where an ontically deterministic dynamics is not completely predictable epistemically. As has been discussed in detail by Atmanspacher (2000), these different perspectives can be conveniently referred to by stability arguments versus information theoretical approaches.

The idea to model neurodynamics in terms of deterministic chaos goes back to early work of Freeman (1979) (see also Amit, 1989). It has been of increasing influence over the decades, and today there is general agreement that chaotic processes play an important role to understand the dynamics of the brain at various levels. Cognitive science and psychology have adopted this idea (Van Gelder, 1998; Beer, 2000). We come back to these issues in Sec. 3.3 and 3.4 in particular.

2.3 Probability and Stochasticity

The concept of determinism is insufficiently represented if it is compared only with causation and prediction. An important arena with its own tradition is the tension between deterministic and stochastic behavior.⁹ Roughly speaking, stochastic behavior is what is left if one tries to describe the world in deterministic terms.

In the theory of stochastic processes, the behavior of a system is described in terms of stochastic variables $x(t)$, parametrized by time $t \in \mathbb{R}$, whose distribution $\mu(x, t)$ is an epistemic state. The description of a system in terms of individual trajectories $x(t)$ corresponds to a point dynamics of an ontic state, whereas a description in terms of the evolution of the associated measure $\mu(x, t)$ corresponds to an ensemble dynamics of an epistemic state.

The limiting cases of infinite and vanishing predictability addressed in the preceding section correspond to special types of stochastic transition matrices. For instance, singular stochastic processes are completely deterministic and allow a perfect prediction of the future from the past. The general case of limited predictability is covered by the notion of a regular stochastic process. This analogy notwithstanding, comprehensive accounts or textbooks dealing with explicit relationships between the theories of nonlinear systems and stochastic processes in general have only become available recently, see Lasota & Mackey (1995) and Arnold (1998). The difference between deterministic and stochastic approaches is made especially clear in Arnold's discussion of conceptual differences between the "two cultures" (pp. 68ff in Arnold (1998)).

A major point of discrepancy in this respect is that (in most standard treatises) stochastic processes are intrinsically understood as time-directed (semigroup evolution). By contrast, the ergodic theory of dynamical systems considers a time-reversal symmetric (group) dynamics, offering the possibility of symmetry breakings that lead to forward as well as backward deterministic processes. In earlier work, Arnold & Kliemann (1983) introduced the concept of Lyapunov exponents for linear stochastic systems (of arbitrary dimension) rather than low-dimensional chaos in nonlinear deterministic systems. More recently, the basis of these approaches, Oseledec's multiplicative ergodic theorem, has been generalized from formulations in Euclidean space to manifolds (Arnold, 1998).

The dichotomy of ontic and epistemic descriptions is also prominent in the theory of stochastic differential equations. For instance, Langevin type equations such as

$$dx(t) = -\gamma x(t) dt + d\xi(t) \quad (1)$$

generally treat stochastic contributions $\xi(t)$ in addition to a deterministic flow in terms of fluctuations around the trajectory of a point x in phase space.¹⁰ Such a picture clearly reflects an ontic approach. On the other hand, the evolution of epistemic states μ , i.e., densities, is typically described by Fokker-Planck type equations such as

$$\frac{\partial}{\partial t} \mu(x, t) = \frac{\partial}{\partial x} \gamma x \mu(x, t) + \frac{1}{2} \frac{\partial^2}{\partial x^2} Q \mu(x, t) \quad (2)$$

⁹We use the terms "stochasticity" and "stochastic behavior" as synonymous with "randomness" and "random behavior", as Halmos (1986) suggested: "'Stochastic' is a learnedly elegant way of saying 'random' ". The notion of randomness seems to be favored in the Russian tradition, whereas stochasticity is more frequently used in the Anglo-American terminology.

¹⁰Langevin equations are linear in x ; nonlinear generalizations are due to Ito and Stratonovich. The stochastic term ξ in Eq. (1) is most often considered to be uncorrelated (white) noise.

with drift term $-\gamma x$ and diffusion term Q accounting for deterministic and stochastic contributions to the motion of μ in phase space. Although both types of formulations can be shown to be “equivalent” in a certain sense (see e.g. Haken, 1983; Gardiner, 1985, for an elementary discussion), this must not be misunderstood as a conceptual equivalence. An epistemic description refers to the knowledge which is empirically available about an ontic state that itself is empirically inaccessible but can nevertheless be modeled in an ontic description.

The concept of probability and the framework of probability theory have become inevitable tools with which stochastic processes are described or modeled. Yet, as Huber (1995) provocatively formulated, “stochasticity has (almost) nothing to do with probability”. For instance, in a gambling system each individual outcome is equally likely, and it is impossible to distinguish stochastic and non-stochastic behavior on the basis of probability theory.

Kolmogorov’s axiomatization of probability theory in terms of measure theory (Kolmogorov, 1933) has been so successful precisely because it is not concerned with individual (ontic) stochastic events and their characterization. Much later, Kolmogorov (1968) re-addressed these issues in a paper introducing the concept of algorithmic randomness, today also called algorithmic complexity. He indicated how the stochasticity of individual events can be founded without any recourse to probability theory. Essentially the same idea was, from different starting points, worked out by Solomonoff (1964) and Chaitin (1969).

With this background in mind, the measures that characterize statistical (epistemic) states μ are reasonably called probability measures.¹¹ Depending on whether they describe fixed effects or random effects in the sense of Sec. 2.1, their dynamical evolution is called a singly or doubly stochastic process (Cox, 1955).¹² Particular complications arise in complex systems where sequences of states or observables are often (or even usually) not stationary, or where limit theorems of probability theory (central limit theorem, law of large numbers) do not apply. In the latter case, the field of large deviations statistics (Ellis, 1985) has become an important tool of choice.

Notes

Probabilistic methods and stochastic dynamics play a prominent role for mathematical models of brain activity, as well as for the description of brain structure. For instance, the essential molecular components of electrical activity in nerve cells, the so-called ion channels, open and close stochastically. They are effectively described by finite-state Markov processes. The associated probabilities depend on circumstantial factors which turn them into powerful switching elements with a rich functionality (see Sect. 3.1).

Trains of action potentials generated by individual neurons are frequently described in terms of stochastic point processes, most prominently the Poisson process. Implicitly, this presupposes that the only relevant aspect of spiking is the time-dependent firing rate of neurons (see

¹¹Note that Finetti (1974), in his definition of *subjective probability*, proposed to utilize the distinction between randomness and stochasticity in the following way. In his terminology, randomness refers to the objects of probability theory, while stochasticity refers to what is valid in the sense of probability theory. As indicated above, we use randomness and stochasticity synonymously throughout this article.

¹²Note that, alternatively, transition matrices (of stochastic processes) are called doubly stochastic if the transition probabilities in both rows and columns are normalized. They are called uniformly stochastic if the distribution of N states is given by $p_i = 1/N$.

Sect. 3.2). More detailed models of input integration in neurons conceive the membrane potential process as a continuous-valued stochastic process, like a one-dimensional random walk (Gerstein & Mandelbrot, 1964; Brunel, 2000). Spiking is induced by imposing a threshold on the fluctuating potential. Standard probabilistic descriptors, like the distribution of first-passage times, then yield a viable characterization of single-neuron dynamics (see Sect. 3.3).

The complex behavior emerging in recurrent networks of spiking neurons has been identified as deterministic chaos in particular dynamical regimes. Nevertheless, generically statistical descriptors (e.g. “irregularity”, or “synchrony”) are much used for the characterization of stationary states. Similarly, a probabilistic description of biological neuronal networks in terms of easily measurable parameters (e.g. coupling probability in random graphs) currently appears to be best suited to cope with the obvious complexity of the underlying circuits (see Sect. 3.3).

2.4 Deterministic Embedding of Stochastic Processes

It is not surprising that deterministic processes such as fixed points or periodic cycles can be considered as special cases of more general formulations in terms of stochastic processes. This is easily understandable if all entries in a stochastic transition matrix are either 1 or 0, thus representing deterministic transitions among states. What comes somewhat as a surprise is the converse, namely that stochastic processes can be understood in terms of deterministic processes. This has been accomplished by means of a mathematical theory of so-called natural extensions or dilations of stochastic processes.

Gustafson (1997) discusses three types of corresponding “dilation theories”. Consider a flow T_t on subsets of a phase space Ω , and consider the space (Ω, Σ, ν) of probability densities μ defined over Ω . Then dilations according to Halmos, Sz. Nagy, Foias, Naimark and others dilate the densities μ , dilations according to Kolmogorov and Rokhlin dilate the flow T_t , and dilations according to Akcoglu, Sucheston and others dilate the reference measure ν . For details on literature see also Gustafson & Rao (1997) and Misra (2002).

The common feature of such dilations is the extension of a (non-invertible, irreversible) Markov semigroup evolution to a (reversible, invertible) unitary group evolution. Applying the dilation theory of exact systems to K-flows (Rokhlin 1961, cf. Sec. 4.5 in Lasota & Mackey (1995)), Antoniou & Gustafson (1997) have recently achieved important progress with the proof of a theorem on the positivity-preservation of densities in unitary dilations (see also Gustafson (1997)). The significance of this theorem is that deterministic embeddings of stochastic processes *exist*; this does not entail an explicit and unique prescription for *how* to construct them.

The conceptual meaning of this important result can be illustrated in the following way. A system that is originally described stochastically, e.g. due to uncontrollable interactions with its environment, is successively extended into the environment as long as all interactions are integrated in the behavior of the system itself. This leads to an increasing number of degrees of freedom, enabling an integration of all previously stochastic behavior into an overall deterministic dynamics. If such a procedure is supposed to be of general relevance, ultimately the universe as a whole has to be considered in order to achieve a complete deterministic embedding. Primas (2002) referred to this idea as hidden determinism, or crypto-determinism.

Notes

If deterministic and stochastic dynamics can be transformed into each other, it follows that corresponding (*epistemic*) descriptions cannot be taken as indicators of determinacy and stochasticity as (*ontic*) features of nature. After all, the existing dilation theorems show that the gap between the two is often a matter of convenience or convention. If a stochastic description of a system seems to be appropriate, this can be simply due to a lack of knowledge about underlying observables and corresponding laws of nature. Conversely, certain idealizations that ignore fluctuations or perturbations of a system can easily lead to a deterministic description.

With particular respect to a number of deep philosophical topics, studies in neurodynamics are hoped to resolve the question whether the brain is a completely deterministic “machine” or a generator of stochastic events with indeterminate connections. Of special interest is the case of “deterministic chaos”, processes that are ontically deterministic but have limited epistemic predictability because of the sensitive dependence of the dynamics on initial ontic states. In Sec. 3.3 we will discuss accumulating evidence for this type of chaos in brain dynamics.

The intricate relations between determinacy and stochasticity raise strong doubts concerning the hope to infer ontologically valid statements from neurodynamical descriptions. These doubts are amplified by the observation that even the kind of description that is suitable depends on the level of brain activity one is interested in. As will be discussed in detail below, moving from microscopic (sub-cellular, membrane-bound molecules) to mesoscopic (neuronal assemblies) and macroscopic (large networks or populations of neurons) levels, completely different kinds of deterministic and stochastic models are suitable and relevant.

For this reason, it is (presently) almost hopeless to defend the position that neurodynamics “is” deterministic or not. This bears significance with respect to all kinds of problems related to “free will”, “free agency” and the like. The point here is not so much that relating neuroscientific and philosophical discourse to each other naively may be a category mistake (which it may indeed be). The point is that pretentious claims as to the brain as a deterministic system are unfounded, and so are any consequences drawn from them.

2.5 Hierarchies of Ontic and Epistemic Descriptions

In a recent article, Keller (2007) has argued that the traditional approach in physics to look for fundamental laws may not be the optimal choice to address complex biological systems. This is certainly agreeable. However, even in physics it is not the case that empirical phenomena are directly addressed by fundamental descriptions. This boils down to the point, emphasized in earlier sections, that epistemic states of a system must not be confused with ontic states. To describe empirically accessible information in terms of a more fundamental theory, the contexts introduced by measuring tools or pattern detection and recognition devices used by the experimentalist have to be taken into account explicitly.

In mathematical terms, a context can be implemented within a fundamental theory by restricting its domain of validity and introducing a new, coarser topology (i.e., a coarse graining, or a partition) compatible with the topology of the underlying fundamental theory. There are many possibilities to introduce such a *contextual topology*. A standard strategy uses singular asymptotic expansions which do not converge in the original topology of the ontic description. Examples

include the emergence of phenomena of geometrical optics (such as “shadows”) in the high-frequency limit, and the emergence of inductors, capacitors and resistors in the low-frequency limit of Maxwell’s electrodynamics. Another instance is the emergence of the shape of molecules in the singular asymptotic Born-Oppenheimer expansion at the singular point of an infinite nuclear mass (see Primas (1998) for more details).

Of course, physical examples are not enough to cover the entire hierarchy leading from elementary particles in physics to chemistry, biology, to psychology and other areas of social science. But they show that for epistemic descriptions the specification of a context is as important as the underlying ontic description. Since there are many levels involved in the mentioned hierarchy, it is reasonable to speak of a lower-level description formulated in ontic terms always as *relative to* a subsequent higher-level description formulated in epistemic terms.

We will outline below how examples relevant for brain science and cognitive science can be constructed. At this point, a simple example for the scheme of *relative onticity* is given by the relation between statistical mechanics and thermodynamics. A statistical description of a many-particle system is clearly epistemic, while the underlying description of many particles in motion according to classical point mechanics is ontic. However, an observable such as temperature is contained in neither of the two descriptions. It *emerges* from a statistical description by implementing the context of thermal equilibrium as a stability criterion (Takesaki, 1970). See Bishop & Atmanspacher (2006); Atmanspacher & Bishop (2007) for more discussion.

The conceptual structure of this construction is: (i) start with a description by ontic states at a particular level, (ii) select properly defined equivalence classes of ontic states, (iii) introduce epistemic states by reformulating these equivalence classes in terms of statistical distributions, and (iv) reinterpret these epistemic states as ontic states with new emergent observables. Contextual conditions at the higher-level description are necessary for the selection of a proper topology (partition) in step (ii) that yields the emergent observables at this level.

The central issue of the concept of relative onticity is that states and observables of a system, which are treated epistemically at a particular level i of description, can be both related to ontic states and their observables at a lower level ($i - 1$) and reinterpreted as ontic states with emergent observables at level i . Emergent observables at successively higher levels of description can be formally addressed by a change of perspective which is not uniquely given but depends on contexts and conceptual schemes that must be selected properly. Depending on what is relevant (and irrelevant) for the particular context under investigation, different contextual topologies must be chosen as appropriate.¹³ The notion of *contextual emergence* has been introduced (Bishop & Atmanspacher, 2006) for this scheme. The significance of such contexts implies that a strict reduction of higher to lower levels of descriptions fails.

The entire approach discussed so far essentially regards successively higher levels of description in the sense of increasing diversity. Generally speaking, moving from one level to the next higher level corresponds to a symmetry breaking. Such a so-called “bottom-up” approach is usually assumed as a proper way to reflect the evolution of more and more complex systems in the material world. But, in addition, the observables of a system at a higher level can also constrain the behavioral options at the lower level.¹⁴ Bénard convection is a good example: the circular

¹³Schulmann & Gaveau (2001) discussed this issue in terms of the question of how to choose proper coarse grainings of physical state spaces.

¹⁴This is often, somewhat misleadingly, called “downward causation”, cf. Sec. 2.2. Another notion, coined by Haken, is that higher-level observables (order parameters) “enslave” lower-level observables.

motion of convection roles in a liquid govern the motion of individual molecules in the liquid.

Usually, the time scale on which the constrained lower-level motion operates is much smaller than that of the constraining higher-level motion. This is similar in the examples mentioned above: the motion of convection roles is slow compared to the motion of the molecules, changes of the temperature of a system are slow compared to changes of the momenta of particles in a many-body system, rotational motion is slow compared to vibrational motion of molecules in the Born-Oppenheimer picture. Time scale separation is an important and useful criterion for the distinction of different levels of description, on which ontic and epistemic states can be discussed. It is likely that space scale separation serves the same purpose.

Notes

The idea to ascribe ontic relevance to a particular level of description only relative to another, epistemic, level of description (Atmanspacher & Kronz, 1999) picks up Quine's proposal of an "ontological relativity" (Quine, 1969). It tries to circumvent the assumption of an absolute ontology (e.g., of elementary building blocks of reality) and requires an ontological commitment for each particular situation to be discussed. For example, classical point mechanics is to be viewed ontic relative to statistical mechanics, but epistemic relative to quantum mechanics. This has ramifications for the design of intertheory relations such as reduction, supervenience, and emergence. While the ultimate goal of reduction in the conventional sense of physics is an explanation of physical phenomena in terms of the fundamental building blocks of an absolute ontology, relative onticity renders the idea of reduction, as well as its alternatives, more flexible.

A sophisticated alternative to reduction was introduced recently and denoted as contextual emergence (Bishop & Atmanspacher, 2006). It is characterized by the fact that a lower-level description provides necessary, but not sufficient conditions for higher-level descriptions. The presence of necessary conditions indicates that the lower-level description provides a basis for higher-level descriptions, while the absence of sufficient conditions means that higher-level features are neither logical consequences of the lower-level description nor can they be rigorously derived from the lower-level description alone.

Sufficient conditions for a rigorous derivation of higher-level features can be introduced by identifying higher-level contexts that reflect the particular kind of contingency in a given situation. These contexts can be implemented as stability criteria in the lower-level description and induce a partition (coarse-graining) as a change in the topology of the corresponding state space by applying techniques of symbolic dynamics.¹⁵ This yields a mathematically well-defined procedure for deriving higher-level features from the lower-level description plus the contingent contextual conditions of the higher-level description.

As demonstrated by Atmanspacher & beim Graben (2007), this method can be successfully used to construct mental states from neurodynamics, a central problem of cognitive neuroscience (see Sec. 3.5). It should be noted that this construction complements contextual emergence by a key issue of supervenience, namely the idea that particular higher-level features can be *multiply realized* at the lower level of description. In this respect, supervenience posits sufficient but not

¹⁵In symbolic dynamics, one tries to map a lower-level dynamics of fine-grained states to the dynamics of coarser equivalence classes of states (Lind & Marcus, 1991). For this purpose one needs to find a partition whose cells are invariant under the dynamics, so that their definition is robust. For nonlinear systems, such partitions (so-called generating partitions or Markov partitions) are generally inhomogeneous and not easy to find.

necessary conditions at the lower level. In the scenario proposed by Atmanspacher & beim Graben (2007) contextual emergence and supervenience together do not simply imply reduction because they refer to different entities: contextual emergence refers to properties, while supervenience refers to states.

In many cases, contextually emergent properties vary on time scales that are longer than the time scale of the dynamics at the lower-level description. However, there are exceptions to this rule of thumb which we will discuss in Sec. 3.2. There are situations in which time scales at different levels of description are similar, so that they cannot be used to separate levels. And even if time scales are different, the higher-level dynamics is not necessarily characterized by the slower process.

3 Levels of Neurodynamics: From Ion Channels to Neuronal Networks

This section reviews some core aspects of neurodynamics. Different properties are salient when studying brain activity at different levels of resolution, as for example ion channels, neurons, or networks. Therefore, the corresponding conceptual frameworks and mathematical models present a picture of neurodynamics that is quite non-uniform. Sweeping from microscopic over mesoscopic to macroscopic components of the brain, deterministic, chaotic or stochastic descriptions can each be adequate. The proper choice for one of them is usually motivated by arguments concerning which features are important and which aspects have little or no relevance at each particular level. This entails that it is often premature – and always risky! – to draw general conclusions from neurodynamics for the organism by taking only a single level of description into account. In fact, an interpretation derived from models at one level may be contrary to the conclusions obtained from another level. We will discuss scenarios yielding different conclusions at the level of stochastic subcellular biophysics, at the level of quasi-deterministic isolated neurons and at the level of large chaotic networks. As a consequence, grounding philosophical discussions on properties of the brain requires us to keep an eye on the many facets of neurodynamics.

Specifically, we will cover a number of issues that were, and still are, intensely discussed in the neuroscientific literature. Section 3.1 about the reliability and precision of individual neurons highlights the fundamental finding that ion channels, which are essential for the functioning of neurons, exhibit stochastic behavior. It also discusses how this influences the dynamics of whole nerve cells, which rely on the joint operation of a very large number of ion channels. Section 3.2 gives an account of the relative contributions of different sources of noise and fluctuations to the neuronal activity dynamics in the intact brain of behaving animals (and humans) and discusses to which degree they can be separated by their time scale.

In Section 3.3 we discuss the emergence of complex dynamics of recurrent cortical networks characterized by asynchronous irregular activity of its neurons, presumably reflecting deterministic chaos. The following Sec. 3.4 on “neuronal assemblies and spike correlations” dwells on Hebb’s original idea that neurons do not operate in isolation, but cooperate with (many) others. We present some modern interpretations of this crucial feature in terms of “combinatorial coding” and “higher-order correlations”. Finally, Sec. 3.5 gives an account of the problems which one meets when assessing the meaning of correlations between brain activity and what it is supposed to encode in terms of mental or behavioral states. We contrast the concept of correlation

with that of causation, and address the role of additional constraints as, e.g., introduced by “embodiment” of the brain.

3.1 Reliability and Precision in Individual Neurons

The biological function of living cells depends on the selective transport of ions across their membranes through ion channels. Channels are macromolecules which are loosely bound to the cell membrane, and which can act as pores under certain conditions. For example, the ability of nerve cells to employ electric currents for signaling is based on a variety of ion channels with different properties. Particularly the ability of neurons to generate short impulses, so-called action potentials or spikes, is owing to specialized voltage-dependent ion channels. The properties of these channels are mainly responsible for the non-linear “all-or-nothing” dynamics of spiking neurons. Spikes reliably cover very long distances without compromising the low noise level of the transmitted signal. This feature is of fundamental importance for the functioning of a brain (Kandel et al., 2000).

Individual ion channels admit a small number of discrete states, defined by the three-dimensional conformation of the molecule. Some of these states are such that ions can traverse the membrane following their concentration gradient (open, or conducting), others are prohibitive (closed, or non-conducting). In their natural environment at room or body temperature, individual ion channels exhibit seemingly erratic openings and closings, at frequencies which depend on circumstantial parameters (Hille, 1992). Multiple random impacts of water molecules are responsible for this behavior, and neither the nerve cell nor an experimenter can gain control over this source of randomness. However, stochastic models describing the memoryless transitions between states (“Markov processes”) have been very successful in quantitatively characterizing the behavior of individual channels (Sakmann & Neher, 1995). Such models assume a probability (rate) associated with each possible transition, and modulatory parameters (like the membrane potential at the spike initiation zone, or the concentration of neurotransmitter in the synaptic cleft) may influence these transition probabilities. Control over probabilities replaces absolute control in a deterministic setting. Almost-determinate (almost-deterministic) behavior is reflected by state (transition) probabilities close to 0 or 1, respectively.

The function of intact nerve cells relies on large populations of ion channels, rather than few individual ones. The compound ion currents resulting in larger membrane patches and whole neurons have greatly reduced fluctuations as compared to single-channel currents. This averaging or smoothing of signals associated with (lower-level) ion channel populations is due to the independent, uncorrelated operation of its constituents. As a consequence, the classical (higher-level) description of single-neuron states and their dynamics including action-potential generation is both determinate (in the sense of Sect. 2.1) and deterministic (in the sense of Sect. 2.2), first given by Hodgkin & Huxley (1952) in terms of non-linear differential equations. Not only was this formal description found very adequate for isolated nerve cells, physiological experiments also demonstrated that real neurons can be extremely *reliable* and *precise*.

In fact, it was demonstrated that neurons effectively operate as deterministic spike encoders, provided the input by other neurons matches natural conditions in terms of its spectral composition (Bryant & Segundo, 1976; Mainen & Sejnowski, 1995), see Sect. 3.3 for further discussion. Although for the neocortex the level of noise (e.g. induced by spontaneous channel openings and unreliable synapses) is still under debate, there is accumulating evidence that these residual fluctuations are negligible at the level of single neurons and networks (Boucsein et al., 2005).

Notes

In appreciation of the biological facts listed above, a characterization of neuronal dynamics in terms of determinacy or stochasticity can be profitably rephrased in terms of reliability and precision. They refer to the aspects of variation and error in the characterization of states (cf. Sec. 2.1) as well as to the aspects of determinism and prediction concerning the dynamics of those states (cf. Sec. 2.2). Both notions, reliability and precision address epistemic issues of predictability horizons and the form of distributions. They avoid ontic connotations or commitments which need to be clarified if one speaks about determinacy and stochasticity.

Reliability and precision are useful to express the relevance of particular phenomena on a microscopic level (e.g. stochastic ion channel openings) for the dynamics on a more macroscopic level (e.g. the operation of nerve cells), and the degree of control that can be exerted either by the system itself or by an experimenter. It cannot be denied, though, that chance phenomena characterize the operation of some subcellular building blocks of neurons in an essential way. These aspects, however, do not seem to play an important role for the functioning of nerve cells, and even less so for the dynamics of the large networks that they constitute.

This is not surprising insofar as an extension of a system into its environment often allows to simplify the description of its dynamics, e.g. by averaging procedures. As indicated in Sec. 2.4, this can lead to a deterministic description if enough stochastic interactions are integrated, i.e. if the system is considered globally enough.¹⁶ The reliability and precision of the behavior of individual neurons enables a deterministic description of neurons despite an underlying stochastic dynamics of ion channels.

Any distribution characterizing a state can in principle be interpreted as due to genuine chance (ontically) or due to ignorance (epistemically). This ignorance, or missing information, can in turn be deliberate, e.g. in order to disregard details that are inessential in a particular context, or it can be caused by uncontrollable perturbations. At the ion channel level, where quantum mechanical effects may occur, an ontic interpretation is possible or likely. But the fact that the stochastic dynamics of ion channels typically leads to highly reliable and precise neuronal behavior suggests that any potentially genuine micro-stochasticity is inefficacious at the neuronal or even network level. Therefore, distributions at the neuronal level are assumed to be of epistemic nature and to have a small variance. Since indeterministic contributions to the dynamics of neurons seem to be of low relevance, the representation of the neurodynamics in a neuronal state space amounts to a fairly well-defined sequence of almost-ontic states, a so-called trajectory.

3.2 Sources and Time Scales of the Variability of Neuronal Activity

Neuronal activity in the active brain is highly dynamic – or variable, depending on the point of view – on multiple time scales. From the viewpoint of a single neuron, this is due to the joint action of many sources of input impinging upon its dendrite, but also additional mechanisms internal to the neuron. The latter include a variety of modulatory ion channels, which can modify the integration dynamics of the neuron (Koch, 1999; Gilboa et al., 2005), but also random effects like spontaneous miniature synaptic events, which also play a role in homeostatic control of network

¹⁶As a rule, this works if the number of degrees is sufficiently large or the fluctuations are sufficiently fast. For instance, moving from a mechanical two-body problem to a three-body problem does not simplify the treatment, but the extension to a many-body problem does.

activity (Sutton et al., 2004). The former reflects both the participation of the neuron in local recurrent networks, where the approximate balance between excitation and inhibition induces fast and relatively large fluctuations of the membrane potential resulting in irregular spike trains (van Vreeswijk & Sompolinsky, 1996; Brunel, 2000). Input from non-local sources, in contrast, may be responsible for the much slower fluctuations of ongoing activity that entrains large neuronal populations as a whole, rather than single neurons individually (Arieli et al., 1996; Leopold et al., 2003).

Can one dissect and separately characterize these different sources of variability from recordings of neuronal activity? This problem is certainly ill-posed in its general form, and only by making simplifying assumptions and considering suitable control experiments can its analysis be attempted. One possible scenario is that the different component processes are independent and operate on separable time scales. Under these conditions, the contributions of the sources are superimposed in such a way that they can be disentangled again. Such a concept has been applied to neuronal spike trains which, under stationary conditions, are described well by stochastic point processes (in particular renewal processes) that mirror the complex dynamics of the local network. An isolated network yields constant firing rates in neuronal spike trains, but perturbations from the environment induce non-stationarities, in particular dynamic fluctuations of the underlying firing rates. The latter can, for example, be caused by ongoing brain processes associated with non-local sources (Rotter et al., 2005a; Nawrot et al., 2008). Spike trains recorded in behaving animals (*in vivo*) are known to be affected by such slow ongoing processes, whereas spiking activity in isolated brain tissue (*in vitro*) cannot not be linked to these sources. A comparison of spike trains obtained in the *in vivo* and the *in vitro* situation leads to the estimate that ongoing activity increases the total variability in the intact brain *in vivo* with respect to the tissue *in vitro* by a factor 2–3 (Nawrot et al., 2000, 2001).

From a conceptual point of view, it would certainly be attractive if brain dynamics at a higher level of organization were generally slower so that they can be separated from the faster low-level dynamics. Although this perspective seems often appropriate, there are cases where it is too simplistic. Two illustrative examples are: (1) the relation between membrane potential dynamics and population activity dynamics in recurrent networks, and (2) the interaction between spike timing dependent plasticity and spiking dynamics in recurrent networks.

(1) The integration of membrane potentials in neurons is essentially determined by the passive electrical properties of the neuronal membrane. This implies time constants in the range of tens of milliseconds. Interestingly, on the level of neuronal populations, the same cells can operate on time scales in the range of milliseconds, if they are part of a recurrent network (Kriener et al., 2008). Population activity is one order of magnitude faster, although it occurs on a higher level of organization. (2) Synaptic plasticity is the presumed cellular basis of system-wide learning and memory in cortical networks. A strong candidate mechanism is spike timing dependent plasticity, which has been shown to apply to many synapses in the central nervous system (Dan & Poo, 2006). The point to be made here is that this Hebbian mechanism (cf. Sec. 3.4 for more details) operates on time scales that do not well separate from the time scales of spiking activity itself. In fact, an intricate balance between recurrent network dynamics and plastic synapses must be established and maintained by the cortical network, the properties of which are just in the process of being explored (Gütig et al., 2003; Morrison et al., 2007). Further contributions by various homeostatic mechanisms (Abbott & Nelson, 2000; Turrigiano & Nelson, 2004) or structural plasticity involving growth and reorganization (Stepanyants et al., 2002) must be taken into consideration.

Notes

The comparison of neuronal activity in isolated brain tissue (*in vitro*) and in the intact brain (*in vivo*) enables studies of the impact of ongoing (background) activity on local subsystems of the brain. As Nawrot et al. (2008) reported, ongoing activity induces strong slowly varying non-stationary contributions to the behavior of spiking neurons. This illustrates how neuroanatomically given differences in size scales are related to differences in the time scales relevant for the corresponding neurodynamics: Smaller subsystems typically operate on time scales that are smaller than those of larger subsystems composed of smaller ones. The comparison of the *in vitro* dynamics of dissected brain tissue with the *in vivo* dynamics of the brain as a whole demonstrates this feature very well. It supports the argument, given in Sec. 2.5, that both size scales and time scales can be used to distinguish levels of description in such a way that lower-level behavior is constrained by higher-level behavior.¹⁷

However, two pertinent examples described above indicate limitations to this argument. In example (1), the fast dynamics occurs at the higher level of neuronal populations, compared to which the behavior of individual neurons changes slowly. The situation in example (2), which has recently received increasing attention, is even more subtle. The reason is that the time scale of the neuronal dynamics (spiking activity) that is supposed to entail the emergence of Hebbian assemblies is of the same order of magnitude as that of the formation of those assemblies due to synaptic plasticity, self-organization, and learning. In such a case, spatial scale remains as an indicator of level distinction: Hebbian assemblies extend over groups of neurons mutually connected with a high density of synapses. But this does not facilitate the analysis of the intricately entangled dynamics in terms of the two kinds of processes.

3.3 Complex Dynamics of Recurrent Cortical Networks

The activity of cortical neurons *in vivo* is generally characterized by highly irregular spike trains (Softky & Koch, 1993; Holt et al., 1996). More precisely, the standard deviation of inter-spike intervals is typically close to the mean interval, a property which is also shared by Poisson processes. This reminiscence of a random phenomenon raises the question which components of single-neuron activity can be considered as a signal, and which aspects must be classified as random noise (Shadlen & Newsome, 1994, 1995). A potential answer is found in the fact that irregular spike trains correspond to strongly fluctuating membrane potentials observed in intracellular recordings *in vivo* (Azouz & Gray, 1999; Carandini, 2004). Comparison with *in vitro* recordings (most afferents cut off) strongly suggests that irregular spike trains *in vivo* are actually caused by deterministic synaptic interactions among the neurons in the network, and that they are not a result of noise processes extrinsic or intrinsic to the network.

Theoretically, it is long established that fluctuating membrane potentials (“random walk” model) in combination with a fixed spiking threshold can, in principle, induce irregular spike trains (Gerstein & Mandelbrot, 1964; Tuckwell, 1988). Membrane potentials fluctuating close to the firing threshold, as observed in many cortical neurons, can be produced by an approximate balance

¹⁷As mentioned above, Haken (1983) coined the notion of the “slaving principle” for such an adiabatic elimination of fast relaxing variables. The variables that exhibit the slow high-level dynamics are often called “order parameters”. They characterize cooperative behavior of a system as a whole which constrains the motion of its components. Analogous to the mentioned example of Bénard convection, a coherent action of a neuronal assembly constrains the activity of individual neurons.

between excitation and inhibition (Shadlen & Newsome, 1998). But do recurrent networks support this mode of dynamic operation?

Modeling studies provide an affirmative answer, suggesting that the emergent complex dynamics might even be chaotic (van Vreeswijk & Sompolinsky, 1996, 1998).¹⁸ Analyses based on a diffusion approximation (Fokker-Planck formalism) of single-neuron dynamics in the high-input regime show qualitatively different types of dynamics of recurrent networks on different equivalence classes of states, depending on the strength of external inputs and on the relative strength of recurrent inhibition in the network (Brunel & Hakim, 1999; Brunel, 2000).¹⁹ One of these equivalence classes of states, briefly “dynamic states”, is characterized by very irregular neuronal spike trains and by a very low level of synchrony across neurons. This “asynchronous-irregular” state, in fact, bears many similarities with spiking activity typically observed *in vivo*.

There is accumulating experimental evidence that neurons in the cortex of awake animals operate in the high-input regime (Destexhe et al., 2003). Under these conditions, the behavior of single neurons is altered with respect to their resting state: neurons become faster and couplings are generally reduced in strength, both due to a decreased input resistance (Bernander et al., 1991). This even leads to a non-monotonic input-output characteristic for neurons, which is at variance with the monotonic sigmoid curves typically assumed in *ad hoc* models (Kuhn et al., 2004). In numerical simulations, asynchronous-irregular states of the network are found to be compatible with the high-conductance regime for synaptic input on membrane potentials. In addition, networks with conductance-based synaptic input, in contrast to current-based synaptic input, exhibit self-sustained asynchronous-irregular activity even without any external input or internal pacemakers (Kumar et al., 2008a).

Notes

To say that recurrent cortical networks have a *complex* dynamics is, to begin with, a phenomenological characterization that says nothing about the deterministic or stochastic sources of that complexity. Similarly, *irregular* spike trains and *fluctuating* membrane potentials reflect the same phenomenological feature at the level of individual neurons. Of course, the question is how these complexities, irregularities and fluctuations are connected and which origin they have. The irregular appearance of neuronal spike trains and fluctuating membrane potentials do not depend on the presence of noise sources, be they extrinsic or intrinsic to the network. They reflect the complex dynamics of a complex, recurrent network.

The empirical, numerical and theoretical pieces of evidence outlined above indicate that significant contributions to these kinds of behavior can be appropriately ascribed to deterministic chaos (cf. Sec. 2.2 for details). Deterministic chaos is often characterized by a sensitive dependence of the dynamics on initial conditions. This leads to time series that appear massively irregular, and standard statistical tools such as Fourier analysis or correlation analysis cannot distinguish deterministic chaos from random noise. Nonlinear times series analysis (see, e.g., Kantz & Schreiber, 1997; Kantz et al., 1998) offers applicable methods in these cases.

The dynamics of a chaotic system takes place on a subspace of the state space that is called an attractor. However, this holds only *cum grano salis*, namely if the transient motion from initial

¹⁸Recent work of Zumdieck et al. (2004) demonstrates that, beyond chaotic attractors, long chaotic transients may abound in complex networks.

¹⁹See Sect. 3.4 for more examples of such types of dynamics and associated equivalence classes of states.

conditions onto the attractor can be disregarded. If such transient motion is not negligible, or if there are many attractors between which the system spends considerable amounts of time, the situation becomes quite sophisticated. For instance, Kaneko (1990) observed *long-time (super-) transients* in studies of complex coupled map lattices, and Tsuda (2001) proposed the scenario of *chaotic itinerancy* with many coexisting quasi-stable “attractor ruins” for neurodynamics.

In such involved situations, irregularities of time series are due to a combination of deterministic chaos and random fluctuations which are hard to disentangle. It is, therefore, often practical to look for an overall stochastic description, for instance in terms of diffusion equations, stochastic point processes, or otherwise. The examples show that this does not imply, however, that the nature of the process is basically stochastic. Mixtures of deterministic and stochastic processes can obviously be described by stochastic evolution operators, although there may be underlying “crypto-deterministic” features. As outlined in Sec. 2.4, even the opposite is possible: Systems that are described deterministically (in a suitably large state space) can have underlying “crypto-stochastic” features as well.

An additional twist on this argument refers to the fact that the network models considered in most studies of cortical dynamics have actually a “random” structure (Brunel, 2000; Voges et al., 2007; Kriener et al., 2008). This means that they have a fixed complex wiring diagram which reflects the cortical wiring in a statistical sense (Braitenberg & Schüz, 1998). The idea is that the kinds of dynamics exhibited by all potential network realizations are statistically equivalent.

3.4 Neuronal Assemblies and Spike Correlations

According to the neuronal assembly hypothesis (Hebb, 1949), neurons organize into groups in a transient and task-dependent manner. The activity of such Hebbian assemblies refers to a mesoscopic level (Kiss & Erdi, 2002) of brain dynamics, situated between the microscopic level of individual neurons and the macroscopic level of large neuronal masses. In theory, such a dynamic orchestration of neuronal resources has many attractive properties, but it was found notoriously difficult to demonstrate it in recordings of neuronal activity.

The idea of combinatorial coding assigns a special role to neuronal synchrony (Stevens & Zador, 1998; Salinas & Sejnowski, 2001; Stein et al., 2005). The bottom line is that synchronized action potentials induce action potentials in the postsynaptic neuron with higher efficiency than the same number of asynchronous ones. In fact, modeling studies indicate an enhanced susceptibility of neurons for correlated inputs (Abeles, 1991; Salinas & Sejnowski, 2000). In recurrent networks, however, correlations also emerge as a result of network structure, due to common input by shared presynaptic populations (Kriener et al., 2008). This complicates the interpretation of correlations between neurons measured in behaving animals.

A delicate sensitivity for higher-order correlations in the presynaptic population is also found in simple model neurons (Kuhn et al., 2002, 2003; Benucci et al., 2007). Specialized circuits of converging-diverging groups of neurons, known as synfire chains (Abeles, 1991; Bienenstock, 1995), have been suggested to exploit this sensitivity for reliable signaling under noisy conditions. Numerical studies of activity dynamics in isolated chains (Diesmann et al., 1999) and of chains embedded into recurrent networks (Kumar et al., 2008b) indeed demonstrate that synchronized volleys of action potentials can survive within ongoing background activity, provided the latter conform to the asynchronous-irregular state discussed in Sec. 3.3. In principle, synfire chains can also explain the abundant occurrence of precise firing patterns in cortical activity, a special

variant of narrow spike correlations (Riehle et al., 1997; Prut et al., 1998).

Beyond the idea that joint activation may be used to define functional neuronal assemblies, Hebb (1949) also suggested a mechanism, now known as Hebb's rule, how such assemblies could actually be established and changed during learning: Neurons that are frequently coactivated by a common cause are assumed to develop strong synaptic connections ("fire together, wire together"). Eventually, a group of mutually connected cells will have the tendency to operate as a whole, if parts of it are activated.

A recently discovered variant of Hebbian learning, which relies on the intricate timing relations of pre- and postsynaptic spikes, is addressed as spike timing dependent plasticity (cf. Sec. 3.2) and has become a significant field of research. A surprising new feature of the resulting synaptic learning rule is the ability to serve as a filter for apparently "causal" relations between presynaptic and postsynaptic activity. While in some parts of the brain, including the neocortex, pre-post sequences are "rewarded" and post-pre sequences are "penalized", synaptic plasticity rules applicable in other brain areas seem to be ignorant of this feature (Abbott & Nelson, 2000).

Notes

Synchronization of action potentials within a group of neurons was suggested as a potential signature of dynamic assembly activation (von der Malsburg, 1995). In this scenario, the assembly members would exhibit specific higher-order correlations. The statistical procedures for the analysis of higher-order correlations from multiple parallel spike train recordings suggested so far (Perkel et al., 1975; Martignon et al., 1995, 2000; Grün et al., 2002a,b; Nakahara & Amari, 2002; Gütig et al., 2002, 2003) suffer from the "curse of dimensionality": the estimation of the necessary parameters (order of 2^N for a population of N neurons) poses serious problems, mainly due to insufficient sample sizes. As a consequence, most attempts to directly observe cell assemblies have resorted to pairwise interactions (Brown et al., 2004).

However, relying on pairwise correlations alone presupposes that higher-order correlations can be exhaustively described by sets of pairwise correlations (Gütig et al., 2003). It is well-known that this is generally not the case,²⁰ so that direct conclusions about the absence or presence of higher-order effects cannot be drawn based on pairwise correlations alone. In a recent approach, we suggested to circumvent the aforementioned combinatorial problems by resorting to a specific model of correlated Poisson processes, which allows to devise powerful statistical procedures for the inference of higher-order parameters (Ehm et al., 2007).

The notion of causality in spike timing dependent plasticity is not literally the same as the notion of causation in the discussion of Sec. 2.2. The difference between "causal" and "anti-causal" order in the context of synaptic plasticity compares the temporal sequence of spikes with the neuroanatomically given asymmetry of presynaptic and postsynaptic structures. A sequence of spikes is called "causal" ("anti-causal") if the presynaptic spike precedes (follows) the postsynaptic spike.

Braitenberg (1974) speculated that "causally" operating synapses, potentially favored in the evolution of cortical networks, can be regarded as reflecting the causal laws governing the inter-

²⁰In a pivotal paper studying correlations between cells in biochemical networks, Boogerd et al. (2005) have shown that emergent systemic properties of a biochemical network depend critically on triple correlations $R(A, B, C)$ that cannot be reduced to pairwise correlations $R(A, B)$, $R(B, C)$, and $R(C, A)$.

actions of external objects in the environment of a perceiving subject. By contrast, one could argue that subjects interpret their environment in terms of causal relations *because of* the pre-post asymmetry of synaptic connections. While Braitenberg's account assumes causality as a key feature of nature, the alternative view would imply that the concept of causality can be considered as a result of the structure of the perceiving brain. This idea might open an interesting way toward an epistemic foundation of causality as, e.g., discussed by Reichenbach (1956) or, more recently, Price (1996).

3.5 Correlations between Brain, Mind, and Behavior

Relationships between brain states, mental states, and behavioral states are at the core of cognitive neuroscience and neurodynamics. While brain states have been discussed extensively in the preceding sections, we need some characterization of mental and behavioral states to begin with. For the purpose of this contribution, the notion of a mental state is intended to cover perceptive, cognitive, affective, and motivational states – briefly everything that belongs to the area of psychology. Within a functionalist tradition, which forms the tacit basis of most of neuroscience, mental states can only be (or, at least, usually are) operationalized by behavioral states such as verbal utterances, reactive movements or other responses to a given cue with which a subject interacts with its environment. Hebb (1949, p. xiii) put it succinctly: “All one can know about another's feeling and awareness is an inference from what he *does*.”

But Hebb's monograph “The Organization of Behavior” has a broader intention which can be rephrased in terms of a search for relations between brain, mind, and behavior. The purpose of it is (Hebb, 1949, p. xii) “to present a theory of behavior for the consideration of psychologists; but another is to seek a common ground with the anatomist, physiologist, and neurologist, to show them how psychological theory relates to their problems and at the same time to make it more possible for them to contribute to that theory.”

In principle, there are four possibilities how brain states, mental states and overt behavior can be correlated with each other: (i) one-to-one, (ii) many-to-one, (iii) one-to-many, and (iv) many-to-many.

(i) “Lower” animals with relatively small nervous systems, like nematodes or slugs or leech, may be of type one-to-one, possibly up to minor noise perturbances in the functioning of nerve cells that are inherited from the stochasticity of their molecular components. Such a straightforward use of neuronal machinery may simply reflect an economical use of biological resources. The nerve nets are the “hardware” implementing a small and fixed set of behavioral rules that allows the animal to survive under well-defined and much constrained environmental conditions. The relative simplicity of the controlling brain appears to be a result of evolutionary adaptation and optimization.

(ii) The option that different brain states give rise to the same kind of mental or behavioral states means that the set of discernible configurations of biophysical parameters of the brain is richer than the observable mental or behavioral repertoire. This is a possible scenario in the presence of strong noise and large “unintended” fluctuations. Suboptimal performance and loss of control would be among the consequences.

(iii) Multiple mental or behavioral states arising from one and the same brain state can, however, be meaningful if an organism needs brain flexibility to explore novel routes of higher-level activities

to adapt to a changing environment and create improved strategies to cope with it. In this case, redundancy would be beneficial, rather than a waste of resources. It would effectively promote survival. It is also a conceivable and interesting option that whole families of mental states are correlated with the same brain state. A pertinent example might be the proposed correlation of the phenomenal experience of different “tokens” of color (red, blue, green) with one and the same correlate for the “type” color (Chalmers, 2000).

(iv) Many-to-many relations between brain states on the one hand and mental or behavioral states on the other are a typical empirical finding in “higher” animals and humans. Based on invasive recordings of neuronal activity in human brains, for example, correlations with complex visual acoustic stimuli (movies) have been investigated (Hasson et al., 2004; Mukamel et al., 2005; Nir et al., 2007). The neuronal activity dynamics underlying perceptual decisions has been intensely studied in behaving monkeys (Britten et al., 1992; Shadlen & Newsome, 2001). The question of whether cortical microstimulation causes the brain activity that corresponds to a mental percept was tackled by Nichols & Newsome (2002), for a review see Cohen & Newsome (2004). The behavioral impact of minimal perturbations of neuronal activity was impressingly demonstrated in recent experiments in behaving rats where evoked trains of action potentials in single neurons could reliably induce whisker movements (Brecht et al., 2004).

An overall assessment of the results of such studies, however, shows that they are still not precise enough to allow final statements with respect to the relevance of many-to-many relations. The main reason is that environmental factors, previous experiences and many other circumstantial variables, which may have a strong impact on brain activity, cannot be controlled well enough in the experiments (e.g. Bastian et al., 1998). A high degree of residual variability remains unexplained even if quite specific neuronal responses can be extracted (Rotter et al., 2005b; Nawrot et al., 2008).

The discussion becomes yet more subtle if one takes into account that straightforward physical constraints influence the behavioral repertoire even in the simplest organisms. This was popularized by Braitenberg (1984) with his “vehicles” early on. The implications of such apparently innocent observations are serious: The dynamics of the brain cannot be understood without reference to its “embodiment”, that is the physical setting of the (biological or robotic) organism to be controlled by the brain. In this respect, the brain acts as a “mediator” in the interaction of the body with its environment, and new dynamical features result from this interaction (Pfeifer & Scheier, 2001; Thompson & Varela, 2001; Cruse, 2003; Pfeifer et al., 2007).

Notes

In all the scenarios outlined above it is strongly recommended to use the notion of causation extremely carefully. The straightforward “bottom-up” version of causation (“brain causes behavior”) is naive and conceptually misleading. Even results from microstimulation experiments, such as reviewed by Cohen & Newsome (2004), do not provide a clear-cut and unambiguous picture of the situation, in view of the recursive nature of the sensory-motor loop any organism (and robot) exhibits. But also the “top-down” version (sometimes termed “downward causation”) is unfortunate because it insinuates a diachronic cause-and-effect sequence where actually synchronic relations prevail. In Sec. 2.2 the term downward constraint has been proposed to address corresponding cases, discussed to some extent in Sec. 2.5.

Many examples for downward constraints upon brain activity at the *behavioral* level can be

found in research on embodiment, as mentioned above. Behavior is always embodied, and it is an established fact that particular brain states (e.g., the neural correlates of proprioception) are critically constrained by embodiment. Braitenberg (1984), using the notion of a “synthetic psychology”, has suggested that embodiment might have decisive impact for our understanding not only of brain and behavior, but also of internal mental states. Downward constraints upon brain activity at the *cognitive* level can be found in various effects of attention (for an overview on attention see Pashler, 1998). Recently, Kim et al. (2007) have shown that attentional effects can severely influence the formation of categories, as neurally implemented by attractor networks.

Relations between brain states, mental states and behavioral states are typically investigated assuming a simplifying hierarchy of successive levels of description. In such a picture, brain states are considered at a lower level relative to mental or behavioral states. As discussed in Sec. 2.2, it is usually inadequate, or at least premature, to use the notion of causation to characterize relations between those levels. In general, these relations are bidirectional and, thus, prevent us from a sound distinction of “cause” and “effect”. It is, therefore, advisable to look for interlevel correlations to study how states and properties at different levels of description are connected.

The different classes of correlations (one-to-one, etc.) between levels of description can be translated into interlevel relations as they are usually addressed in the philosophy of science (and of mind). As formulated in detail by Bishop & Atmanspacher (2006), one-to-one relations, or isomorphisms, can be understood as referring to situations in which the lower level provides both necessary and sufficient conditions for higher-level descriptions. This is the case for strong versions of *reduction*. In general, it is not easy to find clean examples for this type of reduction.

Many-to-one relations indicate that the lower level provides sufficient but not necessary conditions for higher-level descriptions, a case for which Kim (1993) has coined the notion of *supervenience*. A key feature of supervenience is that higher-level properties are multiply realized at the lower level. A well-known physical example is the relation between thermodynamics and statistical mechanics.

One-to-many relations indicate that the lower level provides necessary but not sufficient conditions for higher-level descriptions. Dretske (1981) has influentially argued this way for brain-mind relations, and Atmanspacher & beim Graben (2007) proposed an elaborated scheme, called *contextual emergence*, that has been shown to yield a successful formal implementation of the idea for relations between brain states and mental states. (For a more detailed account of this proposal see Sec. 2.5.) A related approach for the same purpose, but based on statistical correlations rather than dynamical contexts, has been proposed by Amari (1974).

4 Some Conclusions

The preceding text gives rise to quite a number of interesting and important questions, and it provides, so we hope, a number of helpful *caveats* concerning the proper use of problematic notions in the philosophy of science in general and of neuroscience in particular. However, it is clearly impossible to discuss conclusions from all these exhaustively here. In the following we intend to refer to some points which we find most worthwhile to be elaborated in more detail, either because they have a distinct potential for future progress or because they can serve to clarify current misrepresentations and trendy aberrations.

From the rich material presented above we select some aspects of the notion of *causation*, some ideas associated with *relations between levels of description*, and eventually some problems with popular stances concerning the issue of *determinism and free agency* or, as some say, “free will”. As will become clear during the discussion, these three areas have intricate connections with each other which need to be taken into account in serious attempts to move forward toward a resolution of the deep questions they raise.

(1) Causation is a pertinent example for a conceptual term that must be defined precisely in order to be applied carefully. A widely distributed error is the confusion of causation with correlation. The whole huge body of *empirical* knowledge in all sciences is mostly based on correlations; assigning causal relations to them, or interpreting them causally, usually requires a theoretical background, implicitly or (better) explicitly.²¹ (An active intervention into an observed process, leading to a change of the outcome, may be considered as an exception to this rule.) This entails that differing theoretical approaches might lead to different interpretations of correlations.

A nice and potentially fertile example is the use of the term causation in time-asymmetric Hebbian learning, or spike-timing dependent plasticity. The empirical fact that particular temporal sequences of synaptic events support Hebbian learning while opposite sequences obstruct it has been employed to speculate that brain processes are (evolutionarily) designed in such a way that they are capable of representing an assumed (ontic) causal *nexus* of events in nature. However, an alternative interpretation would be to consider these brain processes as the reason why subjects have actually developed the capacity to (epistemically) describe nature by using the category of causation. This refers to a deep philosophical problem to the solution of which detailed research in neurodynamics might be able to contribute.

Another case in point is the notorious claim that brain states “cause” mental or behavioral states. Correlations between brain and mind or behavior are uncontroversial, but assigning causal significance to them is entirely hypothetical as long as the intended mode of causation remains unspecified and no theoretical background is available for a corresponding interpretation. The degree of conceptual naivety with which this keeps being overlooked in many publications by more or less well-known authors is astonishing.

The same applies to the opposite idea that mental states can “cause” brain states, briefly covered by the notion of “mental causation”. Although spectacular experiments utilizing EEG-biofeedback suggest that subjects can bring themselves into particular mental states in order to change their brain states, there is no idea so far how the observed correlations can be causally interpreted in an intelligible way. Conversely, we should add that arguments against the possibility of mental causation, which are based on the so-called “causal closure of the physical”, are equally weak. This will be resumed in more detail further below.

(2) Another area in which a careful discussion of subtle issues is mandatory to avoid fallacies concerns the different levels or (if one wants to abstain from a simplifying hierarchical picture) domains of description. What may be a proper way to address the dynamics of ion channels, might be irrelevant or unsuitable for the dynamics of neurons, and what appears to be appropriate there, may fail to provide a useful picture of the dynamics of neural assemblies or even larger units of the brain. We have discussed scenarios which demonstrate that this is often the case indeed. Moving from these descriptive levels to mind and behavior makes the story even more difficult.

²¹The distinction between effective and causal models in Stephan (2004) takes this point into account.

In general, it is a good strategy to assume that one-to-one relations between states and properties at different levels of description are too narrow to cover the richness of the respective kinds of complex dynamics. This implies that the desirable simplicity of such relations, leading to the option that higher-level properties can be reduced to lower-level properties, is generally unjustified. "Reductionism" is not only simple but, as a rule, also false. This becomes even more manifest if one goes from different levels of brain description to those of mind and behavior.

Instead, we argue that versions of emergence are good candidates for adequate reflections on interlevel relations. A specific one among those versions, contextual emergence, has recently been worked out in formal detail and has been shown to be applicable to empirical data (Allefeld et al., 2008). It mirrors the sophisticated ways in which descriptions of lower- and higher-level features can depend on each other, and it has turned out to be feasible for the construction of emergent higher-level features from lower-level descriptions.

A key element in this construction is the irreducibility of higher-level contexts, which can be formally implemented but are not primarily given at the lower level. These contexts play the role of constraints acting "downward". As an expedient concept for emergence relations we thus propose to replace the misleading notion of "downward causation" by a characterization in terms of downward constraints.

(3) Distinguishing different levels of description provides overwhelming evidence that there is no clear-cut way to decide whether neurodynamics is deterministic or stochastic. Brain behavior is suitably described in more or less stochastic and deterministic fashions, and there is no universal rule of determining how these descriptions vary as one goes through levels. Even worse, it is a mathematical fact that stochastic and deterministic descriptions can typically be transformed into each other. Moreover, there are no convincing arguments available for attributing ontic significance to particular neurodynamical descriptions. All this together throws dark shadows on full-sounding claims as to the determinism of brains, and it renders the decision about determinism in the brain an entirely open question.

In addition to the issue of determinism, the idea of the causal closure of the physical has been increasingly questioned. Roughly, it means that each caused event, or effect, in the physical domain must be caused by another physical event. This would rule out mental causation if the mental is conceived as irreducible to the physical. Some recent objections cast doubts on the principle of the causal closure of the physical (Primas, 2002; Stapp, 1999). Usually, the physical is characterized by the fundamental laws of physical nature. These laws are strictly separate from initial or boundary conditions that are needed to produce solutions of the laws. Any deliberate choice of such initial or boundary conditions, e.g. by experimenters or engineers, thus violates the causal closure of the physical. This argument may be useful to avoid premature no-go statements in informed discussions of (free) agency.

There are already many arguments against popular proposals of how to eliminate the long standing idea of free agency by resorting to brain determinism. From a basic philosophical viewpoint, one would first need to exclude the option that both are compatible with each other in order to start such proposals on firm ground. Implicitly assuming an incompatibility of determinism and free agency may be in accord with common sense – but without further reasons this is not far from folk psychology. Then, we know that emergent features of a system can be entirely misrepresented if one tries to describe them in terms of underlying features. What Bennett & Hacker (2003) called the mereological fallacy arises if one tries to describe capacities of a subject as a whole as if they can be recognized by investigating its constituents.

A lesson to be learned from this contribution is that, in addition to these objections, even neurodynamical observations in themselves are unhelpful for the rejection of a freedom of agency, be it with respect to volition, decision, or action. This goes beyond (or underneath) the criticism that philosophical notions are not precisely enough related to neurobiological notions. The claim of an ontic determinism in neurodynamics cannot be cogently defended on the basis of the currently established body of knowledge, and implications from it bear the risk of being fundamentally flawed.

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