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S.I.: NEUROSCIENCE AND ITS PHILOSOPHY

Structures, dynamics and mechanisms in neuroscience: an integrative account

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Abstract Proponents of mechanistic explanations have recently proclaimed that all explanations in the neurosciences appeal to mechanisms. The purpose of the paper is to critically assess this statement and to develop an integrative account that connects a large range of both mechanistic and dynamical explanations. I develop and defend four theses about the relationship between dynamical and mechanistic explanations: that dynamical explanations are structurally grounded, that they are multiply realizable, possess realizing mechanisms and provide a powerful top-down heuristic. Four examples shall support my points: the harmonic oscillator, the Haken–Kelso–Bunz model of bimanual coordination, the Watt governor and the Gierer–Meinhardt model of biological pattern formation. I also develop the picture of "horizontal" and "vertical" directions of explanations to illustrate the different perspectives of the dynamical and mechanistic approach as well as their potential integration by means of intersection points.

Keywords Dynamical explanations · Mechanisms · Structures · Multi-realizability · Generalizability · Harmonic oscillator · HKB model · Watt governor · Gierer–Meinhardt model · Horizontal versus vertical explanations

1 Introduction

Within recent years there has been much controversy between proponents of the mechanistic approach of explanation and philosophers of science and scientists who cherish

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the dynamical systems approach and dynamical explanations. I consider this controversy as essentially misguided and want to argue for an integrative approach that takes into account that the dynamical and the mechanistic approach follow, on the one hand, two different perspectives of explanation (which I shall dub "horizontal" and "vertical" explanations), but that there exists, on the other hand, a natural intersection between the two. My aim is to scrutinize the nature and the prospects of this intersection by presenting an understanding of dynamical explanations according to which they are structurally grounded. This means that the dynamical equations that build the core of a dynamical explanation pick out the spatiotemporal-cum-causal relational properties of a dynamical system which—and this is crucial—directly correspond to the organizational structure of the underlying realizing mechanisms.

The paper is organized in six sections (including this introduction). Along the way, four theses about the relationship between dynamical and mechanistic explanations shall be developed and defended. The theses include the claims that dynamical explanations are essentially structural, that they are multiply realizable, possess realizing mechanisms and provide a powerful top-down heuristic in a deductive-nomological fashion. I shall use four examples to illustrate my points: the harmonic oscillator, the Haken–Kelso–Bunz model of bimanual coordination, the Watt governor and the Gierer–Meinhardt model of biological pattern formation (there is no one-to-one correspondence between theses and examples, each example helps to support more than one thesis).

In the second section, the opposition between two extreme views which I dub "strong mechanism" and "strong dynamicism" is introduced. The positions are more than just straw men. Various authors have expressed views that fall under their scope. Strong mechanists (Craver and Kaplan in some of their writings among them) tie their view to two constraints: the models-to-mechanism-mapping and the details-constraint. Moreover, they consider their account as an exclusive account of explanation in the neurosciences (Craver and Kaplan 2011). Strong dynamicists, on the other hand, consider dynamical model explanations as decidedly non-mechanistic and self-contained (e.g. Chemero and Silberstein 2008). My first example in Sect. 3, the harmonic oscillator, helps to show where strong dynamicists go wrong (or, rather, overshoot in view of the majority of dynamical systems). The harmonic oscillator provides us with a rather simple as well as ubiquitous example of a dynamical system, and it will be used to introduce and support the first two theses that (1) dynamical explanations are essentially structural and that (2) they are multiply realizable. Thesis (1) indicates a clear divergence from the strong dynamicist position. In most cases in science, dynamic explanations are by no means self-contained and free floating, but are grounded in the "structure" of the underlying and realizing dynamical systems insofar as they pick out their spatiotemporal-cum-causal relations. This immediately makes clear that, as thesis (2) states, dynamical laws are multiply realizable, since their multiple realizability is anchored in shared structure of the realizers.

Section 4 is intended to connect the foregoing results with the mechanist agenda. It starts with a metaphysical interpretation of thesis (1): The realizers of dynamical laws are realizing mechanisms (e.g. the various realizers of the harmonic oscillator). Insofar as the relations that figure in the dynamical law are directly picked out from the realizing systems, the allegedly 'higher-level' structural explanation delivered by the dynamical law and the spatiotemporal-cum-causal structure of the ‘lower-level’ realizing mechanisms can be identified in the strong sense of Nagelian reduction. The widespread ontological distinction among mechanists between the phenomenological level and the level of the components, operations and organization of the mechanism collapses as far as the “structural core” of the dynamical law is concerned. This will be illustrated in Sect. 4.2 by means of two examples: the Haken–Kelso–Bunz model and the Watt governor. Both models can straightforwardly be understood as directly picking out causally relevant relations (certain angles, distances and phase relations) of the organizational level of the realizing mechanisms. This is captured in thesis (3) by claiming that the realizers of dynamical laws *just are* realizing mechanisms (which therefore trivially fulfill the 3M constraint). Since, in view of the first example, the HKB model, proponents of mechanism (Bechtel, Craver, Kaplan) have argued otherwise, the difference between the present approach and the strong mechanist agenda should become clear.

Section 5 abstracts from the particular debate between mechanists and dynamicists and provides us with a more general picture of our analysis so far. It is well-known that mechanistic explanations of restricted generalizablity; they focus on particular, if not detailed causal arrangements. Dynamical explanations, on the other hand, are law-like and quantify over a large class of phenomena. Generalizability and attention to details seem to pull into opposite directions. They even seem to represent incompatible virtues of explanation. The point of the present approach, however, is that you can have the cake and eat it. A full-fledged explanation of a given phenomenon, say, harmonic oscillation of a particular pendulum, should give us both insight into the particular causal mechanism of the pendulum that brings about the particular swinging as well as the fact that the spatiotemporal-cum-causal structure of that particular pendulum is shared by other mechanisms that underlie similar harmonic oscillation phenomena. The stunning fact that allegedly heterogeneous mechanisms can bring about one and the same pattern of behavior, e.g. harmonic oscillation, is only fully explained once we identify them as realizers of the same dynamical law. And a particular mechanism is justified as a realizing mechanism of a dynamical law if and only if it is the case that this very law picks out all and only the causally relevant relations of the realizing mechanism, i.e. its structure. It is, after all, this structure that the particular mechanism shares with all other (albeit, on the face of it, heterogeneous) mechanisms that fall under the same dynamical law.

Now, by digging into the causal goings-on of phenomena and typically even providing us with a hierarchy of nested mechanisms, mechanistic explanations offer a „vertical“ direction of explanation, whereas law-like explanations, such as dynamical laws, embrace a wide variety of phenomena and, hence, work „horizontally“. The terms *horizontal* and *vertical explanation* are introduced to illustrate the orthogonal, as it were, nature of the two virtues of generalizability and causal details in an explanation. The point of the present approach is that, according to theses (1) to (3), horizontal and vertical explanations naturally intersect. This is the integrative aspect of the present approach.

Section 6 adds a further virtue to the integrative approach. Sometimes, horizontal explanations provide a powerful top-down heuristics in a deductive-nomological fashion (thesis 4). Rather than building bottom-up causal models, a research strategy that is often practically impossible due to real-world, biological complexity, it might be easier and perhaps the only feasible strategy to use general recipes and organizational principles as heuristic starting points and guides in search of realizing mechanisms. The fruitfulness of this approach and, hence, the subtle interplay between horizontal and vertical considerations, will be illustrated by a fourth, concrete example: the Gierer–Meinhardt model of pattern formation in reaction–diffusion systems of the activator-inhibitor type. Section 7, finally, concludes the paper.

2 Setting the stage: strong mechanism versus strong dynamicism

Many biological systems can suitably be modeled by the toolbox of dynamical systems. Dynamical systems consist of states given as sets of variables that can be represented by points in a state space where the evolution function is usually the solution of a (system of) differential equation(s). Applications in biology comprise, among others, population dynamics, cell dynamics, enzyme kinetics, metabolic networks, cell signaling networks, predator-prey systems and, particularly, neural dynamics and recurrent neural nets.[1]

There can be no doubt that dynamical systems play a major role in biology and neuroscience modeling. Their ontological and explanatory status, however, remains controversial. It remains particularly controversial whether and in which sense dynamical models and explanations fit into the overall doctrine of mechanism. According to this doctrine, genuine explanations in the life sciences are mechanistic. I shall mainly follow Bechtel and Abrahamsen in their definition of a mechanism:

> A mechanism is a structure performing a function in virtue of its component parts, component operations, and their organization. The orchestrated functioning of the mechanism is responsible for one or more phenomena (Bechtel and Abrahamsen 2005, p. 423; see also Sect. 6).

„Strong dynamicists“, as I dub them, radically disagree with the mechanist doctrine. For instance, Chemero and Silberstein (2008) and Stepp et al. (2011) argue in favor of dynamicism and dynamic explanations as self-contained, i.e. they understand dynamical models as genuinely explanatory whether or not the variables in the explanation refer to mechanisms (another, less radical but still dynamicist position is Ross 2015). Strong dynamicists see dynamical explanations as opposed to mechanistic explanations:

> Dynamical explanations do not propose a causal mechanism that is shown to produce the phenomenon in question. Rather, they show that the change over time in a set of magnitudes in the world can be captured by a set of differential equations... That is, dynamical explanations show that particular phenomena could have been predicted, given local conditions and some law-like general principles (Stepp et al. 2011, p. 432).

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[1] Cf. Izhikevich (2007) and Gerstner et al. (2014) for applications of dynamical systems theory in neuroscience and Brauer and Kribs (2016) for biology in general.

Proponents of „strong mechanism“, on the other hand, consider the mechanistic approach as the exclusive account of explanation in the neurosciences. According to Craver and Kaplan (2011), the philosophy of neuroscience should thus develop „towards a mechanistic philosophy of neuroscience.” Other types of explanation, in particular dynamical, topological, computational and psychological explanations, are either non-explanatory or mechanistic explanations in disguise. As Craver and Kaplan put it:

> we articulate and defend a mechanistic approach to explanation for dynamical and mathematical models in systems neuroscience and cognitive neuroscience... [carrying] ... explanatory force to the extent, and only to the extent, that they reveal (however dimly) aspects of the causal structure of a mechanism. This view contrasts with dynamicist views, according to which explanations need not respect the underlying causal structures that give rise to system-level dynamics (Craver and Kaplan 2011, p. 602).

The authors have tightened their proposal by postulating two rigorous constraints: the model-to-mechanism-mapping constraint (3M) and the “details-constraint”. According to the “3M-constraint”

> ...in successful explanatory models in cognitive and systems neuroscience (a) the variables in the model correspond to components, activities, properties, and organizational features of the target mechanism that produces, maintains, or underlies the phenomenon, and (b) the (perhaps mathematical) dependencies posited among these variables in the model correspond to the (perhaps quantifiable) causal relations among the components of the target mechanism (Craver and Kaplan 2011, p. 611).

According to the “details-constraint”, completeness and specificity about the details of a mechanism is an explanatory virtue, as already Machamer et al. (2000) have pointed out. Kaplan is particularly explicit about this:

> As one incorporates more mechanistically relevant details into the model, for example, by including additional variables to represent additional mechanism components, by changing the relationships between variables to better reflect the causal dependencies among components, or by further adjusting the model parameters to fit more closely what is going on in the target mechanism, one correspondingly improves the quality of the explanation (Kaplan 2011, p. 347).

The upshot of the strong mechanist doctrine is that dynamical explanations are either mechanistic in the sense that they conform to the 3M- and details-constraint or are no explanations at all.

3 Dynamical explanations as structural: the harmonic oscillator

Presumably the simplest and at the same time paradigmatic example of a dynamical system is the harmonic oscillator. The oscillator model may serve us as a blueprint for important and characteristic features of a large class of dynamical systems. The model explains the occurrence of periodic motion behavior in a wide variety of natural and artificial systems (at least to 1st order approximation). The key physical idea is that harmonic oscillation occurs whenever the restoring force is directly proportional to the displacement, hence, $\mathrm{F} \sim -\mathrm{x(t)}$. This leads to the well-known oscillator equation as a dynamical law:

$$\frac{d^2}{\mathrm{dt}^2} x\,(t) = -\,\mathrm{kx}\,(t)$$

Two immediate observations are in order: first, the dynamic equation leaves the intrinsic nature of the oscillating system (almost) indetermined—only up to a constant k that serves to individuate the system—and, second, the harmonic oscillator possesses a wide and impressive variety of (seemingly heterogeneous) realizations by means of pendula, springs, electromagnetic oscillatory circuits, rotating gravitational systems, neural oscillators etc.

The two observations are, of course, connected: The oscillator model depends on one dynamical variable, x(t), only. In broadest terms, x(t) represents some quantity of change, typically a spatial distance such as a displacement or angle, but maybe also a change in concentration, activity etc. What is crucial is that it is a relational rather than an intrinsic property. Hence, the dynamical equation doesn't capture its target system(s) intrinsically, but rather picks out the decisive temporal variation of a relational property that is causally relevant to bring about the observed behavior. Consider two particular instantiations of a harmonic oscillator: a pendulum and an electric circuit. On the face of it, they look different, if not drastically heterogeneous. But they nevertheless share a crucial feature: they both share a relational or structural property that obeys the same temporal evolution. This characteristic carries over to systems of coupled oscillators, in particular to large classes of neural networks. The shared properties aren't intrinsic, they are all and only the structural properties encoded by $\mathrm{d^2x(t)/dt^2}$ and x(t) in the oscillator equation.

Directly related to this is that the harmonic oscillator seems to provide us with a stunning example of multiple realizability (MR). But it isn't a worrisome example for the reductionist. The multiple realizability can be traced back to the simple fact that the oscillator equation picks out a relational dynamical variable without specifying the relata any further. This, in my view, is a general feature of many cases of alleged MR: the instantiations or realizers may only superficially look drastically different, but do in fact share a particular set of relevant properties. It is then perfectly understandable why it is possible to have, on the one hand, a 'higher-level' generalization, while having, on the other hand, the 'lower-level' realizers appear to be different. The 'higher-level' law simply quantifies over the commonalities only: the shared properties of the realizers.

As a simple example, consider billiard sports. The physics of billiards is basically about ball collisions and is captured by the laws of energy and momentum conservation under the assumption that ball collisions are nearly elastic. Ball behavior can therefore be traced back to a few physically relevant properties of the balls such as mass, rigidity, spherical shape and size. Color, however, is not among them; whether a billiard ball is yellow or red doesn't affect its kinetics. One might nevertheless say that billiard balls are multiply realizable by means of differently colored balls. But this is indeed an "innocent" case of MR. It doesn't block the reduction of the higher-level property or type 'billiard ball' to its lower-level properties mass, rigidity, spherical shape and size. These latter, causally relevant properties are shared properties of all billiard balls that show the same kinetics. Whether the balls differ in other properties (color, for instance) is irrelevant. Since the MR argument is sometimes used as an argument against type-reduction, it becomes clear that innocent MR cases cannot be used to fuel the MR argument against type-reductionism. As pointed out in Lyre (2009), the situation becomes somewhat more tricky (but not fundamentally different) in cases where the realizers share all and only relational properties. And as we have seen, the harmonic oscillator is a suitable case at hand. It is an innocent MR case—it involves a shared and causally relevant relational property only represented by the dynamical variable x(t).

The above points and observations may very well be generalized. Dynamical explanations draw on dynamical equations as law-like generalizations. Dynamical equations typically leave the intrinsic nature of their target systems underdetermined. In many (albeit perhaps not all) cases the dynamical equations *directly pick out or highlight the causally relevant relations (i.e. structure) of the dynamical system* under consideration. In what follows, I will *only focus on the class of dynamical explanations to which this qualification applies*. The harmonic oscillator, for instance, clearly falls into this class. Dynamical systems with the mentioned qualification are *grounded* in causally relevant structure, and a structure or set of relations is causally relevant if and only if the dynamics of precisely this set of relational properties brings about the overall behavior of the dynamical system. I will not speculate whether and to which extent the thus considered class of dynamical systems exhausts the class of dynamical systems in general. My strong suspicion is that it at least comprises the majority of cases of dynamical systems in general. But whether and to which extent this suspicion is correct is of no importance for the purpose of this paper. It is sufficient to see that many (if not most) cases of dynamical explanations actually pertain to such structurally grounded dynamical systems.

Our qualification is best captured in the slogan that *dynamical explanations are structurally grounded*. Generally, a structure is a set of relations imposed on a set of relata such that the relata are only defined via the relations in which they stand. However, the structure picked out by a dynamical equation (or set of equations) is of course not an abstract, mathematical structure, but typically a *spatiotemporal-cum-causal structure* in the sense that dynamical equations in natural science will typically involve temporal and spatial derivatives of relationally defined quantities that are causally relevant to bring about the overall behavior of the dynamical system. For instance, in the case of the oscillator equation, x(t) stands for some measure of a relationally defined quantity and $d^2x(t)/dt^2$ for its temporal variation.

Let me summarize our observations in the following two theses:

(1) Dynamical explanations are structurally grounded: they individuate their entities only relationally by focusing on the relevant spatiotemporal-cum-causal structure of their target systems.

(2) Dynamical laws are multiply realizable. Their multiple realizability is anchored in shared structure of the realizers.

4 Realizing mechanisms

The following section consists of two parts. In Sect. 4.1, the observations of the foregoing section, in particular thesis (1), shall now be connected to the mechanist view in terms of our third thesis that the realizers of dynamical laws just are realizing mechanisms. This comes down to saying that the spatiotemporal-cum-causal structure which provides the structural grounding of a dynamical law can be identified with (or, as we shall see, Nagel-reduced to) the causally relevant structure of a mechanism. The thesis will be illustrated by two further examples in Sect. 4.2: the HKB model and the Watt governor.

4.1 Nagelian reduction

Dynamical equations highlight the causally relevant spatiotemporal structure of a dynamical system. We shall now focus on the aspect that the spatiotemporal-cum-causal structure of a dynamical system conforms to the structural core of the system's mechanistic organization. The term "structure" is used here in roughly the same sense as it appears in Bechtel and Abrahamsen's definition of a mechanism (Sec. 1, but see also Sec. 6). Couched in mechanist terms: the spatiotemporal-cum-causal structure of a dynamical system comprises the causally relevant spatial relations of the parts and their temporal operations.

This shall be considered as our third thesis:

(3) The realizers of dynamical laws are realizing mechanisms.

Consider again the harmonic oscillator. The different instantiations of a harmonic oscillator provide different mechanisms: pendula, springs, electromagnetic circuits, etc. In other words, the class of models of the oscillator equation comprises all realizing mechanisms that underlie the phenomenon of harmonic oscillation. To spell out a concrete model means to specify a concrete causal mechanism: the material out of which, say, the stick and bob of the pendulum as the main components of the mechanism consist as well as their particular spatiotemporal and causal arrangement and organization.

A crucial feature of the mechanist doctrine is that mechanisms are said to be multilevel. One particular mechanism at least comprises two levels: the higher level on which the phenomenon occurs and the lower level on which the mechanism's components, their operations and their mechanistic organization "live". As our analysis has shown, this picture is highly misleading if not flatly wrong once applied to the class of dynamical explanations. The reason is that the dynamical, 'higher-level' explanation picks out properties that are already existent on the 'lower level'. The 'higher-level' dynamical equation picks out relational properties of the 'lower-level' realizers, i.e. the components and operations of the realizing mechanisms.

In other words: the relevant ’higher-level’ and ’lower-level’ relations coincide. The dynamical explanation turns out to be a reductionist explanation in the full Nagelian sense (for a recent defense of Nagel’s classic model of reduction that is in tune with the present paper see Dizadji-Bahmani et al. 2010). We may think of dynamical equations as providing us with reducing Nagelian identities: they provide us with an insight into the identity of the structure of the dynamical equation(s) and the structure of the realizing mechanisms. This is the reason why I have used quotes for the terms ’higher level’ and ’lower level’. They are, in fact, not really distinct levels – at least not in any ontologically robust sense. The levels of the realizing mechanisms that underlie dynamical equations collapse.

This reductionist insight about dynamical explanations is notoriously missed by both the camp of strong dynamicists and strong mechanists, albeit, of course, for different reasons. Strong dynamicists will probably argue that even if the reductionist case of structurally grounded dynamical explanations can be granted, not all dynamical explanations conform to this qualification. And they will most certainly insist that those that do not are of more importance for the practice of science. While I have strong doubts that this is correct, I will not delve into this dispute, as already pointed out. Of greater importance for the purpose of this paper is how structurally grounded dynamical explanations fit into the mechanist agenda and that strong mechanists have largely overlooked that dynamical equations may directly touch upon the spatiotemporal-cum-causal structure of the underlying mechanisms. This can best be seen by considering two further examples: the HKB model and the Watt governor.

4.2 Further examples: HKB model and centrifugal Watt governor

The Haken–Kelso–Bunz (HKB) model serves as a well-known dynamical explanation of pattern formation in bimanual coordination tasks (Haken et al. 1985, see also Schöner and Kelso 1988). The model reveals several characteristic features of self-organization in dynamical systems such as multi-stability, phase transition, hysteresis and attractor dynamics. The observed finger movement behavior of human subjects is in perfect accordance with the model predictions: subjects will show two movement patterns – a symmetrical, in-phase mode and an anti-symmetrical, anti-phase mode – at low speed of finger movement (frequency), but only one, the symmetrical mode, remains stable as the frequency is increased beyond a critical value. By means of suitable symmetry considerations, HKB were able to derive a dynamical equation that depends only on the relative phase φ between the fingers as control or order parameter:

$$\frac{d}{\mathrm{dt}}\phi = -\sin\phi - 2k\sin 2\phi.$$

Note that the relative phase is a relational property. The parameter k corresponds to the inverse of the oscillation frequency. The HKB model provides thus a perfect dynamical explanation of bimanual movement behavior in accordance with the foregoing section.

As we have seen in Sect. 2, strong mechanists propose a 3M constraint for any dynamical model to be explanatory in the mechanist sense. Craver and Kaplan have considered the HKB model explicitly and arrive at the following, strange conclusion:

> Mechanists argue that such models are neither mechanistic nor explanatory of the phenomena they describe. […] None of the variables or parameters of the HKB model map on to components and operations in the mechanism... (as required by 3M) (Craver and Kaplan 2011, p. 273).

The authors are eager to declare that “the modelers [themselves] do not intend HKB to be a description of mechanisms”, but the crucial reason for their astonishing conclusion that “none of the variables … map on to components ... in the mechanism” can be found in the footnote

> Models such as HKB at most involve behavioural ‘components’, such as the phase relationship between the index fingers, but these are features of the phenomenon and should not be confused with parts of a mechanism (Craver and Kaplan 2011, p. 286, fn. 3)

and, more explicitely, in a closely related paper:

> The HKB model is a mathematically compact description of the temporal evolution of a purely behavioral dependent variable (relative phase) as a function of another purely behavioral independent variable or order parameter (finger oscillation frequency). However, none of the variables or parameters of the HKB model correspond to components and operations in the mechanism, and none of the mathematical relations or dependencies between variables map onto causal interactions between those system components (as required by 3M). Variables in models of behavioral dynamics, such as HKB, might be said to involve macroscopic or behavioral “components,” such as the phase relationship between the fingers, but these are not components in the sense of being the underlying parts of the mechanism. (Kaplan and Craver 2011, pp. 615–616).

This analysis strikes me as simply wrong. Whatever the biomechanical and neural mechanism underlying the HKB equation may look like in all detail, the phase relation between the fingers will of course be a relation that can be covered as a relation between components within the mechanism’s organization (perhaps the fingers themselves, perhaps their bones and muscles etc.). The crucial point is that the phase relationship can be Nagel-reduced, it is both a ’higher-level’ and a ’lower-level’ feature. Craver and Kaplan’s attempt to distinguish between “behavioural components” and “parts of the mechanism” is misguided. The two levels collapse with regard to the causally relevant structure, in this case the finger phase relation.

The same point can be made rather evidently in connection with another widely regarded and discussed dynamical model: the centrifugal Watt governor. The Watt governor is a simple mechanical feedback controller to maintain a constant speed of a steam engine. Part of its particular mechanistic organization is that the central spindle is linked to the engine’s flywheel and that the motion of the spindle arms is linked to the throttle of the engine. The dynamical equations that can be derived to model the governor will basically depend on the angle of deflection of the centrifugal flyball arm (after suitable linearization). Details aside, the dynamical model can immediately be understood as directly picking out the relevant causal aspects of the underlying mechanistic organization of any particular Watt governor realization. Here again, as in the HKB case, the relevant relations on the phenomenal level and the mechanistic level are simply the same.

Strong mechanists—perhaps—will argue that there is still a difference between the HKB case and the Watt governor. They grant the latter but don't buy the former, since in the HKB case, unlike the Watt governor, the causally relevant variable, the phase relation of the index fingers, is a more abstract, "far less intuitive" relational property of the underlying mechanism. Three remarks to that: First, there's no scientific value in intuitions, they should better play no role in our arguments. Second, there is, as far as I'm informed, no full-blown mechanistic model of the phenomenon of pattern formation in bimanual coordination tasks. It is, thus, not settled that 3M doesn't apply. But let us, third, assume that a full-blown mechanism is available—maybe a detailed story of how the fingers, bones, muscles, nerves etc. are organized together. Clearly, for such a story, the mechanist must be able to individuate the mechanistically relevant parts and operations. How? In order to tell causally relevant from causally irrelevant parts and properties in a mechanism, most mechanists stick with an interventionist approach to causality (cf. Craver 2007, Chap. 3). However, wiggling parts and properties in the mechanism will necessarily bring about the phase relation of the index fingers as a causally relevant operational property of that very mechanism. Hence, by the mechanist's own standards, the phase relation is a relation of the mechanism as good and as identifiable as any other relational property (as, for instance, the dynamical variable x(t) in the harmonic oscillator and the various relevant angles and distances in the Watt governor).

The upshot of our examples and the Nagel identification of the dynamical variables with relational properties of the underlying mechanisms is best captured in our thesis (3) from the beginning of this section that the realizers of dynamical laws *just are* realizing mechanisms. This thesis in connection with thesis (1) makes it immediately clear that structurally grounded dynamical explanations naturally conform to the 3M constraint:

(a) the dynamical variables of a dynamical system correspond (in the strong sense of Nagel identities) to the components and organization of the realizing mechanisms, and
(b) the dependencies among these variables correspond (in the strong sense of Nagel identities) to the causal relations among the components.

Of course, the reason why the 3M constraint in the case of dynamical explanations is almost trivially fulfilled, hinges on the crucial fact that the dynamical equations directly touch upon the spatiotemporal-cum-causal structure of the underlying mechanisms and that therefore no reasonable (let alone ontological) distinction between the 'higher-level' and 'lower-level' structure can be made (but that they must rather be identified). This point has generally been overlooked by the strong mechanists.

5 Generalizability and the "horizontal" direction of explanation

While the 3M constraint is a direct follow-up of theses (1) and (3) and is thus naturally fulfilled by dynamical explanations, the details constraint isn't—at least not in a literal and unrestricted manner. This is another point of departure between the present approach and the strong mechanist agenda.

In fact, the details constraint has recently been under attack by a few authors (Chirimuuta 2014,Levy and Bechtel 2013; Ross 2015). By and large, I agree with their various criticisms. None of the authors, however, arrives at the crucial diagnosis of the present paper. Why, indeed, is a crude "more-details-the-better (MDB) assumption", as Chirimuuta has dubbed it in view of Kaplan (2011) position, flawed? The answer is, of course, that only causally relevant details should count. This is almost analytically true: if we consider mechanistic explanations as a species of causal explanations then, of course, what counts in a causal explanation is all and only the items that are causally relevant. And on a charitable reading, this is even in accordance with Kaplan's quote at the end of Sect. 2, where he talkes about „mechanistically relevant details" (again, an analytic truism: what counts in a mechanism is what is mechanistically relevant). Clearly, we need an independent criterion to tell causally relevant from irrelevant details or properties; and as already mentioned in the preceding section, most mechanists stick with an interventionist approach to causality. I do not doubt that this is a possible option, but want to point out that the present analysis offers a different option. Indeed, the crucial point of the present analysis is that in the case of dynamical laws with realizing mechanisms the causally relevant properties (the properties that bring about the dynamical phenomenon in question as, for instance, harmonic oscillation) are already entailed in the dynamical law—according to theses (1) and (3). Structurally grounded dynamical laws are profoundly economical and effective: they quantify over all and only the causally relevant relations of the whole class of realizing mechanisms that fall under their scope.

This is likewise the reason why dynamical laws and explanations generalize.[2] By way of contrast, a notorious weakness of mechanistic explanations is that they are of restricted generalizability. This weakness becomes particularly pressing in view of the details-constraint, since this constraint seems to be directly opposed to the idea of generalizability. Mechanistic explanations in the strong sense don't generalize because of their unduly focus on details. Strong mechanists, of course, would judge things differently. They don't judge the poor generalizability of mechanistic explanations as a weakness, but rather consider it to be a defining characteristic of their explanatory target fields. The biological regime, so the usual story goes, is mainly shaped by evolution. Evolution, however, is a unique process. Therefore, the biological regime

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[2] As a reviewer has pointed out, the assumption that generalizability and scope are explanatory virtues is already controversial and should particularly be argued for. While a general discussion of the nature of scientific explanation is beyond the scope of the present paper, I like to add this much: explanation raises understanding, hence, an explanatory pattern with a wider scope raises a bigger understanding than with a narrow scope. So far, I take sides with the basic idea of unificationism. I do, on the other hand, agree that many of the well-known standard problems of the classic DN- and unificationist approach stem from the fact that causation has not suitably been taken into account. The purpose of the present approach (and the present section in particular) is to present an integrated picture of a "horizontal" and a "vertical" direction of explanation and to eventually stress the idea that a full-fledged understanding of many phenomena is only brought forth once we understand their particular mechanistic realizations as well as their deep and generalizable structural core. In this respect, the present approach is in general harmony with a recent paper by Bangu (2017) who presents a revised unificationist account that aims to incorporate the causal account as a sub-component.

should not be expected to be regimented by law-like generalizations. Local and short-range mechanistic models and explanations are tailor-made for the biological regime.[3]

Such a line of reasoning, however, is utterly simplistic. Evolution itself is best captured by guiding principles (especially the selection principle) and can be modeled by dynamical equations, as, for instance, championed by Manfred Eigen's model of molecular evolution (Eigen 1971; cf. Schuster 2011). The details-constraint stands also in stark contrast to the *de facto* role of dynamical modeling in the neurosciences and in biology throughout. As our foregoing analysis has shown, there needs to be no categorical opposition between dynamical laws and mechanistic modeling, even the 3M constraint turns out to be naturally fulfilled. On the contrary, dynamical explanations and mechanistic explanations can in principle be united into an integrative account. The point is, again, that dynamical explanations draw on the organizational structure of the realizing mechanisms themselves.

At the same time, dynamical explanations generalize rather straightforwardly, as the paradigmatic example of the harmonic oscillator shows. The oscillator model provides us with a crisp law-like generalization which applies to all realizing oscillator mechanisms (in words: "If the restoring force is proportional to the displacement, then harmonic oscillation occurs"). To combine both approaches, dynamical explanations and mechanistic explanations, means to combine two different types of explanatory interest into one integrated approach. The integration becomes possible because of our key idea (1) that dynamic explanations directly touch upon the organizational structure of the realizing mechanisms.

Figuratively speaking, dynamical and mechanistic explanations pursue different "directions" of explanation. We may very well distinguish between between a "vertical" and a "horizontal" type. Consider mechanisms first. The focus of mechanistic explanations is on local domains. This connects to the restricted scope of mechanistic explanations. At the same time, mechanisms occur in nested multi-level hierarchies. We can think of such hierarchies as vertical towers of nested mechanisms. In this sense, the direction of explanation is vertical. By way of contrast, the direction of dynamical explanations is horizontal. Dynamical explanations focus on long-ranging, generalizable laws with a wide (and potentially even universal) scope. Theses (1) and (3) allow for a natural intersection between the two, orthogonal approaches of explanation: dynamic explanations possess underlying mechanisms not only as realizers, but also as "intersection points" of the horizontal and vertical direction of explanation.

Our analysis has a certain impact on the notorious question about lawhood in general. Ever since the advent of the deductive-nomological account of laws, it has been a point of controversy of how to distinguish between genuine laws and mere accidental generalizations. In a recent paper, Kaplan (2015) remarks that proponents of the dynamical account of explanations *„have failed to address many of the standard objections to the general nomological conception of explanation upon which it is based"*, and that this is mostly due to the fact that in their writings they *„mistakenly imply that virtually any correct generalization taking the form of a differential equation should qualify as a law"* (Kaplan 2015, pp. 774–775). Indeed, in the present paper I

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[3] Of course, as Bechtel (2009) for instance discusses, the possibility of conservation of mechanisms through evolutionary descent allows for a certain, limited generalization of mechanistic explanations.

have invariably talked about dynamical equations as dynamical laws. But keep in mind that this must be read under the qualification associated with thesis (1): it is precisely the class of *structurally grounded dynamical systems* that is regimented by dynamical equations that, in turn, can suitably be considered as providing dynamical laws. Our analysis of a Nagel-identification of the relevant relations that figure in the dynamical equations and the spatiotemporal-cum-causal relations of the underlying realizing mechanisms is, in the present view, the pivotal point of providing us with a precise understanding of why structurally grounded dynamical equations are generalizable and, hence, law-like. They must be: structures (sets of relations) are multiply realizable; in focusing on such structures, dynamical equations generalize over the class of all of their (isomorphic) instantiations, i.e. underlying mechanisms; such structurally grounded dynamical equations, therefore, provide laws. Or, to make the same point in our new terminology: in the case of structurally grounded dynamical systems there is a genuine intersection between the horizontal explanation provided by dynamical laws and the vertical explanation of realizing mechanisms.

Rounding up this section a final mention should be made that Kaplan in his recent (2015) indeed softens his former strong mechanist agenda and calls for a "natural alliance between dynamical and mechanistic approaches" (Kaplan 2015, p. 780) mainly based on the idea of components of mechanisms as "moving parts" with a temporal organization covered by dynamical equations:

> The relationship between dynamics and mechanism is one of subsumption, not competition. In particular, dynamical models are especially well suited to reveal the temporal organization of activity in neural systems. Because dynamical models are subsumed within the broader toolkit for describing mechanisms, their explanatory value can be seen as clearly depending on the presence of an associated account (however incomplete) of the parts in the mechanism (and their interactions) that support, maintain, or underlie these activity patterns. Dynamical modeling approaches do not signal the emergence of a new explanatory framework in neuroscience distinct from that of mechanistic explanation. Instead, dynamical models with explanatory force can readily be understood within the mechanistic framework (Kaplan 2015, pp. 759–760).

According to the present view, of course, the alliance between mechanistic and dynamical approaches is not one of subsumption, but of an intersection of two otherwise orthogonal accounts of explanation with orthogonal virtues: generalizability and "horizontal scope" on the one hand versus faithfulness for particularity (if not MDB) and a "vertical deep drilling" into multiple levels of whole-part-relations on the other hand by means of hierarchies of nested mechanisms. The integration between the two approaches becomes possible, unlike Kaplan's "alliance", because, once more, dynamical laws are grounded in the shared spatiotemporal-cum-causal structure of the whole class of realizing mechanisms that fall under their scope, which is also why the 3M constraint is naturally fulfilled at the intersection point of a horizontal dynamical and a vertical mechanistic explanation.

6 Dynamical explanation heuristic: the Gierer–Meinhardt model

The merits of the horizontal direction of explanation not only lie in the prospects of generalizability or to answer generic why-questions. The horizontal direction of explanation also allows for a most powerful top-down heuristic in science. The potential of this heuristic only comes to the fore by connecting (or intersecting) the two directions, the horizontal and the vertical. This shall be illustrated by a final example.

Consider the class of self-organizing dynamical reaction–diffusion systems that are described by the Gierer–Meinhardt model (henceforth: GM model; Gierer and Meinhardt 1972). The model consists of two coupled and nonlinear partial differential equations for two variables, an activator and an inhibitor. Crucial to the model is the idea that the activator is autocatalytic and short-range, while the inhibitor as antagonist is long-range. In fact, it is only this central assumption that constrains the basic form of the differential equations:

$$\frac{\mathrm{da}}{\mathrm{dt}} = \rho\frac{a^2}{h} - \mu_a \mathrm{a} + \mathrm{D}_a \frac{d^2 a}{\mathrm{dx}^2} + \rho_a \qquad \frac{\mathrm{dh}}{\mathrm{dt}} = \rho a^2 - \mu_h \mathrm{h} + \mathrm{D}_h \frac{d^2 h}{\mathrm{dx}^2} + \rho_h$$

The GM model accounts for a remarkably wide range of phenomena for pattern formation and morphogenesis in developmental biology and neuroscience. Of course, as such, the model provides us with a how-possibly story only. Whether or not particular patterns in nature conform to the model calls for the identification of particular realizing mechanisms (in accordance with the 3M constraint). Two important points shall be noted:

1. It is a remarkable and deep insight in itself to understand that nature uses one and the same organization principle in many domains. In this case: the general recipe of lateral inhibition plus auto-catalytic, short-range activation.
2. It is practically almost impossible to arrive at this general organization principle in a bottom-up fashion, i.e. from scrutinizing the various cellular, genetic and molecular goings-on.

The two points in combination put the deductive-nomological pattern of explanation back on stage. The GM model not only works as a powerful heuristic and guide. It leads to a very strong form of top-down deduction in the sense that the various instantiations or underlying molecular-genetic mechanisms can in principle be deduced from the dynamical model. This is different from Kaplan who, interestingly enough, also stresses the usefulness of the dynamical framework as a “heuristic for mechanism discovery and hypothesis generation”, but at the same time only grants that the “contributions of the dynamical framework are descriptive and methodological, rather than explanatory” (Kaplan 2015, p. 758). However, the explanatory value of a dynamical model such as GM in terms of a top-down deduction can very well be seen in precisely the way Gierer, Meinhardt and many followers have used the model. They used mathematical stability analysis in combination with computer simulations to play with the equation’s constants and parameters and thus to explore the richness of the basic model. Eventually, this led to rather precise predictions and constraints on the particular mechanisms (see the great variety of examples of realizing GM model mechanisms in Meinhardt 1982). The GM model thus allows the modeler to make predictions about the biological realm that are otherwise almost absent from the life sciences.[4] This leads to a final thesis:

(4) Horizontal, dynamical explanations provide a powerful top-down heuristic of the underlying mechanisms in a deductive-nomological fashion.

The top-down heuristic shows a deductive-nomological pattern to the extent that, again, the spatiotemporal-cum-causal structure described by the GM equations is precisely the structural core of the organization of the realizing mechanisms connected with the fact that the various constants and parameters of the model fit the particular cellular, genetic and molecular circumstances.

7 Conclusion

I have argued for the theses that dynamical explanations are essentially structural, that they are generalizable and multiply realizable and that the realizers of dynamical laws in neuroscience are realizing mechanisms. The harmonic oscillator as well as the HKB model and the Watt governor have served as examples. Furthermore, higher-level dynamical models turn out as powerful heuristic guides to discover lower-level mechanisms in a top-down, deductive-nomological manner, as illustrated by the Gierer–Meinhardt model.

The present account is integrative and tries to overcome the opposition between strong dynamicism and strong mechanism. It also shows similarities and affinities to other accounts. Bechtel and Abrahamsen, for instance, argue for a special type of "dynamic mechanistic explanations" by complementing their 2005 definition of a mechanism (see above) with the specification that *"the orchestrated functioning of the mechanism [is] manifested in patterns of change over time in properties of its parts and operations"* (Bechtel and Abrahamsen 2010, p. 323). Zednik (2011) is also liberal in applying the mechanist agenda to a wide variety of dynamical models. Levy and Bechtel (2013) emphasize the procedure of abstraction to understand the mechanistic organization as patterns of causal connectivity. And even Kaplan, as discussed at the end of Sect. 5, softens his former strong mechanist agenda and calls for a "*natural alliance between dynamical and mechanistic modeling approaches*" (Kaplan 2015, paper title). Finally, an emphasis on structures can also be found in Felline (2015) and in Kuhlmann (2014) who offers an understanding of *"explanations of the generic behavior of complex systems ... in terms of … structural mechanisms"*.

None of the accounts, however, arrives at the crucial diagnosis of the present paper: the observation from theses (1) and (3) that dynamical explanations directly touch

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[4] Note that what is 'predicted' here is the existence of a mechanism of a certain type (the GM type, i.e. with a structural core represented by the GM model equations). For instance, to take a most recent research result, the particular GM-type mechanism responsible for the color and pattern of skin scales in lizards (Manukyan et al. 2017). The prediction of mechanism types serves as a research heuristics and should of course not be conflated with the prediction of the temporal evolution of a certain system (e.g. by means of its underlying dynamical equations). To consider prediction in this latter sense as already explanatory is highly controversial (and of course dismissed by most mechanists). But it should be clear that this is a different sense of prediction than what I have in mind here.

upon the structural organization of the underlying realizing mechanisms, and that, therefore, realizing mechanisms can be understood as intersection points within an integrative account of horizontal and vertical directions of explanation.

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