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# Potentiality in the Sciences – Biology

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#### Abstract

We take the potentialities that are studied in the biological sciences (e.g., totipotency) to be an important subtype of *biological dispositions*. The goal of this paper is twofold: first, we want to provide a detailed understanding of what biological dispositions are. We claim that two features are essential for dispositions in biology: the importance of the manifestation process and the diversity of conditions that need to be satisfied for the disposition to be manifest. Second, we demonstrate that the concept of a disposition (or potentiality) is a very useful tool for the analysis of the explanatory practice in the biological sciences. On the one hand it allows an in-depth analysis of the nature and diversity of the conditions under which biological systems display specific behaviors. On the other hand the concept of a disposition may serve a unificatory role in the philosophy of the natural sciences. Towards the end we will briefly come back to the notion of a potentiality in biology.

#### **Main Article**

The term "potentiality" can be understood in various senses. In this paper we will use the term "potentiality" both in a broad sense and in a narrow sense. We will take "potentiality" in the broad sense to be synonymous with "disposition", "tendency", or "capacity". This sense of the term will concern us throughout the whole paper. Based on a better understanding of the nature of biological dispositions, we will discuss various options of a narrower sense of the term "potentiality" towards the end of the paper (Section 10).

The aim of our paper is twofold. First, we want to provide a detailed understanding of what biological dispositions are. On basis of examples from various biological fields we reveal several features that are characteristic for dispositions in biology: the importance of the manifestation process and the diversity of conditions that need to be satisfied for the disposition to be manifest. Second, we demonstrate that the concept of a disposition (or potentiality) is a very useful tool for the analysis of the explanatory practice in the biological sciences. On the one hand it allows an in-depth analysis of the nature and diversity of the

conditions under which biological systems display specific behaviors. On the other hand the concept of a disposition may serve a unificatory role in the philosophy of the natural sciences since it captures not only the explanatory practice of biology, but of all natural sciences. After discussing whether biological dispositions are intrinsic and whether they can be 'reduced' we briefly take up the question whether the notion of a potentiality can be distinguished from that of a disposition.

## 1. Dispositional vs. Categorical Properties

Properties of objects or systems are usually distinguished into dispositional properties and categorical properties. The basis for this distinction is the observation that objects may have properties that are not manifest. For instance, we think of certain people that they are courageous. If we attribute the property of being courageous to a certain person we thereby do not imply that they show courageous behavior all day long. Rather, we expect the person to behave courageous, given certain circumstances. For example, if a group of boys attacks another child we expect the courageous person to intervene. In the absence of situations like this a courageous and a non-courageous person may exhibit the same behavior. Thus, being courageous is a property that one may have ('instantiate') without actually manifesting it. In the case of other properties it does not seem to make sense to distinguish between having a property and manifesting the property. For instance, with respect to an object having the property of being cubic it does not seem to make sense to distinguish between having the property and manifesting the property. A cubic object does not need special circumstances for manifesting its being cubic.

This observation provides the basis for a distinction of properties into dispositional and categorical properties.<sup>1</sup> Paradigm cases of dispositional properties are, for instance, courage, solubility, and fragility; paradigm cases of categorical properties are the shape and structure of an object. For dispositional properties it is important to distinguish between an object *having a property* on the one hand and *manifesting the property* under certain conditions on the other hand. For the purposes of our paper we can define a dispositional property as a property that, if it is instantiated by an object, may nevertheless fail to be manifest. In general, it becomes manifest only given certain conditions obtain. In

<sup>&</sup>lt;sup>1</sup> It should be noted that more recently some authors have started to use these distinctions differently. Alexander Bird distinguishes categorical properties from potencies. This distinction concerns the *essence* of properties, viz., whether these essences are dispositional or not (Bird 2007, 5). We are totally uncommitted with respect to essences of properties. Another example is Stephen Mumford who denies that dispositions (*powers*) are properties (Mumford 2009, 268). Mumford explicitly notes the difference.

the relevant literature these conditions are called 'stimulus conditions' (also: 'triggering conditions', 'manifestation conditions'). A person, for instance, may be a courageous person all his life but may have only few occasions on which to show courageous behavior. Similarly, a glass may be fragile but the disposition will become manifest (i.e., the glass will break) only if specific stimulus conditions obtain (e.g., striking of the glass). By contrast, if objects or systems possess categorical properties (e.g., the roundness of a billiard ball) they will be manifest unconditionally.<sup>2</sup>

## 2. The Importance of Dispositions for the Biological Sciences

Since the 1930s (Carnap 1936) it became apparent that dispositional concepts do play an important role in science. More recently interest in dispositions as an analytical tool for characterizing scientific practice has resurged. Nancy Cartwright, for instance, has argued that what she calls capacities need to be introduced to make sense of certain aspects of causal reasoning in scientific practice (Cartwright 1989).

The concept of a disposition is important for the analysis of science because it points to the fact that the properties or behavior of systems may only be manifest given certain conditions. More particularly, we want to argue that the notion of a disposition is an important tool for the analysis of biology and other sciences dealing with complex systems. It exhibits the dependence of the behavior of complex living systems on specific conditions, especially contextual conditions. As we will show in section 5 and 7, not only the importance but also the *diversity of roles* such conditions play can be adequately explicated in a dispositional framework.

Furthermore, we want to argue that the notion of a disposition allows for a certain unification within the field of philosophy of science. If one looks at the current literature, which analyses the explanatory practice in the physical and the biological sciences, one may

<sup>&</sup>lt;sup>2</sup> Is this definition plausible? Molnar (2003, 84-7) discusses examples, which may be considered to be counterexamples to our definition. (1) Our definition can cope with dispositions that are – as Molnar puts it – continuously manifest, i.e. manifest all the time as long as the object has it. There may be a bendable object that is bended as long as it exists. It is still true that the disposition of being bendable is manifest only if certain contingent conditions obtain (e.g. if someone bends it all the time). However, on the definition proposed one of the examples discussed by Molnar does not count as a disposition: According to Molnar, massive objects continuously manifest their gravitational power. If gravitational power is the disposition to attract massive bodies it would count as a disposition on our account. If gravitational power is identified with the field, it comes out as a categorical property, because it would be manifest necessarily (in virtue of laws of nature). Since the latter case is not an intuitively clear-cut case of a disposition, it does not seem to be a problem. (2) Propensities: A muon does seem to have the disposition to decay but it does not need a specific manifestation condition. That's fine on our account. The essential point is that there is a difference between having the disposition to decay and the muon actually decaying. A muon may have the disposition without manifesting it. So, yes, it does come out as a disposition on our account – which is a perfectly acceptable result.

gain the impression that the two fields have hardly anything in common. While the former still heavily relies on the notion of (cp-)laws of nature, the latter focuses on mechanisms and the role they play in the explanation of biological phenomena. This strict separateness of the biological and physical research practice is called into question by the fact that various kinds of interconnections exist between these fields, especially between molecular biology and physics, - let it be "interfield theories" (Darden/Maull 1977), "multilevel mechanisms" (Craver 2002, 2005; Darden/Craver 2001), or the classical "intertheoretical reductions" (e.g. Schaffner 1993). Phenomena such as the elasticity of DNA and DNA-protein interactions are frequently studied by biologists and physicists working hand in hand. Although we do not intend to downplay the differences between the explanatory practices in physics and biology, the view that hardly any similarities exist between these fields seems to be inadequate, too. In our view the existing interconnections in actual research make it prima facie plausible that the explanatory practices in the biological and the physical sciences are not completely different. Thinking about dispositions provides a conceptual framework that accounts both for the dissimilarities as well as for the similarities between biology and physics. It does so by unifying the talk about mechanisms and about (cp-)laws. As we will argue in detail in section 7, explanations that rely on (cp-)laws and mechanistic explanations can both be viewed as referring to dispositions (of a certain kind).

## 3. Conditional Analysis

Before we discuss biological examples of dispositions it will be useful to make the concept of a disposition more precise and to introduce some distinctions.<sup>3</sup> What are the conditions under which we can legitimately attribute a disposition D to a system s? To give a precise answer to this question requires specifying the relation between having a disposition and manifesting it. One major issue in the debate about dispositions is whether this connection can be made more precise – whether particular dispositions can be defined explicitly in terms of their manifestations and stimulus conditions.

The starting point for such attempts is the so-called simple conditional analysis (SCA). The simple conditional analysis and its modification were proposed by philosophers who wanted to argue that, properly speaking, there are no such things as dispositions. Disposition-talk can be replaced by what is referred to on the right hand side of the simple conditional analysis (see below). We are not in this business and will not defend any view on

<sup>&</sup>lt;sup>3</sup> See Mumford (1998), Mellor (2000) and Choi/Fara (2012) for comprehensive discussions of the notion of a disposition.

whether or not dispositions can be eliminated or reduced etc.<sup>4</sup> Still the SCA is a good starting point because SCA and the discussion of its shortcomings allows for the introduction of some terminology that will be useful.

Let Ds stand for system s having the disposition D, that is, s being disposed to M (manifestation) provided stimulus conditions C obtain. According to the simple conditional analysis the necessary and sufficient conditions for s having D can be symbolized as follows:

SCA:  $Ds \leftrightarrow (Cs \blacksquare \rightarrow Ms)$ 

which is to be read as: s has Disposition D if and only if: If s were confronted with C then s would manifest M. Thus, given SCA and given we know how to test the counterfactual claim "Cs  $\blacksquare \rightarrow$  Ms" we know under which conditions we can legitimately attribute D to s.

There are various problems with SCA as a general explication of the concept of a disposition. One problem with SCA is that manifestations cannot easily be specified. What exactly are the manifestations of being courageous? Likewise, it is difficult to spell out the exact stimulus conditions for a disposition such as fragility, e.g. breaking, hitting, and throwing in particular ways (cf. Prior 1985, 6-10). This is even more problematic for biological dispositions because the way in which the context is involved in the manifestation is diverse and complicated, and the enabling conditions are very complex (see below).

Second, in SCA the manifestation M is a property of the system s. That is fine in the case of courage because the same person that has the property of being courageous – given suitable circumstances – manifests courageous behavior. However, in the case of a fragile vase one may wonder whether the manifestation is the property of the vase. After all, when it is broken it might seem reasonable to argue that the vase no longer exists.

Another significant problem for the simple conditional analysis is a family of counterexamples that shows that contrary to SCA (1) a system s may have D without (Cs  $\blacksquare \rightarrow$ Ms) being true and conversely (2) there are cases such that (Cs  $\blacksquare \rightarrow$ Ms) without s having D. There are various such counterexamples discussed under the headings of 'antidotes', 'finks', 'masks' etc. Let us start with an example for (1). We can understand 'fatally poisonous' (D) as 'disposed to kill if ingested'. Someone might take the poison (S) but nevertheless survive (non-M) because of some antidote that has been ingested as well (Bird 2007, 27). In such a case the substance is fatally poisonous but the manifestation does not

 $<sup>^{4}</sup>$  By the way: Our ability to analyze our notion of a chair in non-chairy terms has never – to our knowledge – been taken as an argument for the non-existence of chairs.

take place even though the stimulus condition (ingestion) did occur. So, there may be possible interferences, which invalidate SCA. A standard example for the converse problem (2) is this: Suppose there is a very robust, non-fragile object. However, there is a sensitive detonator attached to it, such that a bomb will explode and destroy the object if it is struck. So the counterfactual 'If the object were struck, it would break' is true even though the object in question is non-fragile (cf. Bird 2007, 29). Examples such as these are sometimes called "mimics".

What we see is that the manifestation of a disposition requires not only stimulus (or manifestation) conditions but also the absence of all kinds of interfering factors. Only if all of these conditions can be listed explicitly, the SCA would provide an *explicit* definition of a dispositional concept. It is, however, a controversial issue whether it is even in principle possible to list all relevant factors. When we discuss the biological examples of dispositions in the next section it will be important to identify, first, the different kinds of conditions that need to be present (or absent) for a disposition to become manifest and, second, those conditions that need to be explicitly listed in a respective explanation.

As has already been indicated, our project is neither committed to defending nor to rejecting SCA. The reason to present it is simply that the relevant terminology has been shaped by discussions focusing on the tenability of SCA.

## 4. Examples of Biological Dispositions

With the relevant terminology at hand we will now identify examples of properties and processes in the biological sciences, which are best reconstructed as dispositions. From Section 5 onwards we will argue – among other things – that such an analysis eventually leads to a disambiguation of different kinds of conditions that the behavior of biological systems depend on.

In the biological sciences we find only a limited use of predicates such as 'heritability' (of traits), 'toti- and multipotency' (of cells), and 'fertility' (of organisms), which indicate a reference to dispositional properties. However, this observation does not imply that the properties under investigation in these sciences should be taken to be categorical. On the contrary, the examples we list will provide ample evidence for the claim that despite the absence of overtly dispositional language, many biological objects possess properties that are only manifest under specific conditions. We will take the liberty of introducing artificial terms for these dispositions.

In what follows, we introduce a selection of examples of dispositions from molecular biology, cell biology, developmental biology, evolutionary biology, and ecology. In each case we identify the dispositional property, the type of object that possesses the disposition (called 'carrier'), and the manifestation conditions. As will be seen below, the manifestation conditions of many biological dispositions are very complex and often partially unknown. In these cases we can only provide an incomplete and general sketch of those conditions.

## 4.1 Molecular Biology

The first example comes from molecular biology. An important step in the synthesis of proteins in cells is the folding of the amino acid chain into a functioning protein with a specific three dimensional structure. We will call this disposition 'foldability'. It can be characterized as the disposition of an amino acid chain to form a specific three-dimensional structure, which allows the originated protein to perform its functions. Conditions for the manifestation of this disposition are a normal physiological milieu in the cytoplasm (that is, an adequate pH-value, salt concentration, and temperature) and, as recent research has shown (e.g., Frydman 2001), in most cases the presence of chaperones, which guide the protein folding by providing the necessary surrounding conditions for the folding.<sup>5</sup>

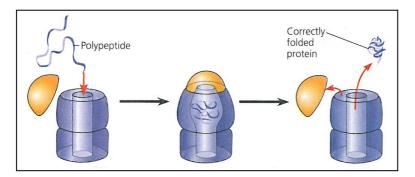


Figure 1: Steps of Chaperonin Action (Campbell/Reece 2005, 85)

The second example also concerns the interaction between macromolecules. It is the disposition of enzymes (a specific type of proteins) to catalyze the chemical reaction of specific substrates by lowering the activation energy barrier for this reaction without being consumed by the reaction. We will call this disposition 'catalyzability'. The conditions under which this disposition becomes manifest are the presence of corresponding substrates and, depending on the ways by which the enzyme is regulated, the absence of inhibitors and the

<sup>&</sup>lt;sup>5</sup> An overview of how exactly chaperones guide the folding of most proteins can be found, for instance, in Alberts et al. 2008, 388-390.

presence of activating factors. For instance, the enzyme threonine deaminase can only catalyze the first step in the reaction from threonine to isoleucine if the substrate, threonine, is present and isoleucine is not bound to the allosteric site of the enzyme. This kind of regulation is called feedback inhibition. It ensures that only as much isoleucine is produced as is needed in the cell.

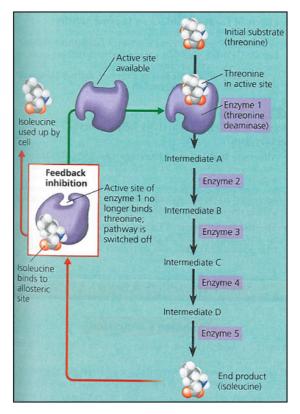


Figure 2: Feedback Inhibition in Isoleucine Synthesis (Campbell/Reece 2005: 157)

As for any cellular process the existence of a normal physiological milieu is another condition needed for the manifestation to occur. Otherwise temperatures, salt concentrations, and pH values that lie outside the optimum range of the proteins would modify the three dimensional structure and thus disturb the adequate functioning of proteins, e.g., the catalyzing activity.

#### 4.2 Cell Biology

The next two examples are phenomena that are studied in cell biology.<sup>6</sup> In order to grow and to replicate animals and plants have to reproduce their cells. This process is called

<sup>&</sup>lt;sup>6</sup> The attribution of dispositions to specific biological fields should not be regarded as too strict. There are many overlapping areas and many phenomena that are investigated in different fields. Especially the distinction between molecular and cell biology is very vague because nowadays much research in cell biology is molecular.

cell division (or mitosis). Almost all cells have the disposition to divide into two complete cells. (Let us call this disposition 'divisibility'.) The process by which this disposition manifests is a complex process that can be partitioned into five different stages (prophase, prometaphase, metaphase, anaphase, and telophase). Since not only the process of mitosis itself but also its control and regulation are highly complex, the manifestation conditions for this disposition are complex too. Rhythmic fluctuations in the abundance and activity of cell cycle control molecules, primarily cyclins and cyclin-dependent kinases (Cdks), play the most important role for the manifestation-process and a fortiori for the manifestation of divisibility. At the beginning, cyclin accumulates and associates with Cdk molecules. The resulting MPF complex initiates the process of mitosis by phosphorylating a variety of proteins, which are thereby activated. This leads to a whole bulk of other processes like, for instance, the fragmentation of the nuclear envelope. During anaphase MPF helps switching itself off by initiating a process that leads to the destruction of its own cyclin.

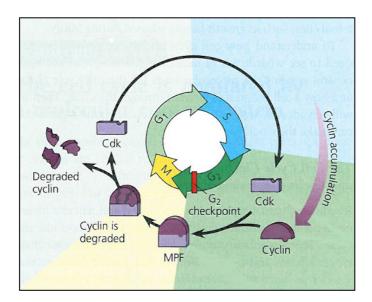


Figure 3: Molecular Control of the Cell Cycle (Campbell/Reece 2005: 230)

Our next example is what we call the 'contractability' of muscle fibers. This disposition can be characterized as the capacity of muscle fibers to actively shorten (or tense) themselves. According to the sliding-filament model of muscle contraction, the manifestation process, that is, the contraction, is due to the sliding of thick and thin filaments past each other whereby the so called I-bands and H-zone are shortened until they, in case of full contraction, disappear.

	I band	A band	I band
	ZIZIE BROWSTON	M line	
Thick filaments (myosin)	Soundational Spinster	ever states	
Thin	Activities of the second	all and	Contraction of the second seco
(actin)	Z line	H zone	Z li

Figure 4: The Structure of Skeletal Muscle (Campbell/Reece 2005: 1067)

The sliding of thick and thin filaments in turn can be traced back to a complex molecular process of energy consuming interactions between myosin (the building block of the thick filament) and actin (the building block of the thin filament). In case where no neuronal stimulation is available, the regulatory protein tropomyosin blocks the binding of myosin to actin. This blocking is lifted when an incoming action potential from a motor neuron triggers the release of calcium ions from sacroplasmic reticulum into the cytosol. The calcium ions bind to another set of regulatory proteins, the troponin complex, which removes the tropomyosin binding sites on the actin filaments. Thus, myosin can bind to the now free myosin binding sites on the actin, the sliding of thick and thin filaments past each other precedes and the disposition of the muscle fibers to contract becomes manifest. Among other factors as the presence of ATP (which causes the transformation of the myosin heads to its high-energy configuration, which is in turn a precondition for the binding of myosin to actin), the presence of an extracellular signal (which affects the release of the calcium ions) and the presence of the troponin complex are the most important manifestation conditions.

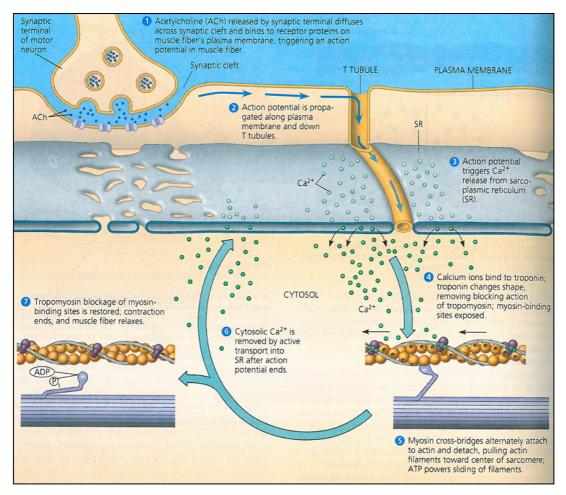


Figure 5: Contraction in a Skeletal Muscle Fiber (Campbell/Reece 2005: 1070)

## 4.3 Developmental Biology

When it comes to the development of animals and plants, the dispositions that are investigated by biologists are even more complex. A major process studied in this field is cell differentiation, that is, the specialization of cells in their form and function. The disposition of cells to differentiate ('differentiability') is closely related to two other concepts that are of great interest for instance in biomedical ethics: 'totipotency' and 'multipotency' (also called 'pluripotency'). Totipotency is the disposition of a cell to develop into a complete, functioning organism. Hence, its manifestation involves not only cell division and cell differentiated cells end up in their appropriate locations). Totipotency includes multipotency, which is the disposition of a cell to develop into any of the three blastodermic layers and the germline, that is, into cells of any type (e.g., muscle cells, blood cells, nerve cells, etc.). Multipotency presupposes differentiability, which is less strict. Cells that possess the disposition to specialize in form and function (differentiability) need not possess the

disposition to specialize into cells of *any* type (multipotency). In this paper we focus on differentiability because this seems to be the most important disposition for developmental biologists.

Like cell division, the process by which a cell differentiates (i.e., manifests its differentiability) is a complex process that consists of many sub processes and that occurs only if a variety of conditions are met. In multicellular organisms differences between cells stem almost entirely from differences in *gene expression*, not from differences in the genome of the cells. Differential gene expression in the early development of an embryo has primarily two sources: either it is caused by cytoplasmic determinants in the egg or by induction from neighboring cells (cell-cell signalizing). The most important kind of information in this process is positional information which ensures the correct development of the spatial organization of tissues and organs in an organism.<sup>7</sup>

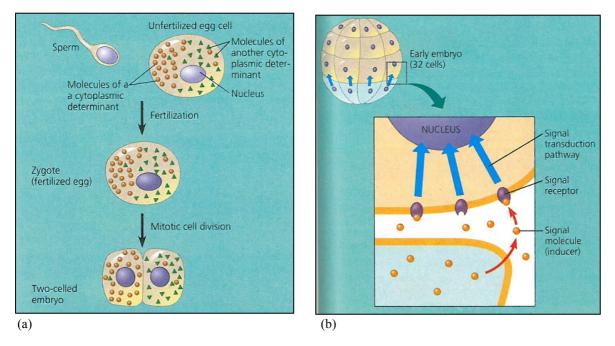


Figure 6: Sources of Developmental Information for the Early Embryo:

(a) Cytoplasmic Determinants in the Egg, (b) Induction by Neighboring Cells (Campbell/Reece 2005: 421)

#### 4.4 Evolutionary Biology

Our next example, biological *fitness*, is a central concept in evolutionary biology and has already drawn notable attention from philosophy during the past decades. It has been

<sup>&</sup>lt;sup>7</sup> This is just a very general characterization of cell differentiation. It should not hide the fact that the manifestation of this disposition is a highly complex process which presupposes that many different conditions are satisfied at different times. For an overview of the details of cell differentiation compare for example Gilbert (2006), chapter 3.

extensively disputed what the appropriate definition of the term 'fitness' is.<sup>8</sup> In this context some philosophers of biology have defended the dispositional nature of the concept of fitness in order to face the criticism that fitness is a tautological concept. Instead of defining fitness as *actual* reproductive success, proponents of the propensity interpretation of 'fitness' (e.g., Mills/Beatty 1979; Brandon 1980; Brandon/Beatty 1984) characterize fitness as the *capacity* of an organism (or genotype) to produce a particular number of offspring<sup>9</sup> or, in other words, to make a certain contribution to the gene pool of the next generation (relative to the contributors of other organisms/ genotypes).<sup>10</sup> According to this approach, organisms with high fitness (relative to the other members of the population) need not actually possess relatively high reproductive success. Rather, the focus is on the "expected ... reproductive success" (Brandon/Beatty 1984, 343). The manifestation of this disposition will only occur if the required environmental factors, the manifestation conditions, are present. For instance, an individual of Phyllium westwoodii (Westwood's walking leaf) whose body exhibits a leaflike coloration and form has the disposition to show a relatively high rate of reproduction despite the presence of insectivores (i.e., an animal that eats insects). However, this disposition will only become manifest in an environment that is dominated by trees with green leafs.

The *evolvability* of populations is a second important disposition in evolutionary biology, which was subject of recent philosophical discussion, too. Some authors think that evolvability is a better object of research than fitness because it provides less reason to argue about the nature of evolutionary theory itself (Love 2003). Evolvability can be characterized as the disposition of a population to evolve, that is, to change its gene or allele frequencies.<sup>11</sup> Biological evolution entails not only processes of adaptive evolution but also of neutral evolution. In the latter case changes in gene frequencies are not affected by natural selection, but by random genetic drift, because the variations of genes are not correlated with variations in reproductive success of the organisms. If only adaptive evolution is considered, the evolvability of a population is the same as its adaptability, that is, its disposition to adapt to a specific environment or, in other words, to respond to natural selection. This narrow

<sup>&</sup>lt;sup>8</sup> For an overview of the various problems with finding an adequate definition of the concept of biological fitness compare for example Rosenberg/Bouchard 2010.

<sup>&</sup>lt;sup>9</sup> As fitness is a probabilistic property and not an all-or-nothing disposition like water solubility, the number of offspring can be various. A high number of offspring corresponds to a high fitness and vice versa.

<sup>&</sup>lt;sup>10</sup> Whether fitness can also be attributed to groups of organisms and whether the fitness of a group is more than the sum of the fitness of the individual group members is a point of controversy in the group selection debate.

<sup>&</sup>lt;sup>11</sup> This characterization of evolvability is constrained to micro-evolutionary processes and is not appropriate with respect to macroevolution, i.e. evolutionary processes at and above the species level (c.f. Stearns/Hoekstra 2005).

understanding of evolvability as adaptability underlies most discussions. As in case of fitness, evolvability is not an all-or-nothing disposition but comes in degrees. In general, the amount of available variation on which natural selection can act is restricted by the functional interconnections between various processes that occur in an organism and its ontogeny. By contrast, four features of biological systems can increase the evolvability of a population: flexible versatile proteins, weak linkage, exploratory behavior, and compartmentation (c.f. Kirschner/Gerhart 1998). Whether the evolvability of a population is manifested by an evolutionary process depends on the presence of selective pressures, which are usually generated by changing environmental conditions.

#### 4.5 Ecology

Our last example is a disposition from ecology that we call 'defensibility'. The value of a resource to a consumer is determined not only by what it contains but by how well its contents are defended. For example, a plant whose leaves contain poison is of less value to an herbivore than a plant without poisoned leaves. Not surprisingly, organisms have evolved various physical, chemical, morphological and behavioral defenses against being attacked. The disposition 'defensibility' captures exactly this disposition of an organism to defend itself against herbivores or predators. The disposition will become manifest if appropriate herbivores or predators are present. The way in which the defensibility of an organism is manifested depends on which of the various defense mechanisms an organism has evolved: defense by secondary chemicals, mimicry (the similarity of a species to another which protects the species members), crypsis (the ability of an organism to avoid observation or detection by potential herbivores and predators), aposemantism (a warning signal that warns potential predators of the existence of another primary defensive mechanism), etc. (cf. Townsend et al. 2008).

#### 4.6 Summary

The following table summarizes the most important features of the examples of biological dispositions analyzed before:

name of the disposition	carrier	characterization of the disposition	manifestation conditions (choice)
(1) foldability	amino acid chains/ polypeptides	disposition to form a specific three-dimensional structure	presence of chaperones

(2) catalyzability	enzymes	disposition to lower the activation energy for chemical reactions	presence of corresponding substrates and activating proteins, absence of inhibitors
(3) divisibility	cells	disposition to divide into two complete cells	rhythmic fluctuations in the abundance and activity of cell cycle control molecules
(4) contractability	muscle cells	disposition to actively shorten (or tense) themselves	presence of ATP, an extracellular signal, troponin complexes, and calcium ions
<ul> <li>(5)</li> <li>(a) differentiability</li> <li>(b) totipotency/</li> <li>(c) multipotency</li> </ul>	cells	<ul> <li>(a) disposition to specialize their structure and function/</li> <li>(b) disposition to develop into a complete, functioning organism/</li> <li>(c) disposition to develop into cells of any type</li> </ul>	presence of specific cytoplasmic determinants and inductive signals, differential gene expression
(6) fitness	organisms/ genotypes	disposition to produce a particular number of offspring	presence of certain environmental conditions
(7) evolvability	populations	disposition to change its allele or gene frequencies	selective pressure, changing environment
(8) defensibility	organisms	disposition to defend themselves against herbivores and predators	presence of herbivores or predators

## 5. Manifestation Process and Manifestation Conditions

According to the tradition ensuing from SCA what is characteristic for a disposition is its manifestation result and the conditions that need to be fulfilled for its manifestation to occur, the stimulus conditions. For instance, fragility is properly characterized by the result of the manifestation, i.e., the glass being broken, and the stimulus conditions, e.g., the glass being hit by a hammer. What the examples from the various biological disciplines discussed in the last section show is

- that a dispositional analysis is appropriate because the behavior of the systems depends on the occurrence of certain conditions, but
- given the variety of conditions that manifestations depend on, the SCA draws an *oversimplified* picture of biological dispositions.

To be clear, our point is not that the additional features we highlight in principle cannot be accommodated by a revised version of SCA, the point is that they have hitherto been neglected.

The first respect in which the (SCA) of dispositions is inadequate in biology concerns the great importance of the *process* of manifestation for biological dispositions. This process of manifestation of a disposition can be distinguished from its *result* or *product*. For instance, the manifestation process of the disposition divisibility is a complex process that can be divided into different stages (prophase, prometaphase, metaphase, anaphase, and telophase). This process can be distinguished from its result, viz. there being two cells. Traditionally, the manifestation result was conceived as being central to the characterization of a disposition, whereas the manifestation process was not taken into account. The manifestation, for instance, of the fragility of a glass is typically taken to be the broken glass. But as we can see for example in the case of contractability, the process of how the manifestation result is generated is equally important for the nature of the disposition as the result of this process. Attributing the disposition of contractability to muscle fibers seems to entail the claim that a specific process, namely the sliding of thick and thin filaments and the myosin ratcheting, will take place which results in the contraction of the muscle fibers. If muscle contraction were brought about by a completely different process we would probably refrain from identifying the relevant disposition as the same disposition. What this suggests is that biological dispositions are individuated not only in terms of stimulus conditions and manifestation result, but also in terms of the manifestation process that yields the manifestation result.<sup>12</sup>

To sum up: the *process of manifestation* of a disposition is of obvious significance in the biological sciences<sup>13</sup> – a significance it does not have in the SCA, nor in every-day cases such as fragility or in physics (one of us has argued that the manifestation in the case of

 $<sup>^{12}</sup>$  Tony Handfield made a similar observation concerning the every-day disposition of the solubility of salt: "Consider, for example, the dissolution of salt in water, as it occurs in a laboratory. Some salt is in a beaker. Some water is added and the mixture stirred. The salt dissolves. This type of process is the way salt manifests its power to dissolve. Although we can envisage deviant ways in which the same end state could be achieved – perhaps with the assistance of a sorcerer, or nanomachines – and we might for convenience call all the various ways of producing such a state 'processes of dissolution', we would be reluctant to say that the salt's power to dissolve is being manifested in such deviant cases. Instead, what is being manifested is a different power of the salt – a power to be put into solution by sorcerers or nanomachines. So not every process in which salt ends up in aqueous solution is a manifestation of salt's power to dissolve in water: only processes of the correct type qualify." (Handfield 2008, 118) However, Handfield draws a slightly different conclusion. He suggests that the manifestation process should be considered as the 'manifestation proper'. We do not agree with Handfield. We think that neither the manifestation result nor the manifestation process alone should be called 'manifestation proper'. Both are important for the individuation of a disposition, which is especially apparent in the biological cases.

<sup>&</sup>lt;sup>13</sup> This does not imply that any difference on any level is important to the individuation of a disposition. In many cases certain micro-level differences are taken to be *unimportant* for the characterization of a biological disposition. For instance, biologists speak about the disposition of organisms to defend themselves independent of what the exact defense mechanism is. Equally, biologists investigate the disposition of organisms to show mimicry (a special defense mechanism) and thereby ignore other micro-level differences, for example, which other organism is imitated.

(some) physical dispositions is an atemporal process – if it is a process at all; cf. Hüttemann 2009).

Taking into account the temporal extension of the manifestation process allows us to identify a second respect in which the traditional picture of a disposition (SCA) needs to be revised in order to capture the specifics of biological dispositions. The received view of the conditions under which a disposition becomes manifest does not account for the *diversity* of roles certain kinds of conditions play for the manifestation of biological dispositions. To begin with, these conditions are more than mere *stimulus* conditions. For this reason we will use the term 'manifestation conditions' to refer to *all* kinds of conditions which are needed for the manifestation of a disposition to occur. According to the traditional view of dispositions, manifestation conditions are conceptualized as stimulus conditions, thus, as mere *input-conditions* to a system which need to be met at the starting time of the manifestation process and then remain fixed or can be neglected. For instance, the fragility of a glass becomes manifest if it is for example hit by a hammer and the solubility of a piece of sugar is realized if it is thrown into water.

What the biological examples clearly show is that this restricted understanding of manifestation conditions is not adequate with respect to most biological dispositions. In many cases (e.g., divisibility, contractibility, differentiability) a variety of manifestation conditions exist, which have to be met not only at the beginning, but at various times during the complex manifestation process.<sup>14</sup> Consider for example contractability. The manifestation process begins with the presence of an extracellular signal. This signal causes the release of calcium ions from the sacroplasmic reticulum into the cytosol, which in turn effects that the blocking of the myosin binding sites by tropomyosin is lifted so that (if ATP is present) the myosin ratcheting can proceed. As this example shows, there are conditions that need to be fulfilled immediately before the beginning of the manifestation process and either are irrelevant at later points in time (e.g., the presence of the extracellular signal) or do not change during this process (e.g., the presence of ATP). But, in addition, many conditions must be met at specific time intervals during the process (e.g., the presence of the extracellular signal, the presence of calcium ions in the sacroplasmic reticulum, the troponin complex, which removes the tropomyosin from the myosin binding sites). In some cases (e.g., cell division) it is actually the presence of a condition (e.g., cyclin) at one time and the absence of the same condition at

<sup>&</sup>lt;sup>14</sup> A related thesis is Craver's claim that phenomena (that are explained by mechanistic explanations) typically are "multifaceted" (Craver 2007, 125). This means that a phenomenon cannot be characterized solely in terms of its input and output conditions, but that other kinds of conditions like "precipitating conditions", "inhibiting conditions", and "modulating conditions" (Craver 2007, 125f) must be taken into account as well.

a later time that is needed for the manifestation process to run correctly and the manifestation result to occur. Since these conditions are crucial for the manifestation process to run through we refer to these conditions as *sustaining conditions*.

Furthermore, the manifestation of biological dispositions presupposes the presence of specific conditions and the absence of disturbing factors which play no explicit role in the individuation of biological dispositions. The presence and/or absence of the relevant conditions is considered by biologists to be 'normal' (whatever 'normal' may mean exactly)<sup>15</sup>. That is why they are usually left unspecified. In case of the catalyzability of enzymes such 'normal' background conditions include, for instance, an enzyme-specific pH-value, salt concentration and temperature. If these conditions were not met the disposition would not become manifest, i.e., the enzyme would not catalyze the specific reaction. This is also true for the presence of corresponding substrates and activating proteins and the absence of certain inhibitors. But the fact that the latter (the substrates, activators, and inhibitors) are in most explanations explicitly cited and the former, i.e., the background conditions, are not, suggests that they belong to different kinds of conditions which play different roles in the explanatory practice of biology.<sup>16</sup>

The diversity we have just encountered can be captured by the following distinction of different kinds of manifestation conditions:<sup>17</sup>

- a) *stimulus conditions*: These are conditions that initiate the manifestation process. For the manifestation to occur, they need to be fulfilled right before the manifestation process starts.
- b) *sustaining conditions*: These are conditions that need to be present or absent at different time intervals during the manifestation process. They ensure that the manifestation process takes its typical course and that the manifestation result obtains.
- c) *background conditions*: These are conditions that are assumed to normally be the case (e.g., a certain environment, the normal physiological milieu, a certain temperature range, the absence of meteors and atomic bombs). They are usually only implicitly included in the characterization of a disposition.

<sup>&</sup>lt;sup>15</sup> For an account of biological normality see, for instance, Weber forthcoming.

<sup>&</sup>lt;sup>16</sup> Contrary to other disturbing factors like very high salt concentrations or the presence of meteors, which are rare or merely hypothetical, inhibitors of enzymes are typically treated as explanatorily relevant and not just as background conditions.

<sup>&</sup>lt;sup>17</sup> Note that all kinds of conditions include presences as well as absences of certain conditions.

The difference between stimulus and sustaining conditions on the one hand and background conditions on the other hand, is a *pragmatic* distinction that is drawn relatively to local explanatory aims and, thus, not entirely dictated by the facts. Background conditions are taken for granted since they are taken to be normally satisfied. It is relative to these background conditions that a disposition is attributed to a biological system. Delegating factors to the background is tantamount to the assumption that they are not explanatorily relevant. We take background conditions to play an analogous role for dispositions as Mackie's causal field does for causes (cf. Mackie 1980, 34/35).

What stimulus and sustaining conditions have in common and what distinguishes them from being mere background conditions is that they specifically trigger the disposition to become manifest (see Woodward's notion of causal specificity; Woodward 2010). Hence, they (in contrast to the background conditions) are included in the characterization of the disposition and in an explanation of the disposition's manifestation. The difference between stimulus conditions and sustaining conditions is temporal: stimulus conditions occur right before the start of the manifestation process and remain unchanged during the entire process, whereas sustaining conditions occur only at certain time intervals during the manifestation process. There is no further (systematic) difference between these conditions. However, the insight that not only stimulus conditions, but also sustaining conditions are crucial for the nature of a disposition is new and needs to be emphasized in order to overcome the oversimplified concept of dispositions that has dominated the general debate on dispositions so far. As our analysis has shown, what is necessary for the manifestation process to take its course and for the manifestation result to occur are not only input conditions (traditionally called stimulus conditions), but also conditions that are met at later times, conditions that are satisfied during specific time intervals only, and conditions that undergo specific changes during the manifestation process.

In sum, our analysis of biological dispositions reveals that there are two aspects of biological dispositions that SCA does not capture: (1) the relevance of the manifestation process and (2) the diversity of manifestation conditions and the different roles they play in explaining why a system shows a specific behavior.

## 6. Dispositions, Mechanisms and (ceteris paribus) Laws

In this section we take up our argument from section 2 that the concept of a disposition is a useful tool for analyzing scientific practice. The usefulness of a dispositional framework has already been indicated in the preceding section where we were led to the distinction of various kinds of conditions that play a role in enabling a system to show a specific behavior. Our aim in this section is to further substantiate this claim concerning the usefulness of the concept of a disposition by indicating how it can serve as a *unifying tool* for philosophy of science in the analysis of the physical and the biological sciences.

In the analysis of the scientific practice of the physical sciences the notion of a law (either strict or ceteris paribus) still plays the central role. By contrast, in the philosophy of biology the notion of a strict law has been rejected for a long time as a quite useless tool for the analysis of the scientific practice. Even the more moderate notion of a ceteris paribus law has been heavily criticized. Sandra Mitchell, for instance, writes:

Critics of the ceteris paribus clause correctly identify the fact that the clause violates the spirit of the concept of "law". I argue that, more importantly, it violates a more pragmatic aspects of "laws" in that it collapses together interacting conditions of very different kinds. [...] Whereas ceteris paribus is a component of the statement of a causal regularity, what it is intended to mark in the world is the contingency of the regularity on the presence and/or absence of features on which the operation of the regularity depends. Those contingencies are as important to good science as are the regularities that can be abstracted from distributions of their contextualized applications. (Mitchell 2003: 164)

One consequence of this kind of criticism is that philosophers of biology have developed their own conceptual tools to investigate the explanatory practice in the biological sciences – most notably the concept of mechanism (cf. Machamer et al. 2000; Glennan 2002; Darden 2006; Craver 2007; Bechtel 2006, 2008). From the perspective of general philosophy of science it may appear as though the explanatory practices in the physical and the biological sciences do not have much in common. While the one is concerned with investigating laws and explaining phenomena by laws, the other studies mechanisms and seeks to explain phenomena by describing the underlying mechanisms. This appears to be a strange kind of dualism if one takes into account the fact that the disciplines overlap in various places and that some scientists move from one to the other area – without, presumably, learning from scratch what a good explanation consists in.

Our claim is that the dualistic appearance is deceptive and that the notion of a disposition allows us to see how the explanatory practices of biology and physics are related and by this serves as a unifying tool. Both, the investigation of (cp-)laws and of mechanisms

can be viewed as an investigation of particular kinds of *dispositions*. With respect to laws this claim has already been advanced by a number of authors (e.g., Cartwright 1989; Hüttemann 1998; Bird 2007). According to these accounts law-statements are reconstructed as attributing dispositions to physical and other systems. The rationale behind this account is that many ascriptions of behavior to systems explicitly or implicitly assume that certain conditions obtain – very often the absence of interfering factors. Thus according to Newton's first law "Every body continues in its state of rest or of uniform motion in a straight line, *unless it is compelled to change that state by forces impressed upon it.*" [italics added] (Newton 1999, 416). In other words, the behavior that law-statements attribute becomes manifest only provided certain manifestation conditions obtain.

We will focus here on the relation between mechanisms and dispositions. To be clear: our argument is not that the concept of a disposition is the *only* way to integrate the (cp-)law based view of physics and the mechanistic perspective on biology.<sup>18</sup> Rather, we think that it is *one* way and that it is a *plausible* way to achieve greater unification in philosophy of science.

How are dispositions related to mechanisms? One might think that mechanisms are subtypes of dispositions. Mechanisms are said to be "entities and activities organized such that they are productive of regular changes from start or set-up to finish or termination conditions" (Machamer et al. 2000, 3). From this one might conclude that mechanisms are dispositions that can be present without being active. And that a mechanism becomes active only if certain conditions ("start or set-up conditions") are present. At first sight, this claim seems to be supported by many of our examples of biological dispositions. What brings about a contracted muscle fiber (i.e., the manifestation end state of contractability) is the mechanism of muscle contraction. Likewise, the defensibility of a buckeye butterfly (Junonia coenia) is manifested by a certain defense mechanism (mimicry), which involves the opening of his wings, the predators being put off by the eye spots on the wings, etc. Accordingly, in many cases we seem to have both a disposition and a mechanism. We think, however, that this does not imply that mechanisms *are* subtypes of dispositions. There is a close connection between them, but one needs to be precise about what exactly the relation is. As one of us has argued somewhere else (Kaiser/Krickel forthcoming), it follows from the dualism about the components of mechanisms (i.e., that mechanisms consist of entities/objects and

<sup>&</sup>lt;sup>18</sup> Alternative integrative approaches might point out the importance of non-strict laws in biology (e.g., Mitchell 1997, 2003) or emphasize the close connection between the concept of mechanism and the concept of law (e.g., Craver/Kaiser 2013).

activities/processes) that mechanisms are not objects or properties, but rather object-process hybrids and, as such, necessarily temporally extended.<sup>19</sup> This implies that mechanisms cannot be dispositional properties themselves (since they are not temporally extended). They can only be manifestations of dispositions, more precisely, the *manifestation processes* of dispositions, which occur only given certain manifestation conditions (among them "start or set-up conditions") are present. In short, mechanisms are not subtypes of dispositions, but subtypes of manifestation processes of dispositions.

To conclude, the concept of a disposition serves as a useful analytical tool because it unifies the (cp-)law based view of the physical research practice and the mechanistic view of the biological research practice.

### 7. Intrinsicality

An instructive debate in the dispositions literature concerns the intrinsicality of dispositions. Roughly speaking, a property is intrinsic if a system possesses the property independently of what is going on in its context. Shape is an intrinsic property, whereas being smaller than everybody else in the room is an extrinsic (relational) property. It will be useful to introduce Lewis' notion of a prefect duplicate (Lewis 1983). Perfect duplicates necessarily have their intrinsic properties in common (that is how they are defined). Conversely, properties not shared by perfect duplicates are extrinsic properties. A perfect duplicate for instance of my water bottle must be made of transparent plastic, must have a certain shape, and its label must be damaged at the upper right side. But in order to be a perfect duplicate it must not stand on my desk close to my phone.

The rationale for attributing a disposition to a particular system seems to imply that dispositions are intrinsic. This can be illustrated by the following example: The phenomenon of sugar dissolving in water is, strictly speaking, a property of a combined system – sugar plus water. If we describe the phenomenon in terms of a disposition being manifest rather than in terms of a property of a compound system, we usually introduce a distinction between a system (e.g., sugar), which is endowed with a disposition, and external conditions (like contextual conditions). If we ascribe solubility to sugar we focus on those conditions for the obtaining of the phenomenon that are due to the sugar only. The disposition (solubility) comprises exactly those conditions of the phenomenon that the system (sugar) possesses

<sup>&</sup>lt;sup>19</sup> This of course forecloses that something like inactive mechanisms exist.

independently of what is going on in its context. Thus, even though the manifestation of dispositions (e.g., the dissolving in the case of solubility) depends on extrinsic factors it is usually held that the disposition itself (e.g., the solubility of salt) is intrinsic. Some even argue that intrinsicality ought to be viewed as a necessary feature of dispositions (Molnar 2003, 58).

But intrinsicality may not be a necessary feature of dispositions (cf. McKitrick 2003; Choi/Fara 2012). A key, for instance, may have the disposition to open certain kinds of doors. A perfect duplicate at another time and in another place, however, will fail to have the disposition if the doors in question have different locks. The disposition in question thus seems to be an extrinsic property. This challenge is particularly clear in the case of some biological dispositions. Take fitness as an example. The capacity to produce five offspring needs to be relativized to a certain environment. Fitness is always the capacity to obtain a certain reproductive success *in a specific environment*. *A fortiori* perfect duplicates may fail to share the capacity to produce five offspring. The fitness of an individual thus appears to be an extrinsic disposition.

Alan Love (2003) has argued for the same point with respect to the evolvability of populations. In many cases external factors are more than the manifestation conditions for biological dispositions. They determine jointly with intrinsic factors the *very nature* of the disposition itself as well as its causal efficacy. For example, whether a population is evolvable or not is co-determined by contextual (environmental) factors such as migratory abilities and landscape topography. Hence, the evolvability of a population appears to be an extrinsic disposition.

There are various options to deal with such (alleged) examples:

- (a) The first option is to take extrinsicality at face value, that is, to accept that some dispositions (such as fitness) are extrinsic dispositions. Whether or not an individual organism has for instance the disposition fitness does not only depend on the organism itself, but also on its environment. This option, however, requires that the environmental factors are something over and above mere manifestation conditions. If this cannot be shown this option falls together with the second.
- (b) A second option is to accept that fitness is a disposition of an individual, but to argue that the environmental factors are merely manifestation conditions. Accordingly, an individual organism might have the disposition to produce a certain number of offspring irrespective of the environment. But whether or not this organism manifests the disposition (i.e., in fact has a certain number of

offspring), also depends on the existence of certain environmental conditions. This approach rejects the above arguments for extrinsicality and insists that perfect duplicates of a particular organism share all their dispositions (among them fitness) even if they are located in different environments.

(c) Finally, one might argue that fitness is a disposition not of the individual organism, but of a compound system consisting of the individual and a certain environment. This approach restores intrinsicality, but at the cost of changing the carrier of the disposition.

One difference between these options is the following: If we assume that an organism has the capacity or disposition to produce five offspring, what we usually mean is: it has the disposition to produce five offspring, given its normal environment (see section 5). What happens if the organism is transferred to a different environment, say to a zoo? If we take option (b) and treat the environment as (usually unstated) manifestation conditions (as we did in section 5), the implication is that the individual retains its disposition in the zoo. On option (a), however, the original environment would *not* be treated as a manifestation condition. It is a consequence of (a) that the individual looses the disposition in question when it is transferred to the zoo. Similarly on option (c): The compound consisting of the organism and its environment looses the disposition in question because the compound no longer exists if the organism is transferred to the zoo.

To conclude, it is not so clear that there are knock-down arguments against one of these options. What needs to be acknowledged is the *source* of the problem: In biology the attribution of dispositions often takes for granted the obtaining of certain background-conditions. The problem of extrinsic dispositions arises as soon as one realizes that the normal background conditions need not obtain.

## 8. Single-track vs. Multi-track Dispositions

Courage, it seems, is a disposition that will be manifested in different situations by different behaviors. This is to say that courage is a multi-track disposition: one disposition, but *multiple possible manifestations*. However, the SCA-tradition has often assumed that dispositions are individuated in terms of one set of manifestation conditions and one manifestation (i.e., that they are single-track dispositions). The drawback of conceiving dispositions such as courage as a single-track disposition is a proliferation of dispositions. Each kind of courageous behavior (e.g., courage in the face of death and courage in the face

of financial stress) is the result of *different* courage-dispositions, not of one and the same disposition.

In biology there are many possible candidates for multi-track dispositions: The manifestation of evolvability for a population can result in different changes of gene frequency of a population. The pluripotency of stem cells can become manifest in muscle cells, bone cells, blood cells etc. But on closer inspection it becomes apparent that the characterization of these dispositions as 'multi-track' depends on a fine grained analysis of the manifestation states. If we choose a more coarse-grained level of analysis, just one and not multiple possible manifestation states can be identified. For example, the disposition defensibility can be conceptualized in two different ways. On the one hand, it can be conceived as a single-track disposition that has just one manifestation state as its outcome, namely the successful defense of organisms against herbivores or predators. On the other hand, defensibility can be characterized as a multi-track disposition that exhibits, according to the different defense mechanisms, various manifestation states. The manifestation of the disposition defensibility can result in the defense of an organism by secondary chemicals, by mimicry, by crypsis, or by aposemantism. But what distinguishes the one manifestation state from the many is only the level of description or, in other words, the graininess of the analysis. Since in many cases both kinds of description can be found in biological research practice, there seems nothing more to argue about.

# 9. Reduction

A further frequently disputed question concerns the issue of reduction. Dispositions such as fragility are necessary conditions for the obtaining of the manifestation (provided that SCA or something akin is correct). This is often analyzed as: Fragility is *causally efficacious* in bringing about the manifestation. An ensuing question that has been widely discussed is whether a disposition can be considered causally efficacious on its own or whether it is causally efficacious in virtue of an underlying causal basis, such as the molecular structure in the case of the fragility of a glass.

We think that it is important to distinguish two issues in this context. First, fragility and other every-day dispositions are *macro-level properties*. It can be argued that macroslevel properties of systems can be reduced to micro-level properties. A glass for instance is fragile in virtue of its molecular structure. If this is true, however, it is true for dispositional and categorical properties alike. The glass has its shape (a categorical property) in virtue of its molecular structure (and/or arrangement) as well. In this sense reductionism does not provide a special challenge for dispositional properties in biology.

A different issue is whether there can be *bare dispositions* or whether every dispositional property can be reduced to categorical properties, such as the micro-structural configuration. The question here is whether there can be irreducible dispositional properties that cannot be identified with a set of categorical (e.g., micro-structural) properties. The physical property 'charge' or other fundamental dispositions might be candidates for bare dispositions because there are no micro-structural properties that they might be identified with.

We think the question should not be whether it is possible *in principle* to find a causal basis of a disposition consisting of merely categorical properties, but whether biologists *actually* specify the causal basis of biological dispositions this way. The answer to the latter question is quite simple: No, they do not. In the biological sciences many cases can be found where the causal basis of a disposition is characterized in a way that it includes categorical properties as well as dispositional ones. For instance, the objects that constitute the causal basis of foldability (like the side chains of the amino acids) possess themselves dispositional properties (e.g., the capacity to form noncovalent bounds). Likewise, the causal basis of divisibility includes for example the protein Cdk (Cyclin-dependent Kinase), which has the disposition to form a complex (called MPF for Maturation Promotion Factor) together with cyclin.

The examples divisibility, contractability and differentiability uncover two other facts about biological dispositions that are worth mentioning here: First, in cases of complex dispositions the manifestation conditions and the causal basis seem to be *interwoven* or *overlapping*. In many cases it is difficult to assign clearly which factor belongs to which group. For example, cells manifest their disposition to specialize their structure and function (differentiability) only if specific cytoplasmic determinants or inductive signals are present, which cause the expression of specific genes. Since these genes and molecules are parts of the cell that has the disposition, they can be characterized both as manifestation conditions and as the causal basis of the disposition. Second, in cell and developmental biology the causal basis is frequently specified in molecular terms. But, in addition, often complementary specifications exist on different levels. Take the example of the contractability of muscle fibers. The manifestation of this disposition is explained by the shortening of the I-bands and the H-zone on the one hand and by the molecular interactions between actin and myosin on the other. Both specifications of the causal basis of this disposition are feasible and actually in use in biology.

## 10. Potentialities in the Strict Sense

So far our discussion has focused on biological dispositions. We have argued that dispositions in the biological sciences are characterized by the importance of the manifestation process and the diversity of conditions that need to be satisfied for the disposition to be manifest.

We think that our analysis of the nature of biological dispositions also delivers valuable insights into the characteristics of biological potentialities because potentialities in the broad sense just are dispositions. One might, however, argue that not all biological dispositions are potentialities, but rather claim that biological potentialities are a *subclass* of biological dispositions. This is to speak about potentialities in the *strict sense* (in the following "potentialities<sub>(strict)</sub>"). We conclude this paper by pointing out a plausible way of how to demarcate biological potentialities in the strict sense from biological dispositions in general.

One idea of what might distinguish potentialities<sub>(strict)</sub> from other kinds of dispositions is that the manifestation process of potentialities<sub>(strict)</sub> brings about a *substantial change* in the carrier of the potentiality<sub>(strict)</sub>. For instance, totipotency and multipotency are potentialities<sub>(strict)</sub> because their manifestation involves the shift from a single, unspecified cell either into a cell of a specific type or into a complete, functioning organism. However, it seems to be terminologically arbitrary that biologists refer to totipotency and multipotency as potentialities, but do not characterize differentiability as a potentiality. The manifestation of the latter may involve a change (e.g., from an unspecified cell to a blood cell) that is as substantial as the change that is involved in the manifestation of totipotency and multipotency and multipotency. This already shows that in some cases it is difficult to specify under which conditions a change should be characterized as "*substantial*" and under which it should not. The coming into existence of a complete organism is a substantial change for sure. But does the division of a cell into two or the folding of a polypeptide into a protein involve a substantial change? A possible way to specify the concept of a substantial change is to claim that changes are substantial if they give rise to the existence of *new objects.*<sup>20</sup> Accordingly,

<sup>&</sup>lt;sup>20</sup> This gives rise to controversial questions concerning the identity conditions of objects. Is an embryo or baby the same thing (or person) as the adult it develops into? When a cell divides into two is one of the daughter cells the same as the cell it originated from or are both daughter cells new objects that came into being by division? Is

divisibility and foldability are not only dispositions, but also potentialities<sub>(strict)</sub> because their manifestation process involves a substantial change that causes new objects to exist (i.e., two daughter cells, a functioning protein). However, in the absence of clear criteria for 'substantial change' or 'new object' it is difficult to see how to avoid the conceptual vagueness and arbitrariness of the notion of a potentiality in the strict sense.

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the functioning protein the same object as the polypeptide from which it arose from, or do these two objects have different identity conditions?

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