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The Subject as Cause and Effect of Evolution

Peter Godfrey-Smith

University of Sydney and

CUNY Graduate Center.

A family of arguments often presented in opposition to mainstream neo-Darwinian views of evolution assert an "active" role for organisms in determining the course of their evolution and other kinds of biological change. I assess several of these arguments, beginning with an early treatment by Lewontin and moving to more recent discussions. I then look at a subset of these phenomena, those in which organisms are efficacious in virtue of features and capacities related to *subjectivity*. In the history of the Earth from the Cambrian onwards, subjectivity has been an increasingly important causal factor.

1. Introduction

In 1983 Richard Lewontin published "The Organism as the Subject and Object of Evolution," my favorite of his more philosophical papers [1]. Initially appearing in the now-defunct journal *Scientia*, it was reprinted in Levins and Lewontin's *The Dialectical Biologist* [2], and in that form has continued to have influence. Lewontin argued that Darwinism and allied parts of biology made progress by turning organisms into "objects" of evolution, pinned between forces – genetic mutation and natural selection – that are "autonomous and alienated from the organism as a whole" ([1] p. 87). Lewontin said we now need to see organisms as *subjects* as well as objects, with respect to both the production of individual phenotypes and their relations to environment; organisms

actively participate in their own development and "construct" the environments they encounter.

Both themes have figured in recent debates about whether there is a need for large-scale reform and an "expanded synthesis" in evolutionary biology [3]. Does the field suffer from habitual reliance on simplistic causal models, or are all the phenomena Lewontin and other critics talk about handled perfectly well by mainstream approaches? This paper will not be primarily concerned with whether there are errors in mainstream views, but with how we should think about the active, subject-like features of organisms and their place in evolution. Do claims about the active role of organisms specify a definite class of evolutionary possibilities? Is this just a picturesque way of describing all, or almost all, cases?

After looking at those questions I'll make extensions to another project. For Lewontin, the term "subject" referred to a *role* organisms could have, initiating and guiding change rather than responding to other forces. In a different but related sense, a subject is a kind of entity, something that experiences the world and acts. Very roughly, subjects in this sense are a subset of organisms, but it is more accurate to say that organisms can be more or less subject-like, can realize subjectivity to a greater or lesser degree. Subjects, like organisms, are both products of evolution and evolutionary causes. The latter part of the paper will use my treatment of the debate about the active organism to look at the place of subjectivity, in this second sense, within evolutionary processes.

I'll begin with general arguments about the active role of organisms (section 2), discussing phenotypic plasticity, niche construction, and ecosystem engineering. All these concepts are surrounded by active empirical debates about particular organisms and ecological systems. Writing here as a philosopher, it is not my project to assess those disagreements. Instead I attempt some progress on the theoretical side. I then turn to aspects of living activity that involve subjectivity, and connect these ideas to events in the history of life.

2. Phenotypic Plasticity, Niche Construction, and Ecosystem Engineering

Lewontin's 1983 paper opposed the idea of the organism as "alienated" from its evolution, with respect to both the role of environmental pressures and the genetic causation of phenotypes. The breadth of Lewontin's complaints makes one wonder what would count as an alternative – how else things might work. Lewontin saw earlier views that recognized a large-scale role for *will* or internal volition, as in Lamarck [4], as genuinely different. Those theories are long gone and should not be revived, but Lewontin saw views that treat phenotypes as joint products of genes and environments, via plasticity in developmental pathways, as relevantly similar with respect to the active role of organisms.

As well as internal forces imposing themselves on the organism, there are external ones that squeeze it – environments seen by neo-Darwinism as implacably posing problems and assessing solutions. Instead, Lewontin claimed that organisms *construct* their environments, as well as being shaped by them. "Construct" in what sense? Lewontin gave two families of arguments on this point. First, organisms through their capacities determine what is *relevant* to them, filtering external factors insofar as they operate as evolutionary causes. Second, organisms physically remake environments through their biological activity.

I have argued that Lewontin was wrong to see these two phenomena as both pointing towards a kind of construction of environments [5]. A "filtering" or making-relevant is not construction. The two families of phenomena he cited do both push against a certain kind of externalist causal model, a model in which external forces determine how organisms change and not *vice versa*. But otherwise they are different, as one set of phenomena concerns how organisms *themselves* change in response to what they encounter, and the other concerns the effects organisms have on the world beyond themselves. Conflation of these two leads to overstatement of the extent to which organisms construct environments.

The decades since 1983 have seen extensive work in all these areas. I'll revisit these themes and the relations between them, distinguishing three ways that organisms can be seen as "active" in ways that matter to evolution.

2.1. Phenotypic Plasticity

The first part of Lewontin's 1983 presentation of organisms as subjects looked at the role of genes. He sketched, and then opposed, a view of organisms as the mere products of the shuffling of genes introduced periodically by mutation. For any given genotype, the phenotype or form of the organism depends on its environment according to a "norm of reaction," a mapping from environments to phenotypes that applies to that genotype [6, 7]. When the norm of reaction does not map all environments to the same phenotype, we have a breakdown of the simplest kind of genetic causation of traits.

A reasonable initial response might be is that no one has ever denied that environments make a difference to phenotypes; the simplest kind of genetic determinism is not a real position. Further, how is the effect of the *environment* on phenotypes something that makes *organisms* into active players?

The answer I would give to this question differs from Lewontin's. To some extent, plasticity is inevitable. But plasticity itself can also be adaptive, and the mapping from environments to phenotypes can be tuned by natural selection. A developing organism may pair an environmental state with a phenotypic response not out of accident, or biochemical necessity, but because that mapping has been selected for. In general, the implementation of the mapping requires some sort of sensing or tracking of the environment, and the forging of a link between the tracking mechanism and an appropriate response [8, 9]. Such links may involve signal transduction pathways, integration of cues, and feedback mechanisms [10, 11]. In these cases, plasticity has a *proto-cognitive* character; it shares some of the form of the arc from perception to adaptive response seen in animal cognition and action. Because of this need to implement the mapping, although an adaptively tuned reaction norm is often said to be associated just with the genotype, in fact it involves the entire organism's (or cell's) capacities.

So far, the point being made is one applicable on the time scale of individual development, and the next stages of the story might, in principle, follow the most orthodox neo-Darwinism. The relevance of these phenomena can be extended to evolutionary change, though, as argued by Mary Jane West-Eberhard [9]. She claims that many cases of evolutionary innovation occur through a process in which the first step is a novel phenotype brought about through a plastic response to a new environment,

followed by "genetic accommodation" of the innovation; hence, "genes are usually followers, rather than leaders, in evolutionary change." ([9] p. 29).

The importance of "plasticity-first" sequences of this kind has been discussed extensively [12, 13, 14]. I think this debate now features a mix of stronger and weaker claims about plasticity, some with limited bearing on the viability of standard views, and others that do mark something distinctive.

I'll start with a typical scenario discussed in this literature. A population might contain individuals that all look similar, but have different underlying genotypes. When environmental conditions change, differences become manifest. "Cryptic genetic variation" is revealed, as genotypes that produced similar phenotypes in the old environment do not so in the new, and some produce novel phenotypic forms. Fitness differences result, and further mutations also follow, tuning the reaction norms present in the population. These might remain broad (retaining a lot of plasticity) or become narrower, so that a trait once produced only rarely and in specific conditions comes to be produced routinely.

So far, it may seem that nothing unusual is happening from a mainstream neo-Darwinian point of view, and I think that is right. Once norms of reaction are recognized as traits in their own right, they are candidates for evolution by ordinary natural selection. "Cryptic genetic variation" is also interesting, but not disruptive of mainstream views. A way to look for a more substantial evolutionary role for plasticity is to pose the question as follows. Suppose some individuals in the population come to produce a new trait, T , in a new environment by means of phenotypic plasticity, and then at a later time, T (or a refined version of it) is produced reliably across the whole population. In one sense, there was "plasticity first," and genetic change "followed" a plastic response. But the neo-Darwinian can ask: suppose some individuals had *not* produced T plastically at the earlier stage, what would have happened differently in the longer term? If trait T is the best option in the new environment, it seems that mutations should eventually have arisen that gave rise to T obligately, and the plasticity-based production of T was a temporary stage that played no role in determining where the population ended up. Can the plastic production of T make more of a difference than that?

As I count them, there are three ways. One is by giving the population a kind of "breathing space" in the newly challenging environment; perhaps the population would not have still been around, or would not have been large and healthy, if some individuals had not been able to produce T by means of a plastic response [13].

A second way is via a mechanism emphasized by West-Eberhard. It may be that the plastically produced version of T at the earlier stage makes available a genetic *path* to a reliably-produced version, a path that would not otherwise exist or be as accessible. The presence of the plastic version of T provides a kind of phenotypic scaffold, and successive genetic changes then build a less-plastic version of the trait around it. T when produced plastically then makes a difference, because new mutations and combinations of alleles that would not usually be favored, if they arose in the absence of T , are now favored and enable T to be "canalized" [15, 16].

A third way gives a still stronger causal role to the plastic response. In the two scenarios above, T is assumed to be the best phenotype in the novel environment, and what arises at the end is just the best response to those new circumstances, with help from plasticity along the way. But it may be that what made the reliably produced version of T adaptive in the later stages *was* the plastic production of T earlier on. Once some individuals are producing an initial version of T facultatively, other individuals also benefit from producing T , and there may be selection to produce it more reliably. The initial plasticity-based production of T itself sets the path. This process will be restricted to traits for which feedback of this particular kind is possible. Plausible examples would include communicative behaviours [17]. Outcomes where the eventual state is one where the population produces something *similar* to the plastically produced trait T can also be recognized as a special case: plastic production of T at the earlier stage might lead to something very different being favored later, if the best response to T is to do something else.

So plasticity as a factor in individual development can give organisms an "active" role, insofar as the adaptive matching of phenotype to environment has a proto-cognitive character. On the evolutionary side, the fact that norms of reaction are important traits in their own right is not very disruptive to mainstream views. But there are some ways in which the plastic production of a phenotype can alter an evolutionary path or send an

population to a different eventual state from the one it would have reached if that phenotype had not been facultatively produced.

In almost all of this first cluster of phenomena, the environment that is being responded to, and that is affecting phenotype via the norm of reaction, may be fixed and impervious, or exogenously changing. And no one outside the evolving population in question need be affected by what is going on. The last mechanism discussed, in which the plastic production of a trait affects what it is advantageous for others to do, is one where the effects of an organism's behavior start to ripple out a little. Next I'll look at phenomena in which these effects become broader.

2.2. Niche construction

Lewontin claimed that another subject-like role for organisms is their "construction" of environments. Above I set aside one family of arguments he offered on this issue, and I'll now look at cases I see as more substantial. I'll recognize two categories, using the term "niche construction" for situations where organisms have physical effects on their environment that feed back and affect the ongoing evolution of those organisms (the population or species). Cases where the activities of one species affect others will be discussed separately. In niche construction, the activities of organisms at one time lead to changes to their environment that affect selection pressures present at later times, and also change the environment in which development takes place.

The "active" role of organisms now extends outside them. Niche construction need not involve proto-cognitive mechanisms of the kind that can give substance to the subject-like role of organisms in phenotypic plasticity. In niche construction, the subject-like role of organisms involves their being initiators of change, not necessarily "smart" ones in even a minimal sense. The organisms might be inflexible, with a gene-to-phenotype causal path that is simple and largely unconditional, but where this path features downstream effects that form a loop in an evolutionary context.

We can also add the two phenomena covered so far – phenotypic plasticity and niche construction – and further phenomena result. One is what Odling-Smee, Laland, and Feldman [18] call "ecological inheritance." Too much is sometimes included in that category, as many ways that niche construction can have effects on future generations do

not amount to *inheritance* in an evolutionarily relevant sense, as they are not mechanisms that produce parent/offspring similarity. But inheritance can arise by combining niche construction with plasticity. Assume that organisms are plastic, sensitive to the details of their environment as they develop, and that they also *change* the environment in a way relevant to that norm of reaction. Then cycles can arise; organisms respond to their circumstances, and do so in ways that affect their environment, where the resulting environmental conditions affect the next generation of plastic organisms in a way that results in the same phenotype being produced once again. If those affected are differentially the biological offspring of the niche-constructors, then the result is the inheritance of phenotypes over generations.

A causally minimal but empirically important version of this combination is the *copying* of behavior, especially by offspring. Then an "environmental" change barely stretches outside the producing organism at all, just far enough to be seen, but this can be an important mechanism for cultural evolution [19]. Some kinds of imprinting have a similar character. Parents make nests out of certain materials, which offspring imprint on, and use to make nests later in life. Niche construction can also be symbolic and communicative in more paradigmatic ways. Signaling, in its general causal pattern, can be seen as a combination of niche construction and phenotypic plasticity (Ben Kerr, personal communication, 2013). A sender or producer of signs makes some change to the environment that is perceived by a receiver who responds plastically. If there was no plasticity at the receiver end, no tendency to respond differentially to what is seen, there would be no point in the producer constructing the sign.

2.3. *Ecosystem engineering*

My third category is the same as the second on the "cause" side – organisms act in ways that transform their environments. What is different is the effect side, which now involves ongoing evolution not of the same population, but of others.

The term "ecosystem engineering" was coined by Jones, Lawton, and Shachak [20]. "Niche construction" is sometimes used as a broad term for both categories.

That is a reasonable usage, but here I use "niche construction" for effects on self (one's one population) and "ecosystem engineering" for effects extending more broadly – the term "niche" indicates the reflexive nature of the former category.

Niche construction and ecosystem engineering blend and combine. *Coevolution* is evolution in which the evolution of population *A* affects how population *B* evolves, which in turn affects *A* again. This is only a marginal case of ecosystem engineering if the abiotic environment is not much affected, but it can certainly be important. Coevolution both has a niche-constructing character – as *A*'s actions eventually affect the environment relevant to its own later evolution – and it is ecosystem engineering – as *A* affects others as well.

An example emphasized by Lewontin was change in the mix of gases in the Earth's atmosphere, due to the metabolic outputs of organisms. In those cases, just about everyone is affected by the re-engineered environment. Other cases are found in forests, where earthworms, fungi, and microbes continually reconstruct the soil.

Ecosystem engineering (along with niche construction, its cousin) is inevitable to some degree. No organism could fail to have some effects on its environment, as metabolism itself involves the exchange of materials with one's surroundings. The questions relevant in each case concern the extent of these effects and their evolutionary importance. There is also no sense in which ecosystem engineering and niche construction are denied within mainstream neo-Darwinism. More contentious is whether mainstream views have downplayed these things, or underestimated their role. I think that in at some contexts one might see habits of thought that tend to accentuate the environment→organism causal paths and downplay the others. This cannot be said about coevolution; that is squarely in everyone's mind and almost always has been. But with respect to the abiotic environment, there is perhaps a tendency to cast it in models as fixed or exogenously changing. This can be justified in a modeling context as a deliberate simplification, but I wonder if there is also some role for implicit habits of thought. I am receptive to this idea because of my experience with the only empirical system I've studied in detail, an octopus field site in Australia [21-23]. The site was found by a recreational diver, Matthew Lawrence. It is a dense bed of shells in a flat sandy area, and octopuses live there in unusually high densities. Initially I saw the shell bed as just a

special patch of habitat that was generating unusual behaviors in octopuses. One day I wondered: where did the shell bed come from? Lawrence replied that he thought the shells had been brought in by the octopuses themselves.

The point was obvious once he said it – obvious as a possibility, anyway. Odling-Smee, Laland, and Feldman [18] use a passage attributed to George Orwell for the epigraph of their niche construction book: "To see what is in front of one's nose requires a constant struggle." Indeed. What we now think about this octopus site is that a single discarded human-made object "seeded" the site by creating one good den (or a couple of them) in an otherwise difficult setting. Octopuses living there brought in scallops to eat, and as shells accumulated, so did opportunities to build more dens, in a process of positive feedback.

Running through the phenomena above, this case includes plasticity – a special environment induces unusual behaviors through individual-level adaptation. It also features ecological engineering – many species of invertebrates and fish are found at unusually high densities on the site [22]. Do the octopuses' effects on their environment change selection pressures for later generations of those animals? Not much, because this is a tiny site and, when octopuses of this kind reproduce, their larvae disperse as plankton and, as far as is known, do not make their way back to sites occupied earlier by their parents. Non-genetic inheritance from parent to offspring is also unlikely. Instead, unusual patterns of behavior continually *recur* at the site, through being reconstructed by new generations of octopuses who happen upon this unusual environment and, through their foraging behavior, maintain and extend it.

3. Subjects as Evolutionary and Ecological Causes

I've looked at organisms as agent-like factors in evolution, and will now look at a subset of these phenomena. In Lewontin's 1983 paper, the word "subject" referred to a role organisms can play – "The Organism as the Subject and Object...." A "subject" in this sense is an initiator or driver of events. In this section I'll look at subjects in a different sense, a subject as a kind of entity.

What I have in mind is roughly an entity or system that has cognitive or mental properties, but properties of a particular kind within that family, and "mental" is too

strong a term for much of what I'll discuss – I will mostly be looking at very minimal forms. A subject, in this sense, has a pair of linked features: (i) a point of view on the world, and (ii) an agenda. Subjects act in ways that reflect both.

This section will be about the role of those things both as evolutionary products and as causal factors. My choice of focus here is partly a reflection of philosophical goals, and of what I regard as the right approach to the mind-body problem in classical form – the project of making sense of the place of the mental in a material and biochemical world. The main thing this project requires is giving an account of what minds are and how they came to be, but a contribution also comes from saying what role they have, what they do.

Clearly *behavior* has an important role in evolution, as a determinant of fitness and as part of the context most organisms confront. There is a common way of looking at the intellectual landscape in which noting the importance of behavior is not seen to tell us much that is helpful. This is because, as well as the information-processing or cognitive side of minds and brains, there is said to be another side of the mental whose role is mysterious, the "qualitative" or "phenomenal" – roughly speaking, the "feel" of our mental lives [24]. I think, instead, that while there is a side of the mental that does pose special problems for a materialist world view, it can be approached through the idea of subjectivity, a concept which is a bridge between biology and the more puzzling features of the mind [25, 26]. Subjectivity evolved to *do* things for organisms, and the actions that result from these capacities have further ramifying effects. In this paper I will not make the argument that subjectivity is the right concept with which to meet the (reasonable side of) the demands of the classical mind-body problem; instead I'll assume a view of this kind and sketch an evolutionary approach to subjectivity, drawing on the ideas above. Aside from the philosophical goals, I think this development of the organism-as-cause theme may be productive even if one thinks about just the biological side.

Some recent literature has looked at the idea of biological *agency* of simple kinds [27, 28]. What are the relations between *agents* and *subjects* in my sense? Both concepts in their pre-existing forms are vague and flexible. The idea of agency is more output-oriented, tied to action. In the notion of a subject, the experiential side is emphasized, though each side might, in some way, imply the other. In this discussion I am aiming at

the duality – sensing and acting as two sides to the mind, running far back in evolutionary history as complementary capacities. A subject in my sense has, I said, both a point of view and an agenda, so agency is in the picture as well as receptivity.

Looking at the world, or perhaps a single ecosystem, as a large and diverse causal network, a subject is a special sort of node within the network, a center of a certain kind of causal influence. Subjects affect things in ways that other natural objects do not. When subjects are present, events have effects that are filtered through those subjects' points of view and agendas. The effects subjects have include, at a local level, the fulfillment of those agendas and their immediate consequences. The effects also include large-scale changes that occur not because they are sought, but because the pursuit of agendas by a collection of subjects has further ramifications.

The role of *subjects* as causes is one aspect of the role of *organisms* as causes, a subset of those phenomena. Does that mean that subjects are a subset of organisms? Not exactly. All cellular life has some subject-related features. Entities can be more or less subject-like, can have subjectivity-relevant features in more or less marked ways. Subject-status is present in degrees, including cases best seen as *proto*-subjective and cases, especially in animals, where this side of life becomes more elaborate [29-31].

Cellular life is characterized by a set of distinctive chemical and thermodynamic features. Living systems are "dissipative" systems interacting with a milieu that is a source of energy and sink for higher-entropy outputs. (These are features of metabolism that make some degree of ecosystem engineering inevitable in every case.) A cell is a center of an input-output flow of a particular kind, as well as being a system that maintains, demarcates, and rebuilds itself. In a *very* minimal sense, these features suffice to give all cells the beginnings of the pair of subjectivity-related features I mentioned above – a point of view and an agenda. Where exactly those features begin – the border between their presence and absence, and how to think about the most marginal cases – is interesting but not the topic of this paper. Steps that take us to clearer territory come quickly. One such step is sensing, and the use of *indicators*.

Indicators are events and variables that have importance to an organism through their status as predictors of the state of *other* variables [32, 33]. The adaptive role of an organism's response to one stimulus variable, a cue or signal, involves the coordination of

the organism's activities with something else. Use of a stimulus as an indicator, in this sense, is contrasted with situations where the adaptive response to a stimulus is driven entirely by the stimulus' intrinsic properties (its being an energy source, or a toxin). Light, for example, can be used as an energetic resource and as an indicator of other conditions. Even before eyes exist, light may be used by organisms as a cue to the time of day, or the height of an organism within the water column (Dan-Eric Nilsson's "class I" category of photoreceptor-controlled activity [34]; see also [35]). Light can also be used as a resource *and* an indicator, via autocorrelation – the presence of light here and now may be a predictor of the same thing at future times. Bacterial chemotaxis is generally characterized by that kind of mix; chemicals can be both resources and guides, as when a bacterium follows a gradient towards a source of the same food. The chemical sensed is intrinsically important *and* is input to a control system in virtue of its features as an indicator. Something else often present even in unicellular organisms is a degree of informational *integration* – of sensory inputs with each other, or of present with past experience. In either case, a present stimulus has its effects only in combination with other things sensed now, or what was sensed before.

Specialized sensory structures focus the receptivity of living systems and accentuate their "point of view" features. The same is true of integration. Through even these simple cases, we can also start to glimpse the shape of subjectivity as a causal factor. Subjects are sensitive; they scoop up information and act in response. Those actions contribute to survival and reproduction, and this fact takes causal paths down particular directions. All objects are sensitive to events around them in some ways (a wine glass breaks when struck, and may also be affected by one stimulus in a way conditioned by another earlier or simultaneous one) but living things, which use indicators in the service of staying alive and reproducing, respond to events differently from other systems.

In animal evolution these capacities related to subjectivity take on a larger role, as a consequence of multicellular organization, and the integrated form of multicellular collectivity that most animals exhibit. Multicellular sensory systems, which utilize the spatial organization of complex parts, give animals different ways of responding to the

world, a point of view on a larger scale. Action is expanded with multicellular effector arrays.

On the sensory side, image-forming eyes are a paradigm example. Image-formation in general relies on the spatial arrangement of receptive elements that are themselves complex, like cells. Directional photoreception – enabling some tracking of the direction of light – is found in various protists and does not require multicellular organization. From there, image-forming eyes of low resolving power ("class III") evolved a number of times, and high-resolution vision ("class IV") perhaps just four times [34]. To a good approximation, image-forming vision is multicellular. This generalization is not quite exceptionless. Some unicellular dinoflagellate protists (warnowiids) have eye-like "ocelloids" with a lens and retina, accepted by Nilsson as genuine eyes. This eye truly probes the boundary between unicellular and multicellular structure, however, as several of its components are derived from endosymbionts – plastids and mitochondria. So it has much in common with a multicellular structure, though it is housed within one cell ("The first description of a warnowiid was dismissed as a cell that had scavenged the [multicellular] eye from a jellyfish" [36]). At an even smaller scale there is a case of an eye-like photoreceptor system in a cyanobacterium [37]. In this case the problem of space is overcome (to the extent that it is overcome – it is not yet clear what this system does) by focusing the incoming image on the cell's outer membrane itself, by "using the whole organism as an imaging device" [38]. In general, image-formation is achieved by spatially organized collections of cells.

Sensing as it becomes more complex achieves directedness on distal objects and states of affairs. One kind of "directedness" on the distal is present in virtue of the most basic features of indicator use, which I described above as responding to one variable in a way conditioned by its predictive relationship with another. An additional kind of involvement with distal affairs, one that can still be found in relatively simple sensory systems, is discussed in Dretske's information-theoretic analysis of perception [32]. Assume a causal chain from a distal variable, via a more proximal variable, to an inner state of an organism (see Figure 1). The state of the organism has causal connections to both the proximal and distal variables, but may only have an *informational* connection to the distal, if the values of the proximal variable are not a difference-makers of the right

kind. If the organism goes into the same internal state in response to any of a set of proximal stimuli, all of which are produced by a single distal condition, then the inner state carries no information (does not reduce uncertainty) about which of those proximal states obtains, but may still carry information about the distal "source." A response that is indifferent to the proximal in this way thus has an informational directedness on the distal state.

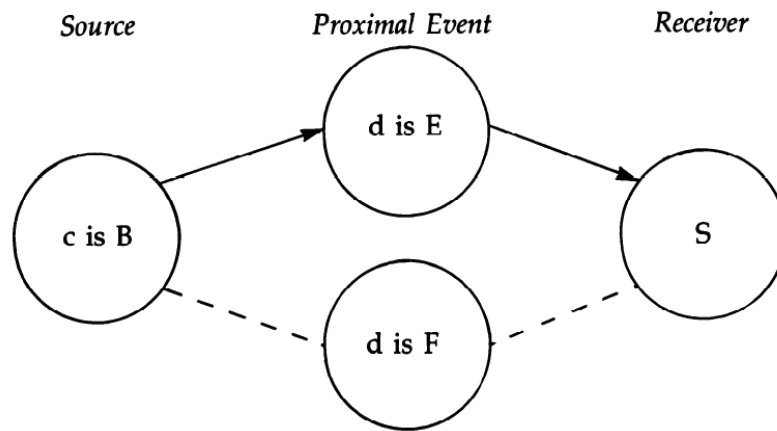


Figure 1: Dretske's information-theoretic treatment of perceptual directedness on distal events. Solid lines represent actual causal relations and broken lines represent counterfactual ones – alternative causal paths. The state of the receiver is informationally associated with the state of a distal source, c , but not with the state of the proximal cue, d , as the state of d (with respect to the values represented in the figure) makes no difference to the receiver. From [32].

The loss of information about proximal states along chains, and the retention of information about more distal ones, is also found outside the domain of life and subjectivity: the state of a roadway carries information about the presence of earlier rainfall, but not about the details of how the raindrops fell. This pattern of information loss and retention has special consequences, however, in a context where a selection process is shaping a response at the end of the causal chain. That response can be targeted specifically on a distal event.

The information-theoretic directedness of sensory states on distal objects of perception described by Dretske is a first move towards what in more elaborate sensory systems are referred to as *perceptual constancies* [27]. Here there is more substantial

transformation of sensory input, not merely designed indifference to some proximal details, that enables the organism to "look past" features of stimulation that are due to quirks of circumstances, to track what matters in the environment. These capacities, which rely on nervous systems, are seen by Burge as marking a transition to the representation of objects.

What is the relation between the achieving of distal reference and the spatially organized mapping of stimuli, as in image-forming eyes? Spatially organized mapping does not inevitably involve reference to the distal, though it often does so. Spatially organized sensing does change the kinds of responsiveness of organisms to their environments in other ways. It enables a response to environmental patterns that exist only at macroscopic scales in space [31]. Unicellular organisms are often able to find partial ways round the constraints of their small size; *E. coli* chemotaxis, for example, uses time to adapt the cell to space. A food source generates a chemical gradient, but a bacterium is too small to have sensors that detect the direction of the gradient directly, so it uses temporal structure to adapt itself to space, following straighter lines when chemical conditions are improving over time and making random deviations when they are not. Multicellular collectives can track spatial structure more directly, as in the case of high-resolution vision. Distal reference and spatially organized mapping both enable new kinds of directedness in behavior in subjects, with consequences for the objects around them.

Above I introduced the integration of processing as a subjectivity-relevant feature [39]. This includes integration of present input through various senses, integration of present experience with the past (memory), and integration of what is presently sensed with details of the state of the organism (eg., satiety). Integration enables the organism to respond to non-trivial functions of environment conditions, such as conjunctions and disjunctions. Integrated processing is not peculiar to animals, but neurons, with their branching dendrites and other projections, are ideal means for enabling integration. What is especially relevant here, again, are the ways that this feature affects the shape of causal networks in systems that include subjects of this kind. Consider a combination of distance sensing and integration of senses. There is detection by an agent of what is happening at X and at Y , and the response made is a function of both, perhaps in conjunction. What

happens next *at X* – and/or at *Y*, and/or at other places – depends on both states and how they are combined by an agent. The same applies in the case of time; what is done now can be a consequence of the state of environment sensed now *and* the state sensed in the past, again as filtered through an agent's agenda. Integration of this kind both creates a more definite point of view – an integrated outlook on the world – and is relevant to the subject as cause, creating different kinds of dependence between events.

On the sensory side I discussed directedness on distal things, via "looking past" proximal stimuli. There is a complementary phenomenon on the effector side. It could be called *distance-action* – that term suggests a paradoxical character, but it works analogously to distance-sensing. An animal can set only proximal objects in motion, also imitating a causal chain. But as with Dretske's point on the input side, it is possible for motor programs and other output-side structures in an organism to have an informational directedness on a more distal effect. Actions can be varied across conditions in a way that reliably brings about a distal outcome, and does not reliably go via a particular proximal means. Looking back at Dretske's diagram (Figure 1) and imagining the left hand side now as an agent and the right hand nodes as effects of what is done, again we find there can be more robust correlation between an agent's state and a distal event than between the agent's state and the proximal links, by producing different outputs that have, in the circumstances, equivalent downstream consequences.

Extending the analogy further, there can be *action constancies* as well as perceptual constancies. The analogy is not exact, as in order for the same distal effect to be achieved through variation in means, there must be a sensing of features of the local circumstances that make different actions necessary (or perhaps feedback from the failure of initial attempts to bring about the distal result). The kind of "constancy" seen in the case of action requires that certain kinds of sensing also be present, whereas in the case of perceptual constancies, there is no necessary role for adjustment of action, of a kind that would establish symmetry between the two cases.

In other ways, the two kinds of involvement with distal affairs are similar. In the case of action as well as perception, there are both low-level and fine-grained adjustments that are not conscious, and also more deliberate measures. As you reach for objects, you may make small adjustments with a homeostatic character that are not consciously

accessible [40]. These homeostatically guided small adjustments have analogies to subpersonal perceptual constancies. There are also deliberate personal-level measures in both cases. On the action side, there is deliberate use of tools as means to achieve distal results – acting on X with the intention to affect Y . *Intentions* are psychological states mediating action constancies. On the perceptual side, there is the deliberate or personal-level use of observable cues to draw conclusions about more distant events – inferring from tracks, traces, and news reports.

Above I said that looking at the world, or an ecosystem, as a large causal network, a subject is a special sort of node within the network, a center of a certain kind of causal influence. I discussed several features of subjects that make a difference in such settings, including directedness on the distal and integration. The first is a kind of "reach"; the second is a bringing together, or focusing, of causal paths. What occurs at one place can depend systematically on what happens at various others in space and time, as filtered through a point of view and subjected to an agenda.

4. Evolutionary and Ecological Roles

This section applies ideas above to some stages in the history of life, looking at organisms as causes of large-scale events, and then at organisms *qua subjects* as causes.

An example highlighted in Lewontin's 1983 paper was change to the Earth's atmosphere early in the evolution of life, especially changes in the levels of oxygen in the form of O_2 molecules (dioxygen). The "natural" atmosphere for a planet like ours is very different from our present atmosphere; if the Earth's atmosphere were allowed to reach an equilibrium, the oxygen would disappear and the atmosphere would be nearly all carbon dioxide. Earth's oxygen-rich atmosphere is a product of organisms, via photosynthesis.

The role of oxygen as effect and as cause has since become a topic in debates about several episodes in the history of life, especially the appearance of animals. From an initial state of the atmosphere with almost no oxygen gas, the rise of atmospheric oxygen, beginning perhaps 2.3 billion years ago, was due to photosynthetic activity of cyanobacteria. The crucial transition was not just the evolution of photosynthesis itself, as most forms of photosynthesis invented by prokaryotes do not have a role for oxygen. Cyanobacteria have a more complex photosynthetic system.

[O]xygenic photosynthesis is an intricate construction that unites several distinct molecular innovations to form a unique functional system. From an ecological perspective, this concatenation might well be regarded as the central event in the history of life, because it liberated biology from hydrothermal vents and other environments where locally strong redox gradients could support chemosynthetic life, allowing organisms to spread across the planet.... And it only happened once. ([41], p. 5).

After the first billion years or so of this activity, some cyanobacteria were taken up as wholes by other cells, in an endosymbiotic event that in time gave rise to green algae and land plants.

Levels of oxygen remained low for some time from the invention of oxygenic photosynthesis, though, until a sharp rise less than 1 billion years ago, perhaps due to the filling of geochemical sinks, first in the ocean and then on the surface of the earth, that had absorbed photosynthetically released oxygen up to that point.

The rise in O₂ levels right around the Ediacaran (635-540 mya) has suggested a role for oxygen in the early evolution of animals and then the Cambrian explosion. One view has it that, before this time, O₂ levels in the oceans were so low that the number of cell layers an animal could support was very restricted, as oxygen had to move through animal bodies via diffusion [42, 43]. Without cell layers there is little possibility of differentiation within bodies. According to Knoll, this constraint was relaxed around 580-560 mya. With more available oxygen, the radiation of animals and increases in size and activity were possible.

Some recent work has denied that animal life at this stage was so limited by oxygen; animals can get by at low levels [44]. And though animals and oxygen levels rose at roughly the same time, there is some evidence that animals predated oxygenation of the ocean. Further, the causal pathway need not be one in which oxygen levels rose and animals simply followed. Butterfield [45, 46] argues that extra atmospheric O₂ could have had little role in the beginnings of animal evolution, given the physical condition the seas were in. The seas were changed, in another large-scale case of ecosystem engineering, by early animals themselves.

The seas, for Butterfield, have two stable states and shifted between them. The old regime was one of turbid, stratified waters, dominated by cyanobacteria. With early

animals, the regime changed. Suspension-feeding animals such as sponges cleared and mixed the water, and broke down ocean layers. Early animals "engineered an alternate clear-water state" [46]. As animal evolution accelerated, a transition was completed from a comparatively static microbial world, with huge populations and very little extinction, to a world featuring smaller populations of larger organisms, long food chains, and waves of extinction and reinvention. That world also features ongoing engineering of environments by animals, due to a cluster of features in various combinations – animals are heterotrophic, often motile, usually carrying around an "an evolutionarily optimized chemical reactor" in the form of a gut.

I won't try to assess the empirical side of this view, but it is important in principle, given the context of this paper. The effects Butterfield cites are in a sense intermediate between the effects on the Earth of organic activity that is not much tied to subjectivity-relevant capacities – exemplified by photosynthesis and its effect on the atmosphere – and later roles stemming from behaviorally complex animals with substantial nervous systems.

That next stage in the story begins in the Cambrian. There remains uncertainty about the Cambrian "explosion," but one influential family of views gives sensing, information processing, and behavior a pivotal role [47]. The Cambrian sees the rise of bodies with hard parts, means for motion and manipulation, and better senses – especially image-forming eyes, including both the compound eyes of arthropods and camera eyes in vertebrates. Rapid evolutionary change in the Cambrian may have been due to the coevolution of bodies and behavior, including arms races, especially those between predators and prey.

Arthropods appear to have led the way as predators, prompting evolutionary responses from other groups [48, 49]. In this picture, directed action – by way of complex sensing and new means for mobility and manipulation – plays a central role. The Cambrian appears to have seen new levels of *involvement* of animals in the lives of others, and a rapid and far-reaching regime of coevolution between bodily forms and behaviors. Oxygenation of the seas (with or without the engineering posited by Butterfield) may still have played an important role as cause in this process. Oxygenation may have made possible physiologies, morphologies, and behavioral profiles that were

not achievable earlier, including the bodily means for the new behaviors characterizing this period, including larger size, more cell layers, and mineralized shells and armor [50].

So a sequence of linked and overlapping stages begins with cyanobacteria and their slow oxygenation of the atmosphere, a case of ecosystem engineering that does not involve subjectivity-relevant capacities. If Butterfield is right, then in a second stage early animals cleared and mixed the oceans, making additional oxygen useable to marine animals and initiating further processes of engineering, also setting in place new evolutionary and ecological regimes. This stage depended on features that are characteristic of animal life but less related to subjectivity. In the Cambrian, perhaps aided by oxygenation, animals began a process of rapid coevolutionary innovation, due in large part to animals becoming able to direct action in new ways by means of complex senses, effectors, and neural control systems. These are animals that can move, track macroscopic environmental structure, and direct action in real time on distal objects, including each other.

The story has a fourth stage that I will register only briefly, the stage involving human technology. It may be controversial whether there is good reason to recognize a new period in the history of the Earth, the "Anthropocene," dating from the late 18th century [51], but it is not controversial that human behavior and technology have transformed the Earth, and have done so in a way guided by the mental states and agendas of human agents.

5. Consequences

I will finish by making connections to two other themes, one in biology and one in philosophy. An idea in the vicinity of these views about the transformation of the physical environment by organisms is the "Gaia" hypothesis [52], the idea that the Earth as a whole is an organism or exhibits organism-like features. Gaia was the over-extension of an insight. The insight is recognition of the effects of life on a planet's physical and chemical properties. According to Knoll, Gaia did spur a shift in thinking on these matters: "Jim Lovelock's advocacy of metabolism as a key set of processes in the Earth system was an important catalyst of modern Earth system science. The roots of geobiology go back to Vernadsky and Baas Becking, but debate over the Gaia hypothesis

did lead to more quantitative, mechanistic approaches to the subject" (A. Knoll, personal communication, 2015).

The idea of the Earth as organism was not just an exaggeration, but the assimilation of an insight to the wrong pre-existing model, the model provided by our familiarity with organisms. The Earth, seen as a maintained product of ecosystem engineering, is one kind of unit, and organisms are *parts* of such an entity. Organisms are forged in micro-evolutionary competition, and hence exist in populations within larger systems. It is an error to have an organism-like view of the Earth itself; the whole has different properties, which our usual habits and intuitions perhaps don't do well handling – the Earth is not an organism, but it is not impervious either to life. It has been successively re-engineered by the living organisms that are among its parts.

Another connection, more on the philosophical side, involves one kind of "idealist" tradition in philosophy. At the start I said that the focus on subjects in this paper is due in part to a philosophical agenda, an attempt to show the place of the mind in a materialist view of the world. The familiar alternative to materialism at present is *dualism*, though alternatives in the past have included various kinds of *idealism*, views in which all (not just some) of reality is seen as having an ultimately mental or spiritual character. Some idealist views have been motivated by the problem of explaining how we could have knowledge of a world of material objects – they have been motivated by our limitations – but the appeal of this family of views has also sometimes stemmed from the *efficacy* or importance they give to the mental in their account of what is going on in the world, especially in how the Universe's apparently disparate parts are tied together.

Both idealist views and the usual ways of rejecting them were criticized by John Dewey in *Experience and Nature* [53]. Idealists, he said, seek to see the mind as responsible for everything. The problem with the usual alternatives – "realist" and/or materialist views (the landscape here is problematic) is that they seem to say that the mind is responsible for *nothing*, or next to nothing. Did opponents of idealism mean to say this? No, of course humans with minds decide and do things, so minds have effects. But why do philosophers often say that the world "exists independently" of the mind? Dewey thought that the resolution of this misconceived debate is to note the partial, historically contingent, and local way that some of the world depends on the contents of

minds – on what we want, what we see, what we think. Much of what is around us is a product of intelligence and the pursuit of agendas. The building you are probably in as you read this – certainly the artifact, printed or electronic, on which these words are displayed – are consequences of what some people wanted and believed. The "constructive" role of the mental goes via ordinary action.

Idealism, historically, neglected the role of ordinary action; it was a wholesale view: *everything* is conditioned by the mental. Idealism neglected the limited and before-and-after nature of the mind's efficacy. But this tradition was the only part of philosophy that seemed to acknowledge the efficacy of the mental in the world's operation at all. As Karl Marx said, "the active side was developed by idealism" [54]. The right approach is to reject idealism but acknowledge the mind's efficacy, via the material but mentally conditioned channels of action.

I broaden the point. Dewey saw the "mind" as something dependent on human forms of social interaction and on language. I take the story hundreds of millions of years further back. But the thrust of his point does apply. We *do* live in a world that was shaped first by life and then by minds – by the evolution of subjects, who sense the world and act on it. The difference it makes to have subjects around is not just a matter of buildings and computers, but also the kinds of causal dependencies they engender, tying bits of the world together.

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