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Discussion

The Return of the Replicator: What is Philosophically Significant in a General Account of Replication and Selection?

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Abstract. The aim of this paper is to outline a typology of selection processes, and show that different sub-categories have different explanatory power. The basis of this typology of selection processes is argued to be the difference of replication processes involved in them. In order to show this, I argue that: 1. Replication is necessary for selection and 2. Different types of replication lead to different types of selection. Finally, it is argued that this typology is philosophically significant, since it contrasts cases of selection (on the basis of the replication processes involved in them) whereby selection causes adaptation – and, therefore, can be used in explanations of the (real or apparent) teleology of Nature – and cases in which selection lacks such explanatory power.

Key words: adaptation, interaction, replication, selection

As the evolutionary approach is becoming more and more popular in a large number of different disciplines,[1] there is a strong need for a typology that shows what is similar and what is different in all these evolutionary models. Also, a general conceptual framework would be needed in which these different evolutionary models can be analysed. The endeavour of this paper is to examine the possibility and the philosophical significance of such conceptual analysis.

Such general accounts of selection have been given by several philosophers, most notably by Darden and Cain (1989), and recently by Hull et al. (2001). My endeavour is slightly different from theirs. Instead of using only one notion of selection I argue for a broader typology of different *types* of selection. To put it differently, instead of trying to answer the question of what selection is, I would like to address the differences between various forms of selection. According to the literature on selection a phenomenon is either selection or it is not. My question concerns *what type* of selection it is.

I have argued elsewhere that this more general and more inclusive typology might more effectively face the possible challenges to a general account of selection (Nanay 2001). The most serious such challenge is the claim that selection lacks the explanatory power that has been attributed to it.

It has recently been argued that selection cannot be used to explain adaptation, therefore it cannot be helpful in explaining the teleology of Nature (or explaining the fact that Nature appears to be teleological). In other words, selection is a philosophically rather uninteresting notion without any serious explanatory power (see Sober 1995; Walsh 2000). I would like to point out that different types of selection have different explanatory power, and selection restricted to one sub-case of the typology can indeed be used to explain adaptation. The importance of such typology lies precisely in differentiating between selection processes with different explanatory power. Hence, this typology is not just a *l'art pout l'art* conceptual analysis without any philosophical significance.

The general account of selection is given indirectly. First, the concept of replication is analysed, and it is shown that replication is necessary for selection. Then a typology of replication processes is offered, and this typology is matched with the typology of selection processes. Finally, it is pointed out that the explanatory power of different types of selection depends on what type of replication process is involved in them. In other words, *selection processes with different types of replication have different explanatory power*.

Replicators and interactors

First of all, two central concepts of evolutionary biology and the philosophy of biology have to be introduced: replication and interaction. According to David Hull selection consists of repeated cycles of replication and interaction (Hull et al. 2001: 53; Cf. Hull 1981: 40–41). He analyses selection conceived traditionally as "heritable variation in fitness" as cycles of a copying process (replication) and the interaction with the environment. The replication-interaction distinction needs some clarification (Cf. Brandon 1996).

Hull defines the replicator, that is, the unit of replication as "an entity that passes on its structure largely intact in successive replications" (Hull 1988: 408; Cf. Hull (1980: 318) for a slightly different definition.). The interactor, that is, the unit of interaction, on the other hand, is defined as the "entity that interacts as a cohesive whole with its environment in such a way that this interaction causes replication to be differential" (similarly Hull 1988: 408; Cf. Hull 1980: 318).

For example, in the most standard natural selection case the replicator is the gene, whereas the interactor is the organism itself. The genes are passed on and the organism interacts with the environment in such a way that this interaction causes the replication of genes to be differential. In other words, those genes that are responsible for the development of organisms that are more successful are more likely to replicate.

Several points need explanation here. First of all, it has to be noted that the replicator is only one of the numerous factors that are causally relevant in the formation of the interactor (Cf. Griffiths and Gray 1994, esp. p. 298ff and see Sterelny, Smith and Dickison (1996) for a critical overview). In the gene/organism case, for example, the development of the organism is influenced by numerous factors unrelated to the genes.

Another point of possible misunderstanding is implied in the semantics of the word "replicator". It is not clear whether the replicator is the entity that copies or the one being copied. Or maybe both of them at the same time: the entity copying itself (Cf. Lewontin 1991: 48–49). Again, the gene/organism case shows that genes are copied by a complicated mechanism; genes do not copy themselves. I will use the term replicator to refer to the entity being copied.

With all these clarifications in mind I turn to the analysis of the concept of replication. In the next section I argue that replication is necessary for selection. The analysis of replication is crucial in the discussion of selection, since the main claim I would like to make is that *selection processes with different types of replication have different explanatory power*. The first step of arguing for this claim consists of finding a general definition for replication and showing that replication is necessary for selection. After that I'll turn to the differences between the sub-cases of replication responsible for the differences between the explanatory power of various selection processes.

What is replication?

We have seen that the replicator has been defined as "an entity that passes on its structure largely intact in successive replications". In this section I would like to examine the possible interpretations of this definition.

We are faced with the question of what "passing on the structure" implies. Intuitively two aspects of "passing on" or "copying" seem necessary: similarity and causal connection. This intuition has been captured by Peter Godfrey-Smith's definition. He coins the term "replicate":

> Y is a replicate of X if and only if: (i) X and Y are similar (in some relevant respects), and (ii) X was causally involved in the production of Y in a way responsible for the similarity of Y to X (Godfrey-Smith 2000: 414).

Replication is defined as any process by which a replicate is produced (Godfrey-Smith 2000: 415). It is important to note that this is a very weak notion of replication. According to this definition, photocopied pages or raindrops following the same trickle on the window also count as replications for example.

Interestingly enough, in the same paper where Godfrey-Smith gives this definition he argues that even this weak notion of replication (conceived in the above sense) is not necessary for selection (Godfrey-Smith 2000: 413). I accept his definition of replication, but I would like to challenge his claim that replication is not necessary for selection.

I would stop for a moment to make it clear what the logical structure of my claim is. Godfrey-Smith argues that even if we take the weakest possible notion of replication it will not be necessary for selection. With this he undermines every possible stronger account of replication, since if he showed that replication in this weakest sense is not necessary for selection, then any stronger definition of replication would automatically count as not being necessary for selection.

I do not want to propose any stronger definition of replication; I accept Godfrey-Smith's, but I would like to show that replication as he defines it is indeed necessary for selection. Since the concept of selection has not yet been analysed, in this section I will use the classical definition: "heritable variation in fitness" (Lewontin 1974), which (unlike Hull's definition, for example) does not presuppose the concept of replication. I will return to the question of the definition of selection later.

Godfrey-Smith has two independent arguments to support his claim that replication is not necessary for selection. The starting point of the first argument is a thought experiment:

> Imagine there is reverse translation, from protein primary structure to nucleic acid sequence, as well as forward translation. Then we can imagine an organism in which the genetic material initially contributed by parents is in the form of DNA, but once the new individual has used these genes to manufacture proteins, the DNA is broken down. (The proteins regulate their own activities during this middle stage.) At the end of the cycle, new genes for the next generation are made by reverse-translating (and reverse-transcribing) from protein to nucleic acid (Godfrey-Smith 2000: 417).

The logical structure of the counterexample can be summarised as follows (the same letter signifies similar entities, that is, X-s are DNAs, whereas Y-s are proteins):

Entity X_1 causes the entity Y_1.
Entity Y_1 causes the entity X_2.
Entity X_2 causes the entity Y_2.
Entity Y_2 causes the entity X_3.
Etc.

Godfrey-Smith points out that X_n (proteins) and Y_n (DNA) are not similar, therefore the X_n (proteins) cannot be the replicate of the Y_n (DNA) and the Y_n (DNA) cannot be the replicate of X_n (proteins). Also, even though X_{n-1} and X_n are similar, there is no *direct* causal link between the two generations of X_n (DNA) that would be responsible for this similarity. However, he favours an interpretation of the causal link necessary for replication that involves *indirect* causation. But even if we conceive causation as indirect, Godfrey-Smith argues, we would double-count the replicators, since we would have to regard both X_n (DNA) and Y_n (protein) as replicators (Godfrey-Smith 2000: 418). His conclusion is that neither the DNA nor the proteins can be regarded as replicators.[2] Therefore this imagined selective process does not involve replication.

Two possible lines of counter-argument could be given. The first would be to argue that X_n and Y_n (DNA and protein) are indeed similar in some relevant respects. X_n and Y_n (DNA and protein) are similar in the sense that they carry the same information. The notion of information, however, is one of the most obscure notions in evolutionary biology, and this weakens the counter-argument. I would like to propose another one, which does not rely on the concept of information.

My proposition is that even if neither X_n nor Y_n could be regarded as replicators in this process, the *sequence* of (X_n and Y_n) together fulfils the criteria of being a replicator.[3] The sequence of (X_1 and Y_1) is similar to the sequence of (X_2 and Y_2). Similarly, the sequence of (X_1 and Y_1) is causally involved in the production of the sequence of (X_2 and Y_2) in a way responsible for the similarity between the two sequences. After all, there is nothing in the definition or replicators that would exclude entities that consist of materially (and temporally) distinct parts from being replicators.

The other argument given by Godfrey-Smith in favour of the claim that replication is not necessary for selection is logically independent from the one discussed above (though he tries to combine them). He writes:

> We [. . .] can imagine a complicated role for other causal factors in modifying the transmission of the variations. As the causal web gets more complicated, it becomes less and less appropriate to try to identify a

> replicator [. . .]. The more factors that are involved in creating a new Y that is similar to X, and the more places in the network at which dissimilarity could be introduced, the less true it is to say that "X was causally involved in the production of Y in a way responsible for the similarity of Y to X," as the definition requires (Godfrey-Smith 2000: 418).

This argument is somewhat surprising in the light of Godfrey-Smith's criticism of the view (expressed by Dawkins (1982: 99), for example) that replicators are "directing their own replication and the production of whole organisms" (Godfrey-Smith 2000: 407). He agrees with Sober and Wilson (1994) and Lewontin (1991) that replicators do not "replicate themselves"; they are only one of the many causal factors involved in the production of the next generation of replicators and in the production of the interactor (Godfrey-Smith 2000: 411–412). Moreover, in his definition of replicate he uses the phrase "X was causally *involved* in the production of Y"[4] indicating that the causal effect of X on Y does not have to be the only causal effect responsible for the similarity.

Let's analyse the logical possibilities in the scenario outlined in Godfrey-Smith's counter-argument. Three cases can be differentiated.

1. There is one and only one entity X that is similar to Y and also causally responsible for this similarity. This is the standard case of replication: according to the definition, Y is a replicate of X, therefore the process is replication.
2. At least two entities are similar to Y and are causally responsible for this similarity, let's say, X, X' and X". In this case, Y is the replicate of all three of them, since all of them fulfil the definition: each of them is similar to Y and causally involved in the production of Y in a way responsible for this similarity. Hence, this process is a replication process.
3. There are no entities that are both similar to Y and causally responsible for this similarity. Here, three sub-cases must be differentiated:

3.a. There are no entities that are similar to Y. It is easy to see that in this case the process is not selection at all, since there is no similarity between the generations. Therefore, one crucial element of selection is missing, namely heredity.

3.b. Some entities are indeed similar to Y, but they are not causally responsible for this similarity. Furthermore, no other entities are causally responsible for this similarity either. In this case, this similarity is purely accidental, therefore the process cannot be selection, since heredity is missing again.

3.c. Some entities are indeed similar to Y, but they are not causally responsible for this similarity. There are entities that are responsible for this

> similarity, but they are themselves not similar to Y. The set of entities that are similar to Y and the set of entities that are causally responsible for this similarity are disjunct. Let's say, Z is the entity that is causally responsible for the similarity of Y to X. Z (or an entity with the same causal power: Z′ or Z″ etc.) must be present in every generation, in order to assure the similarity between generations. The question is what is responsible for the presence of Zs in every generation.[5]
>
> If it is Z itself, then we have found an entity, Z, that is (1) similar (in causal power) to an entity in the next generation, Z′, and (2) causally involved in the production of it in a way responsible for this similarity. In other word, Z is a replicator.
>
> If, on the other hand, it is another entity (Q, let's say) that assures the similarity of Zs across generations, then we face the very same question again, of what is responsible for the presence of Qs in every generation. This clearly leads to infinite regress.

It has been shown that the process outlined above is either replication (cases 1, 2, 3.c.) or is not selection (cases 3.a, 3.b.). Thus, selection without replication is not possible; replication is necessary for selection. Note that the only aspect of selection I used in the above argument was the non-accidental similarity between generations.

Godfrey-Smith is right in pointing out that there is no rigid borderline between replication and non-replication, and I think it is an important point to emphasise. However, it may well be the case that replication is necessary for selection, but there is no rigid borderline between the replicative selective processes and the non-replicative non-selective processes.

Varieties of replicators

We have so far seen that replication (as it was defined by Godfrey-Smith) is necessary for selection. However, this definition sets very weak criteria for replication: that of similarity and causal link responsible for this similarity. A possible worry is that this definition is too broad; it includes cases biologists would not want to include.

Godfrey-Smith points out that photocopying, for example, is a replication process according to the definition he has given. Also, I would like to argue that trickles of raindrops on a window are replicators as well, since they are similar and one trickle is causally involved in the fact that the next raindrop will follow the same trickle.

Furthermore, one could argue that any sustaining object is a replicator. Object P at T_2 is the replicate of the same object P at some earlier T_1 (where T_1 and T_2 are standing for different moments), since object P in T_2 is definitely similar to object P in T_1 and object P in T_1 is in a way causally involved in the production of object P in T_2 in a way responsible for this similarity.[6]

These cases may qualify as cases of replication processes, but they are not very interesting ones. I'll call a process trivial replication if no new, spatially distinct entity is formed during the replication process. If new, spatially distinct entities are formed, then the replication is non-trivial. This is the first distinction within the category of replication processes. The second one is somewhat more interesting, involving one of the keywords in evolutionary biology: variation.

The question is whether replication produces variation or not. In the gene/organism case it does, but variation is not a necessary feature of replication. Not every non-trivial replication produces variation. If the fidelity of the replication is absolute, then all the replicates of the same replicator will be the similar. Hence, replication leading to variation – which I call 'replication with variation' for simplicity – is a sub-category of non-trivial replication.

These two distinctions made above will be important in the discussion of selection processes. The different cases of replication are summarised bellow:

a. Trivial Replication.
b. Non-trivial Replication without Variation.
c. Non-trivial Replication with Variation.

Selection processes

We have seen that replication as defined above is necessary for selection. In this section I examine the relation between the different kinds of replication processes and selection. It has been shown that a variety of replication processes has to be taken into consideration. The question is whether a variety of selection processes have to be differentiated as well. In other words, do the different kinds of replication processes lead to different kinds of selection processes?

My starting point is Hull's notion of selection: "repeated cycles of replication and environmental interaction so structured that environmental interaction causes replication to be differential".[7] I will examine how this notion of selection is related to the different types of replication processes.

Selection in the above sense can clearly occur in the case of non-trivial replication. Two sub-cases of such selection processes have to be differentiated though. If the replication produces variation, then the most successful one(s) of these variants will serve as the original replicator(s) that produces variation in the next generation. Therefore, the replicator will be slightly different in each generation: the changes accumulate. I will call this sub-category of selection '*cumulative*'.

It has to be noted that this does not imply that replication with variation automatically leads to cumulative selection. My claim is that non-trivial replication with variation is *necessary* for cumulative selection; I by no means claim that non-trivial replication with variation is *sufficient* for cumulative selection. It certainly is not: a number of other conditions has to be fulfilled.[8] Replication with variation is the necessary but not sufficient condition for cumulative selection.

In the 'replication without variation' case the generations contain completely similar replicators (since there is no variation); therefore the most successful replicator may spread and make all the others extinct, but by doing this it will not change. An example could be the Bedau-crystal that is growing faster than the other crystals in the same pool (Cf. Bedau 1991; Walsh 2000: 142–143). It is easy to see that the growth of the crystals satisfies the conditions of replication. After a certain time the fastest growing crystal will be the only one in the pool, but its structure will not change in the process. The replication of the crystal belongs to the 'non-trivial replication without variation' sub-category, and its selection is a *non-cumulative* one.

We have so far seen that replication with and without variation leads to different selection processes. Now I turn to the question of whether these different selection processes have different explanatory power or not. My claim is that cumulative selection can be used to explain adaptation, whereas non-cumulative selection lacks such explanatory power.

The logical relation between selection and adaptation has been the focus of severe debates recently. It has been argued that natural selection cannot serve as explanation of adaptation, since (1) it cannot explain the creativeness of adaptation and (2) the *explanandum* and the *explanans* are phenomena at different levels: selection is a population-level phenomenon, whereas adaptation occurs on the individual level (Sober 1984, 1995, Walsh 2000). Selection can explain the frequencies of traits in populations, but it cannot explain why individual organisms have certain traits (Sober 1995: 384).

Karen Neander has argued against these claims at length. She points out that cumulative selection could indeed explain adaptation. She agrees that non-cumulative selection cannot explain adaptation, but she argues that cumulative one can. Her conclusion is consistent with Dawkins' famous claim: 'Cumulative selection is [. . .], I believe, the force underlying all adaptive complexity.' (Dawkins 1983: 21)

Instead of repeating Neander's argument I would like to focus on another question that she does not address. Even if her argument is correct, one could still argue that the distinction between cumulative and non-cumulative selection is vacuous, since cumulative selection is precisely the kind of selection that leads to adaptation; thus, the account is circular. This point is similar to the one Walsh makes in his recent paper:

> I am willing to accept that adaptive complexity comes about when selection is ‘cumulative’ [...], but I submit that this gets us no closer to uncovering the causes of adaptation. We still have no inkling of what makes selection operating over populations of *organisms* ‘cumulative’ in a manner sufficient to produce adaptations, whereas selection operating over populations of crystals or convective cells is not (Walsh 2000: 143–144, his italics).

The aim of the first half of my paper has been to give independent criteria for the difference between cumulative and non-cumulative selection. I argued that the difference between the two types of selection stems from the differences between replication. Hence, the difference between cumulative and non-cumulative selection has been established without any reference to whether they lead to adaptation or not, solely with the help of the nature of replication processes involved in them. Therefore, the account has turned out not to be circular, after all.

The difference between these two types of selection processes is crucial, since if a type of selection process (cumulative selection) leads to adaptation, then it can be used to explain the teleological nature of the world (or to explain why it appears to be so). If, however, it does not, it cannot be used in such explanations. Hence, these two types of selection processes have very different explanatory power.

We have only one replication process left, the relatively uninteresting case of trivial replication. Perhaps we can talk about trivial selection as well, where the environmental interaction causes the trivial replication to be differential (that is some objects remain the same, some do not), but I do not think this notion would be philosophically, let alone biologically interesting. This type of selection probably lacks any serious explanatory power.

Conclusion

The relation between the different replication and selection processes is summarised below:

Replication	Selection	Example
Trivial replication	Trivial selection	Any persisting object
Non-trivial replication without variation	Non-cumulative selection	Bedau-crystals Benard-cells
Non-trivial replication with variation	Cumulative selection	Natural selection, immune system, operant conditioning?

It is important to point out that there is not necessarily a strict boundary between the types of selection processes outlined above. If the difference between different selection processes is indeed a matter of degree, then a more pluralistic typology could provide the conceptual framework for examining these types of selection processes as well as the gradual transition between them.

It is worth summarising the argument presented in the paper. I have outlined a typology of selection processes, and showed that different subcategories have different explanatory power. The basis of this typology of selection processes was argued to be the difference of replication processes involved in them. In order to show this, I have argued that: 1. Replication is necessary for selection and 2. Different types of replication lead to different types of selection. Finally, I have argued that this typology is philosophically significant, since it contrasts cases of selection (on the basis of the replication processes involved in them) in which selection leads to adaptation, and can therefore be used in explanations of the (real or seeming) teleology of Nature and cases in which selection lacks such explanatory power.

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Notes

[1] The most important of these disciplines are probably the teleological approach in the philosophy of mind (Millikan 1984, 1992, 2000; Papineau 1987, 1993; Dennett 1995), evolutionary psychology (Buss 1994, 1995; Pinker 1997; Plotkin 1997; Barkow-Cosmides-Tooby 1991), evolutionary epistemology (Popper 1972; Campbell 1974), neural Darwinism (Edelman 1987; Adams 1998; Changeux 1985), and memetics (Dennett 1995; Dawkins 1976).

[2] It is not clear in his argument why it would be a problem to double-count the replicators, but assume that it is and question Godfrey-Smith's conclusion instead of his premise.

[3] Godfrey-Smith hints at this solution, but he regards it as "pushing the boundaries of the concept [of replicator], but not too far" (p. 418).

[4] My italics.

[5] There is a possibility that Z is a constant environmental factor: it is automatically present in each generation. An example could be the process of mass-production, whereby similar entities are produced, but the similarity is not assured by any of these entities but by the mass-producing machines. In this case, however, we clearly cannot talk about selection.

[6] I leave aside the question of whether objects have temporal parts or not and assume that they have. If they do not, it is even better: the case of the persisting object does not represent any challenge to the definition of replication.

[7] Hull et al. 2001: 53. Cf. Hull (1981: 40–41) where he claims: “A process is a selection process because of the interplay between replication and interaction.” This view is consistent with Vrba’s somewhat different characterisation of selection: “Selection is the interaction between heritable, emergent character variation and the environment [. . .]” (Vrba 1984: 319).

[8] One of these conditions of cumulative selection is that environmental interaction should influence the next replication. This is argued to be the difference between single step selection and cumulative selection (Dawkins 1986: 45; Neander 1995a: 72–75, 1995b: 583–584; Nanay 2001).

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