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Choices by organisms: on the role of freedom in behaviour and evolution

KALEVI KULL*

Department of Semiotics, University of Tartu, Jakobi St. 2, 51005 Tartu, Estonia

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Neo-Darwinian biology has demonstrated that it is possible to construct a theory of life that excludes the role of organisms' free choice. In a richer theory, the latter as a possibility needs to be taken into account. For that purpose, it is necessary to introduce the biological concept of choice, analyse its structure and roles, and consider some implications for biological theory. It is argued here that the conditions for free choice emerge together with umwelt—the space of synchronous options. Basically, choice does not require purpose. This leads to the conclusion that freedom is an attribute of life.

ADDITIONAL KEYWORDS: biosemiotics – free choice – habit – knowledge – possibilities – recognition – theory of evolution – umwelt.

INTRODUCTION

> External stimuli [...] approach the animal in the form of questions (Jakob von Uexküll, 1992 [1934]: 323).
>
> Life is not a sequence of cause and effect, but *choice* (Viktor von Weizsäcker, 1940: 126).

Expressions like 'habitat choice', 'choice of food', 'choice of partner' and 'choice of direction of movement' are rather common in biological discourse. The process of choice itself, which presupposes some *freedom* of doing as such in order to be identified as *choice* and not as a random or a deterministic process, is however seldom explicitly defined and analysed in biological theory.

I suspect that this situation is due to the use of a loosely defined anthropomorphic concept of choice, the relevance of which for other species is unclear. Introducing a non-anthropomorphic understanding of free choice, its widespread existence in the living world can be observed. This is the basic hypothesis of this study. If true, the implications for biological theory will be discernible.

This article is organized as follows. The first section briefly describes the situation in the use of the concept of choice in biological theories. The second section introduces the key definitions, and describes the conditions and structure of organismic choice. The third section presents some implications from the understanding of choice for biological theory.

ON THE CONCEPT OF CHOICE IN BIOLOGY

Choice is a strange concept because it fundamentally includes a feature, due to which it has been largely avoided in the natural science: indeterminacy. Choice is the phenomenon that is situated precisely at the border between physics and semiotics, between the natural sciences and the sciences of mind, between the study of causes and study of freedom which means it will also allow us to connect these two areas of study, that now largely belong to separate academic cultures.

In biology, the problem of choice is fundamentally related to the theory of evolution, and is at the heart of a contemporary remarkable paradigm change in the understanding of evolution. Namely, the contrast between the neo-Darwinian and the post-Darwinian paradigms includes some oppositions which concern the role of agentive activity: (1) either organisms are replication-devices, or they are interpretive agents; (2) either environment selects, or organisms choose; (3) either the main factor of evolution is a passive natural selection, or an active organic fitting.

These are not necessarily alternatives. Every experienced biologist certainly understands that

*E-mail: kalevi.kull@ut.ee

evolution is based on both. But this does not resolve the problem, because then the question will be 'in what relationship?' In order to answer this, the precise definitions of terms (including *choice*) will be required.

A focus on the concept of choice in an evolutionary context appeared at the end of the 19th century. George Romanes, in the first chapter of his *Mental evolution in animals* ('The criterion of mind') writes: 'What activities of an organism are to be taken as indicative of consciousness? The answer that comes most readily is, — All activities that are indicative of Choice; wherever we see a living organism apparently exerting intentional choice, we may infer that it is conscious choice, and, therefore, that the organism has a mind' (Romanes, 1883: 17). And he concludes: 'the distinctive element of mind is consciousness, the test of consciousness is the presence of choice, and the evidence of choice is the antecedent uncertainty of adjustive action between two or more alternatives' [(Romanes, 1883: 18); see also comments on Romanes in Maher (2021) and Ginsburg & Jablonka (2019: 195)].

Charles Darwin (1871), when famously introducing the term 'sexual *selection*', not only speaks also about 'sexual *choice*' (indeed referring to choice in a direct sense), but sees choice as the main factor of sexual selection: 'Hence in these classes, such as the *Protozoa*, *Cœlenterata*, *Echinodermata*, *Scolecida*, true secondary sexual characters do not occur; and this fact agrees with the belief that such characters in the higher classes have been acquired through sexual selection, which depends on the will, desires, and *choice* of either sex' (Darwin, 1871: 321, emphasis added).

The roots of the current post-Darwinian (as different from the neo-Darwinian) paradigm go back at least to the concept of organic selection, as defined by James Mark Baldwin (1896: 444): 'Whatever the method of doing this may be, we may simply, at this point, claim the law of use and disuse, as applicable in ontogenetic development, and apply the phrase "Organic Selection", to the organism's behavior in acquiring new modes or modifications of adaptive function with its influence of structure'. Baldwin does not use here the word 'choice', but his meaning of the 'organic selection' that is due to agent activity is close enough to it. As Piaget (1971: 299) commented: 'When Baldwin talked of "organic selection", it was still only a word and a rather ambiguous word at that, for although external selection may proceed by eliminations and survival of the fittest, any organic or internal selection is much more like a "choice" of a more or less active kind, which means that i[t] is, properly speaking, a regulation.'

Conwy Lloyd Morgan had similar ideas, and provided a criterion for choice as 'an alteration or modification of response in the light of individual experience' (Morgan, 1896: 265). However, his own other principle, formulated as Morgan's Canon or principle of parsimony, was later used to reduce the enthusiasm to apply psychological concepts in biology [see also a comment on Morgan in Ginsburg & Jablonka (2019: 197)]. Behaviourism refused to use psychological concepts, and the ethological tradition could mostly do without a direct reference to the subjective experience of animals. Accordingly, the study of human choice behaviour has developed along very different lines, compared to the study of choice in animals (see Staddon, 2016: 270). In the studies of animal choice, what has mainly been meant by choice is preference. This is common in the studies of animal learning, which focus on the changes of preference under various conditions (e.g. reinforcement) and in Edward Thorndike's law of effect.

In her critique of Darwinism, Lynn Margulis emphasized that: 'organisms choose' (Margulis & Sagan, 1995: 222). Sagan (2021: 6) adds:

> The prototactical associations and living choices made by organisms, always members of communities in identifiable ecosystems, may lead directly to evolutionary consequences: origins of new species. [...] But if we accept Darwin's sexual selection, and most biologists have, why then do we not also consider other kinds of organism-level choice-based selection? Prototactical living beings actively decide with which other life forms to associate. Which ought they try to eat? With whom ought they band for protection? Who might they inhabit for shelter? These "artificial selection" decisions of the living have evolutionary consequences that are not to be confused with the "mechanical" – such as the inanimate interactions in random or deterministic behaviours of billiard balls, moving electrons, other elementary particles or solid bodies.

The concept of prototaxis was introduced by Ivan Wallin, to denote an association more general than symbiosis, involving any innate tendency of any particular species, organism or cell to respond in a specific way (associative or dissociative) to any other sort of species, organism or cell (Wallin, 1923). This concurs with Janzen's (1985) observation that species coexistence in ecosystems is not due to slow, long-term co-evolution, but due to their ecological fitting, which is a quick, real-time process. More generally, ecological fitting may include any relationship an organism establishes as a result of search and choice. Its general role in ecosystems has been rather well demonstrated (see, e.g. Araujo *et al.*, 2015).

Likewise, for instance, Williams (1994: 84) writes, with a reference to Herrnstein (1970): 'all behavior is choice, in the sense that there are always alternatives other than the response measured by the experimenter. Thus, the animal is always "deciding"

which response to perform.' In ethology, 'free-choice conditions' is used as one of the experimental settings (Graham *et al.*, 2018).

Thus, the idea that organisms make choices is not new. Young (1987: 148) mentions: 'The realization that choice is a property of all living things gives us great help in understanding the world and our place in it'. However, it is important to notice that animal choice is sometimes understood as being strictly computational (e.g. Real, 1991), which would exclude free choice.

More recently, the natural history of freedom has received attention in biology (Ho, 1996; Heilinger, 2007; Hoffmeyer, 2010). Yudanin (2020) provides a rich review of the studies of animal choice. One of the conditions for choice he points out is self-determination (Yudanin, 2020: 64).

Among the attempts to describe the mechanism of choice, an account by Noble & Noble (2018) builds it to the harnessing of stochasticity. Their description divides the process of choice into five stages (Noble & Noble, 2018: 3):

1. A challenge has occurred—as a puzzle analogous to the form of a template for which a match is needed.
2. The organism searches amongst existing stored possible fits to the problem template.
3. The organism activates stochastic processes within itself to generate further possible new solutions.
4. The organism returns to direct control at this stage, which is to compare what is thrown up by the stochastic process with the problem template to determine what fits.
5. Implementation of the discovered action to solve the problem.

Delafield-Butt (2021: 80) points out the anticipatory aspect of choice: 'Anticipatory motor control with its sense of possible futures affords the organism *choice*. It is the pivot on which sits immediate experience and agency. In mammals, this pivot rests on a tripartite of information integrated from the *exteroceptive* senses of the outside world (i.e. sight, sound, touch, taste), *interoceptive* senses of visceral and vital physiological need (e.g. hunger, thirst, thermoregulation), altogether with *proprioceptive* senses of the body-in-motion. […] Agent action of this kind is common to all vertebrates, and the basic system of "sense, evaluate, choose" common to all organisms.'

Since consumer choices are an important focus in economic theories, some work which links the biological and economic models of choice was carried out (Akçay, 2015). If related to humans, choice is seen as dependent on free will. Literature on free will is vast, but free will is seldom seen as a biological problem to be studied and solved by biologists—which it certainly is, particularly as the study of capacity to choose (cf. Brembs, 2011). In the contemporary philosophical literature, for example, it is most often discussed in the context of neurobiology (e.g. Ansermet & Magistretti, 2007; Lee *et al.*, 2012).

My own attention has been on the role of choice in the processes of semiosis and interpretation, from a biosemiotic perspective. Our analysis of meaning-making or semiosis has shown that choice is its necessary component (Kull, 2015, 2018a, b).

What can be concluded from this brief review is that the concept of choice has a place in biological theory; however, it is not well explicated and accordingly the content of this concept varies. In the next section I attempt to clarify the meaning of the 'choice process'.

THE WORKING OF CHOICE

Here the aim is to formulate the necessary and sufficient conditions for a process to be qualified as choice—by which is meant an indeterminate non-random action (Kull, in press). The latter is emphasized because the term 'choice' is used by some authors for certain algorithms of determinate actions. A little scheme might be of some help in which a random process is compared with choice (Figs 1, 2).

A random process can be modelled as a landscape with branching channels, upon which a ball is rolling downwards (similarly to the classical picture of an epigenetic landscape as a representation of an aspect in developmental differentiation, provided by Waddington, Fig. 1). The pathway which the ball takes at any given branching point is random in this situation, if no additional conditions are applied. Although, for the ball, there may be a short-term unstable moment at the branching point of the channel, the ball does not 'see' both available channels. The two pathways are not 'options' for the ball, these are options only for an external observer. The ball simply follows one of these pathways by chance due to micro-determination.

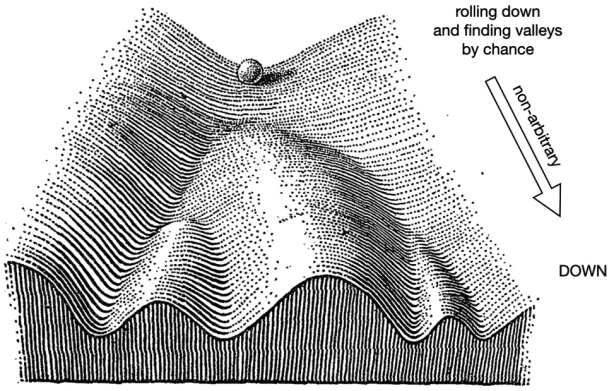

Figure 1. A simple model, in which the selection of pathway is random (modified from Waddington, 1957: 29).

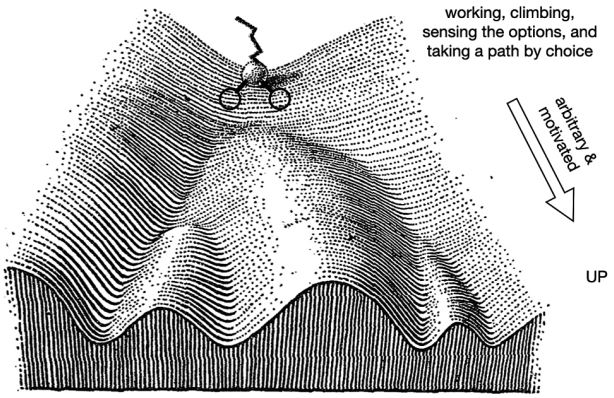

Figure 2. Agent's choice between options as an elementary interpretation.

The branches of the pathways that were not taken by the rolling ball do not exist for the ball, nor have they ever. Which means its turns are not choices, no matter how many 'options' may appear, to the observer, to be present in the landscape.

Thus, if rolling downwards, then at the branching points, at bifurcations, there is not a choice—it is rather a case of pure chance. But change your perspective and assume that the closer end here is the higher one (Fig. 2). If climbing upwards, i.e. when doing work, as any agent does, the situation could be different than in the earlier picture. Still, if the climber has no representation of possibilities, then the situation is not much different from the previous one—the path taken will be random. But if the climber is not 'blind', which means if it has receptors which can provide a *sign in advance* about the two or more possibilities, then the choice can be made. All that is needed is that both paths are represented simultaneously. Obviously, at least two receptors are required for creating such a representation.

In the case of choice, in place of the passively rolling ball, we now have an active agent that can move itself, and that can somehow register or 'sense' the different pathways that are now available before it. The existence of different pathways upon which to go—i.e. the possibilities, the options—being 'sensed' by the agent, now have to be actively *chosen*. Such choice, in order to *be* a choice (which means not determined by a randomizer or any other determinator), means, by definition, that there is no force or pre-given algorithm or rule that has to be necessarily followed. Such *non-algorithmicity* is necessary in order for the event to be a *choice*, and indeed makes it a *free choice*. This meaning of 'free' here, however, requires some further discussion.

Freedom emerges from an additional feature that is implied—from simultaneity of represented possibilities, which means a brief moment of present, the finite Now. This is a tiny period in which what is presented can be synchronous, can be seen or felt together, without determined sequence. Simultaneity of options is an elementary and fundamental condition of freedom in the context of choice. Collecting information about options can be sequential, while for the options to work as possibilities free to choose from, these should be represented together. Choice itself creates the conditions for choice.

From this description, one can notice that in such cases of free choice, there still can be some additional *limitations*, *restrictions*, *preferences*, *motivations* and *intentions* to choose, for instance, the 'left path' instead of 'right path', without such motivation being the strict determinator of the resulting selection. Such preferences or motivations work as memory traces from earlier behaviour, making some paths easier to use. This means that preference or motivation does not remove the *condition* of the choice being *free*, so long as the preference or motivation are not algorithms that must by necessity be followed.

Accordingly motivation or preference is not the *opposite* of arbitrarity or free choice, but one of its important *features*. An arbitrary choice, or free choice, may include more motivation or less motivation in some direction, but so long as the motivation is not a necessity, and so long as there is still the capacity to behave against the motivation, against an acquired preference, the choice is free, and it is still a choice.

Thus, we arrive at a very important and fundamental point for biology—the non-anthropomorphic description of the structure of *free choice* (which is also the key to the structure of *semiosis* or meaning-making in the pre-linguistic realm).

The necessary and sufficient conditions for free choice include: *work*, *simultaneous availability* (i.e. 'sensing' the existence) of alternative options (possibilities) and *indeterminacy*, i.e. the absence of a controlling force or algorithm which would make one of the options *necessary* to pick [see also a similar approach in Laskey (2018)].

First: the condition of the need for work. In cases where work is being applied, the situation of bifurcating pathways is different than it is when small stochastic fluctuations alone determine the continuation of the process (i.e. the path taken) at the bifurcation point. In the cases of 'choice', the energy that is directed towards pushing the behaviour is larger than the energy of fluctuations, and is therefore decisive for the selection of the pathway. The randomness of fluctuations, therefore, is not what plays the principal role in path-selection when an agent's work is applied to the process.

Second: optionality in the sense of the simultaneous availability of possibilities, which can be described as simultaneously representing the existence of more

than one pathway, and which requires the co-existence of more than one elementary receptor in the same agent. Assuming that one elementary receptor can detect the existence of something only once at a time, at least two receptors are required in order to detect two simultaneously existing elements at the same time, i.e. to create non-sequentionality necessary for indeterminacy. If the two are detectable only one by one, then they are not true options that must now be chosen from.

A receptor can be defined functionally as an organ or organelle that is connected to an actor via habit. If an agent has multiple receptors, linking to multiple habits, then the situation of *incompatibility* may occur. The state of incompatibility is the state of an agent in which two (or more) habitual connections (i.e. habits) are simultaneously excited yet cannot be simultaneously executed.

What happens in the coexistence of incompatible habits is that a new dimension becomes created. This new dimension is *the perceptual simultaneity of more than one*—i.e. the creation of a map, the model of space, the subjective space (if space is defined as something that consists of more than one point). The realization of, and access to, this 'space' or 'representation', is the prerequisite of choice.

This new dimension is relational, it is logical, not physical. The incompatibility that characterizes options cannot be based on physical necessity, which is why it requires habits, since habits are the carriers of acquired relations (which by definition are not based on physical necessity).

Choice requires simultaneity of options. If options are not represented simultaneously, they are not options. Simultaneity is possible—as there exists the specious present, the subjective now. The existence of subjective present in animals has been confirmed [see references in Kull (2018b)]. Such simultaneity is illusionary in the same manner as logical relations are illusionary, or as subjectivity is illusionary. In other words, choice creates subjective reality.

At this point a slight further generalization is possible. 'Choice' can be defined as what happens in the situation where there are possibilities present (this being equivalent to the condition of semiosis, or interpretation). Possibility, by definition, cannot be single. The field of possibilities provides the condition of choices; moreover, it makes the choices inevitable. And there are two main types of choices—strongly motivated [for instance recognitions, readings or measurements in the broad sense of Pattee (2007)] and weakly motivated (commonly called 'free') choices. A choice is called strongly motivated if bias or preference towards one of the possibilities is strong. A choice is called weakly motivated if bias towards any of the possibilities is not strong. The boundary between these two types is not strict, and both provide knowledge (*sensu lato*) to organisms via their consequences.

IMPLICATIONS

Choice, according to the definition exemplified in the previous section, requires the simultaneous representation of something more than one, something multiple (characterized as possibilities—habits that can be executed). This implies that the existence of choice is coextensive with subjective time and space—i.e. umwelt, as defined by von Uexküll (1928). Consequently, all organisms who can make a choice have an umwelt. And since umwelt is the space of possibilities, precisely those who have umwelt can choose.

The existence of umwelt and choice in particular organisms should be established by detailed research. A liminal example often mentioned in this respect is plant heliotropism. If heliotropism is not an acquired feature, then it cannot be a plant's choice. If heliotropic movement has been acquired, but works completely deterministically, then it also cannot be a choice. However, the hypothesis that the choice conditions are met during the period of acquisition of such a reaction to sunlight, is quite plausible.

The situation of choice requires the simultaneity (synchronicity) of options. An organism can only have the freedom to make a decision if several possibilities are presented and available at the same time. From the physicalist point of view, this may seem impossible—time is continuous and there is at least a microscopic difference between events, thus everything is sequential. However, from an organism's point of view, perceived time has a certain finite interval which is interpreted as present. From the physiological point of view, the specious present (Varela, 1999) appears due to the finite relaxation times of coupled functional cycles. In this case, before a functional cycle can culminate in action, there is another functional cycle that would lead to an alternative action, and if the actor is the same, then there is an incompatibility between the operations, hence there occurs a true situation of indeterminate choice. Moreover, the moment of choice is related to an organism's meaning making. This can be seen as the fundamental point that connects phenomenology, semiotics and physiology, where these three converge.

A structure that can support the conditions for choice is paired receptor organs. In particular, this is the case in organisms with bilateral symmetry—as in the clade Bilateria among Eumetazoa—which, of course, does not exclude the existence of necessary integration between receptors in the organisms of other forms and taxa, in principle even including unicellular organisms with membrane receptors.

According to our conceptualization here, possibilities are habits. An appropriate definition of habit can be one from Gardner (2015: 277): 'habit is a process by which a stimulus generates an impulse to act as a result of a learned stimulus-response association' while reading it as compatible with Peirce's concept of habit (West & Anderson, 2016). As this definition says, habit is what mediates ['generates an impulse towards action' (Gardner, 2015: 280)]. What can be added here is that habit, in order to be a habit, should not be completely automatic or deterministic; a principal feature of habit is at least a minimal freedom of it not to be followed—only then can a habit be a possibility.

Habits—the possibilities with strong preferences—as acquired and as the results of learning, carry in themselves an anticipation about what may happen. This is because the main types of learning—imprinting, conditioning and imitating—that create (correspondingly) either iconic, indexical or emonic relations. Symbolic relations, as acquired by convention, are an exception, as they may not correspond to any earlier regularity [for terminology, see Kull (2020: 15)]. These relations, other than symbolic, acquire (we can also say 'they model') the relationships or regularities that exist around the organism. This is why Peirce can say that 'knowledge is habit' (Peirce, 1906: CP 4.531). Since possibilities are habits, and habits embed in themselves the local regularities, every choice includes an anticipation as based on these regularities.

Choice (as described) does not require purpose. Choice happens because organisms face alternatives and have the capacity to take one. Consequently, purpose itself is free. Why organisms choose is not because of some purpose, but because of umwelt, their *now*, which *is* the field of alternative possibilities, of options; that is what behaviour *is*—to do this or that. Accordingly, the formation of purpose is secondary in relation to choice.

In the context of biological debate between teleology and teleonomy, the understanding described above can be seen as a 'third way'. This is neither teleology nor teleonomy but semiotics. There is free choice but not necessarily any purpose. Purpose as such presupposes freedom, because the concept of purpose is defined as not applicable to deterministic or random processes. The directionality in behaviour can be a consequence of preferences to which choices contribute. The preferences in choice making are the features of habits, and there may be several alternative habits which fit the same situation. Thus, there is no ultimate purpose like survival or anything else that would determine the choices.

Work alone is insufficient for choice or for intentionality. For example, various engines (including chemical ones) do work without any aboutness or purpose. An additional necessary condition is perception of possibilities together with choice making, but even this is insufficient for purposefulness. Simple playful behaviour includes choices with no purpose as such.

Together with the subjective world (umwelt), the existence of choice implies the existence of meaning making, i.e. semiosis. This is because umwelt consists of the relations in which the organism is a part; umwelt is the organism's interpretative world. Interpretation, which is semiosis by definition, presupposes the potential of alternative interpretations—which is choice.

One of Karl Popper's writings was entitled as 'A world without natural selection but with problem solving' (Popper, 2014). The 'problem solving', if not just a metaphor for certain deterministic processes, assumes indeterminacy, motivation and choice, referring to some fundamental freedom in the behaviour of organisms. A problem, or a problem situation, in the general sense, is a situation in which the behaviour has to be indeterminate, and a choice making has to be possible. This occurs if coupled functional systems face mutual incompatibility. For instance, perceptions from two sense organs order the opposite actions of the same effector. Or, if a perception orders two effectors that lead to opposite actions. This is a situation in which behaviour is not fully determined by any rule, i.e. when an organism is a little bit confused. This kind of indeterminacy appears precisely together with umwelt.

Finally, only a process based on choice and learning, i.e. on semiosis or interpretation, provides an adaptiveness profoundly independent of natural selection. In a more detailed analysis, six principal types of transformations in living systems can be distinguished (Table 1).

Thus, there are three independent sources of innovation: mutation, environmental influence and choice. Mutation initiates genetic modification, environmental influence modifies physiological

Table 1. The principal types of transformations in living systems (see text)

	Mutational	Plastic	Interpretative, meaningful
Neutral	Random **drift**	Self-organizational **shift**	Weakly motivated **choice**
Adaptive	Natural **selection**	Homeostatic **adjustment**	Strongly motivated **choice**

processes, and choice modifies habits. One should notice that self-organization and self-assembly as the processes largely responsible for plasticity but also quite common in non-living systems, may not be teleonomically accommodative or functionally adaptive. There are also three independent test processes for congruence or functionality, i.e. processes that can turn the modification adaptive: natural selection, homeostatic feedback and problem solving via choice [regarding the last, cf. Gregory (1980) on perception as hypothesis]. These are very different processes, but all may result in adaptive behaviour. Since all these can to some extent be heritable, either genetically, epigenetically or ecologically, it should be concluded that there exists at least three independent processes of evolutionary adaptation.

Whether the indeterminacy based on incompatibility of behavioural habits, and its solution via choice, exists only in animals with a nervous system, or can be identified also in other organisms, including at least some types of cells, remains to be carefully studied. Where it exists, it provides a process for end-directed changes—given that choices are based on alternative habits. This is a process of internal teleology, as referred to by Woodger [who added that 'it would doubtless be desirable in biology to avoid the term "teleology" if a suitable substitute could be found' (Woodger, 1929: 453)], and can be identified with a kind of agency. Plasticity, excitable membranes and signal transduction (e.g. Baluška *et al.*, 2022; Gilroy & Trewavas, 2022) are necessary but not sufficient conditions of indeterminacy (as described above) for an agent's capacity to make choices.

CONCLUSION

The initial conditions for the behaviour of an organism are not causal relationships but the possibilities that it is free to choose. Therefore, biology has to start not from the study of causes, but from the study of freedom. This is a fundamental, however seldom invoked, assumption in theoretical biology which is necessary to make in order to arrange the conceptual system of biology correctly.

A concept well suited to describe the field of possibilities is the *momentary umwelt* as defined by Uexküll. The process of choice happens if possibilities as options are simultaneously provided, as they are in any umwelt or subjective space. Synchronicity in the sense of simultaneity of possibilities is the *sine qua non* of choice—and of meaning relations or semiosis as well. In the condition of umwelt—which is the space of possibilities, i.e. the space of some freedom—the organism has no choice but to choose. An organism's behaviour is organized by preferences—i.e. by the possibilities which are biased and habit based. Innovative adaptivity is greatest where there is freedom.

Freedom is not a quality of being alive, it is what defines being alive. Life is choice making, choice making is freedom. Freedom is an attribute of life. It is here that the main problem of biology for our era lies.

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DATA AVAILABILITY

This article is based on information available in the published literature.

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