Circadian clocks signal future states of affairs

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Abstract

On receiver-based teleosemantic theories of representation, the chemical states of the circadian clocks in animal, plant and cyanobacterial cells constitute signals of future states of affairs, often the rising and setting of the sun. This signalling is much more rigid than sophisticated representational systems like human language, but it is not simple on all dimensions. In most organisms the clock regulates many different circadian rhythms. The process of entrainment ensures that the mapping between chemical states of the clock and the daily light-dark cycle is adjusted to deal with seasonal changes. In regulating anticipatory behaviour, the states of the clock look forward both to the time the behaviour is supposed to happen and the later time when the anticipated circumstances are supposed to arise. The case of the circadian clock shows that purely indicative signals can arise in very basic biological systems and brings into sharp relief the trade-offs involved in characterizing representational systems. On receiver-based teleosemantic theories, future-directed signals are not restricted to complex multicellular organisms but are ubiquitous in the biological world.

Keywords Signalling · Teleosemantics · Representation · Circadian cycles · Millikan · Neander · Arabidopsis thaliana

Introduction

Signals of future states of affairs have not received much attention in the teleosemantic literature. The usual examples — the nectar-locating bee dances (Millikan 1984), the predator warning calls of the vervet monkeys (Cheney and Seyfarth 1985), the frog's fly catching reflex (Fodor 1990), the imaginary kimu (Pietroski 1992), the

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arrow worm (Price 2001), the rooting reflex in young infants (Abrams 2005) — all concern signals which are produced and acted on immediately. Circadian clocks have received some attention from various philosophical angles. Gallistel (1990) has discussed them as part of his general account of learning. Bechtel (2016) has considered how some clock activities fit a control-theoretic account of representation. Morgan (2018) claims that what he calls 'tracking theories' of content, including teleosemantic theories, are inclined to attribute representational capacities to non-psychological states like those of the circadian clock. Butlin (2018) considers a circadian rhythm to be a 'questionable' case of representation. I am not, however, aware that there has been any detailed consideration of how teleosemantic theories might interpret the activities of circadian clocks.

I argue that on a receiver-based teleosemantic view of signalling circadian clocks produce signals of *future* states of affairs which are used to synchronize an organism's behaviour with external conditions, though theories based on the sender's response functions (e.g. Neander 2017) probably do not. In some cases, the behaviour regulated by the clock prepares the organism to deal with states of affairs that have not yet arisen at the time the behaviour takes place. All of this is done at a genetic level, through patterns of gene expression. Simple signals of future states of affairs arise even in single celled organisms. In some cases, signals generated by the clock interact with learning mechanisms to allow more flexible adaptation of behaviour to environment. Signals of non-immediate events are often thought of as a mark of more sophisticated signalling systems, but the clock case shows us that signals of future states of affairs are not the preserve of more complex creatures, not even of multicellular creatures. The signalling capacities of the clock are rudimentary in some respects, but much more sophisticated in others. They require us to consider novel trade-offs when deciding what kind of systems should count as representational.

Biological background sets out the basic biological facts about circadian clocks. In The base case I argue that on receiver-based teleosemantic theories, the chemical states of the clock signal the future events with which they are supposed to correspond. More sophisticated cases explores cases where the clock participates in more flexible and sophisticated signalling. Broader implications discusses some of the ways the clock differs from other representational systems. In Conclusion I sum up.

Biological background

Many overt biological rhythms — flowering, mating, sleeping, producing digestive enzymes etc. — are not triggered by the organism registering a regular external stimulus like the rising or setting of the sun, but endogenously, by a molecular clock. The overt rhythms persist without external stimuli. For example, they persist for some time, though not indefinitely, if the organism is kept in constant darkness.

The best understood of these molecular clocks are circadian. They track the light-dark cycle and control daily biological rhythms. Similar processes, however, control monthly and annual rhythms (Boden and Kennaway 2006; de la Iglesia 2013). Circadian clocks are found in a very wide range of organisms, from cyanobacteria to plankton, funguses, plants, fish, birds and mammals.

Circadian clocks are set by the process of entrainment, which adapts the clock's cycle to some external condition, the synchronizer. This is usually light, but sometimes food (Sect. Clock regulation of anticipatory behaviour). Circadian cycles are not exactly 24 h long, perhaps because the difference makes entrainment easier (Pittendrigh 1960).

How the clock works

In all organisms, with the possible exception of cyanobacteria, the clock works through a negative gene feedback loop. Simplifying a little, a clock gene in a cell acts as a template for the synthesis of a protein product which excites the expression of a second gene. The protein product of the second gene inhibits expression of the first gene.[1] Decay of the second protein relieves this inhibition and synthesis of the first protein picks up again. The rates of synthesis and decay, and hence the concentration of the proteins in the cell, follow a regular rhythm with a period of around 24 h. The first protein stimulates the expression of clock-controlled genes, whose products do not feed back into the operation of the clock. The clock-controlled genes regulate overt rhythms: they control the activity of gene complexes that generate biological processes like sleep or digestion.

In Sect. The base case, I will concentrate on the case of mouse-ear cress (*Arabidopsis thaliana*). This is a small flowering plant native to Eurasia and Africa, often found in waste land or by roadsides. It is a widely used model organism and was the first plant to have its entire genome sequenced. As a result, we know a good deal about the feedback loops that drive its circadian clock. The positive element of the main feedback loop consists of the proteins LHY and CCA1 and the negative element consists of TOC1 (Fig. 1). As in most taxa, there are other related loops (Merrow and Maas 2009, Oakenfull and Davis 2017).

The same feedback principle applies in other organisms, although the genes and proteins may differ. In mammals, the circadian clock is largely localized in the suprachiasmatic nucleus, a portion of the hypothalamus. In other taxa, clock functions are more widely distributed throughout the body.

Evolution and adaptive importance

It appears that circadian clocks have evolved independently at least twice (Rosbash 2009). The main circadian proteins in animals seem unrelated to those in cyanobacteria and the rhythms in gene expression which drive the mechanism in animals and plants are less important in cyanobacteria. It is not clear whether the clocks in plants and animals evolved independently. The key genes and proteins in plants and animals are different but it is possible that a common ancestral structure diverged in the two lineages with each acquiring non-homologous components over time (Farré and Liu 2013).

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[1] There are many gene concepts and considerable discussion about which are useful and how they are related (Griffiths and Stotz 2006). I will be using 'gene' to mean a length of DNA which acts as a template for the synthesis of a protein or structural RNA.
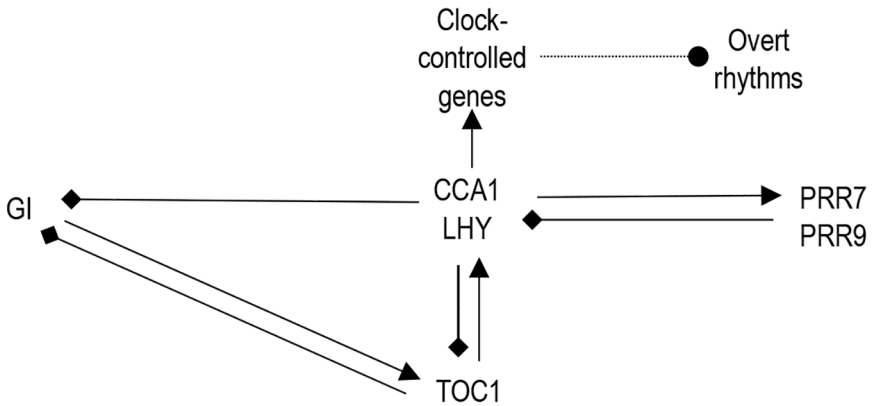
Fig. 1 The clock genes in mouse-ear cress Note: Arrowheads indicate a positive effect on protein synthesis; diamonds indicate a negative effect. The circle-headed arrow indicates that the links between the clock-controlled genes and the overt rhythms may involve the expression or inhibition of other genes.

While the selective history of circadian clocks is not known with certainty, we can make some reasonable guesses about the ways in which circadian clocks have contributed to the fitness of the containing organisms. Within individual organisms:

- An endogenous clock allows the organism to prepare for future conditions in an environment where there is no reliable cue preceding those conditions. For example, mice drink more before sunset to avoid dehydration at the end of the night (Gizowski et al. 2016). The circadian clock regulates the expression of fat-metabolizing genes in zebra fish so as to synchronize the production of digestive enzymes with the likely availability of food (Paredes et al. 2015).
- Probably, the clock plays a role in maintaining internal coordination of different biological processes. For example, in cyanobacteria photosynthesis and nitrogen fixation are important but incompatible processes; the circadian clock helps keep them temporally separate (Bhadra et al. 2017).

The clock also helps organisms deal with predators, prey and potential mates:

- Some food sources are available and some predators present a threat only at certain times of day and often a reliable environmental cue for these times is not available. For example, in the absence of environmental cues, honeybees forage more intensely for food sources late in the day (Moore et al. 1989; DeCoursey et al. 2000). Synchronizing biological processes with the likely availability of food seems to be important for the maintenance and replacement of the protective epithelial barrier in the gut and for gut immunology (Scott-Phillips 2008).
- If all the members of a species look for mates at the same time of day they will have more success than if they look for mates at different times (Vaze and Sharma 2013).

These considerations suggest that the clock is of adaptive importance but we also have direct experimental evidence in plants, bacteria, mammals and flies (Beaver et al. 2002; Tauber et al. 2004; Dodd et al. 2005). Individuals whose clocks are synchronized with the environment do better than those whose clocks are not.

The base case

In light of this background, it seems prima facie plausible that the chemical states of the clock signal the times of day with which they are supposed to correspond. But we must look more carefully.

Senders, signals and receivers

Teleosemantic theories are based on the idea that content arises from functional relations between a sender, a signal, a receiver and some represented state of affairs. What might they be in the cress case?

The expression of clock-controlled genes in the adaxial cells of a leaf stalk, the ones on the upper side of the stalk, causes those cells to elongate and thus open the leaf. The expressed clock genes are a natural candidate for sender status and the expressed clock-controlled genes a natural candidate for receiver status. Between the two we have the chemical states of the cell, the concentrations of clock gene products in the cytosol. These states are a natural candidate for the role of signal. Both sets of genes are well-defined in physical terms, naturally arising and non-gerrymandered. The chemical state of the cell is more complex but the concentrations of clock gene products in a cell at a time still constitute a well-defined, measurable physical state in the cell at that time — the unit in the International System of Units for each product is moles per cubic metre (mol/m^3).

Senders, signals and receivers may also arise at the leaf or plant level. The clock genes and clock-controlled genes in the adaxial cells of a leaf or a plant at a time are well-defined physical collections with a common causal history based on the meiotic event that originally gave rise to the plant. The fact that they are collections of smaller items need not worry us. Liver cells have functions and livers have functions. Individual army ants have functions and castes of army ants have functions.

The collection of concentrations of clock gene products in the adaxial cells of a leaf (or a plant) at a time is a large and messy collection but so is a collection of liver cells or a caste of army ants. Different cells have slightly different concentrations of clock gene products at any given time — just as some liver cells and some ants will not perform their functions perfectly — but this does not imply that there is no signal being sent.

A natural alternative suggestion is that one chemical state of a cell is a sender and its successor state a receiver. That is, it might be the function of one chemical state to produce the next chemical state. It is certainly true that many representational systems involve chains of senders, signals and receivers, where the function of one receiver is to do some processing send a signal to the next receiver in the chain,
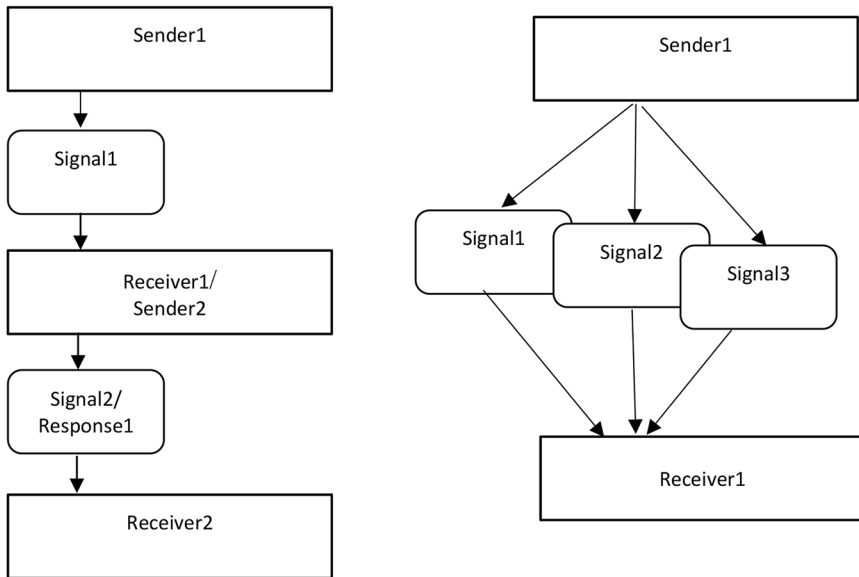
Fig. 2 Chains of signals and multiple signals

depending on the outcome of that processing. Visual processing is an example (Shea 2018).

The difference is that in the clock one state neither produces the state that is supposed to arise immediately after it nor prompts some other receiver to do so. The clock genes, together with general purpose genetic machinery, produce each successive state. The distinction is illustrated in Fig. 2.

So the clock genes, the chemical states of the cell and the clock-controlled genes are plausible candidates for the roles of sender, signal and receiver respectively. In what follows, I will mostly discuss plant level collections of genes and chemical states, since that is the level with the closest causal connection to the opening of the leaves, but the reasoning extends straightforwardly to the cell and leaf levels. We must now consider whether these candidates have the right functional relations with one another and the external world to count as signals.

Functions

Teleosemantic theories are based on the notion of function. What X is 'supposed to do' is what it is its function to do. In the non-human biological domain most functions arise from natural selection: roughly, Z-ing is a function of X iff Z is an effect of X for which X has been selected (Neander 1991; Price 1998; Arp 2007).[2] For example, it is a function of an eagle's talons to seize prey because seizing prey is something talons

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[2] Not everyone thinks that teleosemantics should be based on of selective function, e.g. Hall (1990), Abrams (2005) and Bauer (2017). But even if we adopted a different account of function for a receiver-

do for which they have been selected. The functions in the basic circadian clock cases are selective functions.

The broader idea underpinning selective function is that a function of a thing is something it does that, at least in part, explains why it exists with the properties and relations it has (Wright 1973). For example, the fact that the liver purifies the blood explains in part why livers are around now and why they purify blood. This idea yields bases for functions other than natural selection. The function of a learned behaviour, for example, is an effect of the behaviour that explains why it has been learned. As we will see in Sect. Timekeeping and learning, systems with such functions sometimes interact with the circadian clock to produce more flexible representational systems.

Function, intermediation and response

In this paper, I will concentrate on receiver-based theories, which are the most fully developed in the literature, and argue that on such theories:

- the chemical states of the clock are indicative signals tracking future states of affairs; and
- some states are also imperative signals guiding responses to both future and current states of affairs.

In the base clock cases, though, sender-based teleosemantic theories will also recognize signals in the operations of the circadian clock (Sect. Sender-based theories).

The idea behind receiver-based theories is that something is a signal if its relationship with some state of affairs — usually thought of as a functional relationship — has the function of helping the receiver deal successfully with that state of affairs.[3] The content of the signal is determined by the functional relationship between the signal, the receiver and the state of affairs.

Consider Millikan's account under which the broadest category of representational phenomena comprises all signals that are supposed to intermediate between a sender and a receiver, which are adapted to one another, so that the receiver can perform its functions in particular circumstances (Price 2001; Millikan 2004; Stegmann 2009).

Do the chemical states of the clock intermediate between the clock genes and the clock-controlled genes? Some of chemical states of the clock usually trigger a response from the clock-controlled genes in the adaxial cells and some do not.

Suppose that the leaves of mouse-ear cress usually open when enough adaxial cells elongate and that a cell usually elongates when the concentration of clock gene product P in the cell reaches M_1. Given the highly integrated nature of the clock, we may be confident that it is the function of the clock-controlled genes to respond to an

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based teleosemantics — e.g. Cummins' (1975) or Bigelow and Pargetter's (1987) or Aristotle's for that matter — we would end up with much the same content ascriptions.

[3] Things get more complicated when the interests of the sender and receiver diverge, e.g. in cases of threat or deception between different creatures (Planer and Godfrey-Smith 2020). Success for the receiver might be disaster for the sender. In the clock cases, though, the interests of the senders and receivers are well aligned.

M_1 state by elongating the cell and hence opening the leaves. So M_1 states certainly intermediate between the clock genes and clock-controlled genes.

Suppose, however, that it is the function of the clock genes to produce a K state at three in the morning and that K states have no triggering function. (It is at least possible that neither now nor in the past have K states triggered a process that has contributed to the fitness of the plant's ancestors.) Even here, however, K intermediates between sender and receiver. It is the function of the clock genes to produce a K state at a particular time and if they fail to do so, the clock-controlled genes will be unable to perform their function. So K intermediates between sender and receiver, even though it is not the receiver's function to respond to K.

There is little doubt that the clock genes and the clock-controlled genes are adapted to one another. The clock's accurate and intricate machinery and its powerful contribution to fitness (see Sect. Evolution and adaptive importance) strongly suggest that the clock genes and clock-controlled genes have coevolved to produce and respond to the chemical states of the cell: unless they do so, the clock-controlled genes cannot perform their function, i.e. they cannot synchronize overt rhythms with external states of affairs. We certainly know of no other function that these genes could be performing. (I will not press this point each time it arises, but it is important to note that for teleosemantic theories, identification of selective function is crucial to the attribution of status as a signal and of content to signals. In the clock case, such identifications seem relatively secure but we only know so much about the selective history of the clock in different taxa, so we must acknowledge that some uncertainty remains.) On this kind of view, then, the chemical states of the clock qualify as signals.

In many teleosemantic theories (Millikan 1984; Shea 2007; Butlin 2018), a core condition for X to be a signal of a particular state of affairs is that the functional relationship between X and the state of affairs must be a necessary part of an explanation of how the receiver performs its functions in relation to the state of affairs. In our case, the fact that it is the function of the clock genes to produce a K state three hours before sunrise is necessary to an explanation of how the clock-controlled genes elongate the cells and open the leaves at sunrise. We cannot explain the opening of the leaves without referring to the relationship between the chemical states of the clock, including K, and the light-dark cycle. Again, the chemical states of the clock will come out as signals under this kind of theory. It appears then that under receiver-based teleosemantic theories, the chemical states of the clock are signals. But what are they signals of?

Imperative and indicative signals

Receiver-based teleosemantics has a natural way of distinguishing between imperative and indicative signals (Millikan 1995). In imperative cases, if there is full alignment of interests between sender and receiver, it is the function of the sender to elicit a particular response from the receiver by sending the signal. In indicative cases, a mapping between the signal and some state of affairs is necessary to explaining how the receiver performs its functions.

In some cases, a single signal can be both imperative and indicative, i.e. a pushmi-pullyu signal in Millikan's terminology. For example, rabbit danger-thumps tell

nearby rabbits to take cover but are also supposed to correspond temporally and spatially with danger for rabbits. The base circadian clock case, however, is more complicated: triggering states are pushmi-pullyu but non-triggering states are only indicative.

Triggering states. These are pushmi-pullyu signals, both imperative and indicative. They are imperative because:

- it is the function of the clock genes (the sender) to produce an M_1 state (the signal) at a particular point in the light-dark cycle; and
- it is the function of the clock-controlled genes (the receiver), to respond to M_1 by opening the leaves.

What is content of the imperative signal? On a receiver-based theory, the content of an imperative signal must be *something* the receiver is supposed to do in response to the signal, but the clock-controlled genes are supposed to do many things in response to an M_1 state: act as a template for the synthesis of particular gene products, elongate the cells, open the leaves, help the plant perform photosynthesis, help the plant reproduce (Neander 1995). One option would be to take all of these to be contents of the signal and live with the indeterminacy but it seems reasonable to impose some restrictions on which of the selected effects of the receiver's response can count as the content of the signal: it should be an effect for which the receiver is primarily responsible — this rules out photosynthesis and reproduction — and it should be the effect which makes a direct contribution to the interests of the receiver, which rules out protein synthesis and elongation (Price 1998, 2001). On this account, then, M_1 states are imperative signals with content like 'Open the leaves now.'

Triggering states are also indicative signals. How does M_1 help the clock-controlled genes open the leaves at sunrise? The regular rise and fall of clock gene products maps onto the daily light-dark cycle so that M_1 bears a specific temporal relation to sunrise, i.e. it is supposed to (and usually does) arise at sunrise. Any explanation of how the clock-controlled genes do their job must refer to the fact that M_1 maps onto sunrise.[4]

Non-triggering states. In my view, non-triggering states, e.g. K states, are not imperative signals because it is not a function of the receiver, the clock-controlled genes, (or of any other receiver) to respond to K. To argue that K states have imperative as well as indicative content, something like 'open the leaves in three hours' time', would be to ignore an important distinction between K states and M_1 states. In normal circumstances — the circumstances in which ancestral senders and receivers have acquired their biological functions — an M_1 state causes the leaves to open without the sender, the clock-controlled genes, sending any further signals. It is true

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[4] Here a single physical state of affairs is supposed to do two things: to occur when the sun rises and to trigger the expression of the clock-controlled genes that open the leaves. Is it one signal with both imperative and indicative contents or two signals, one imperative and one indicative? On a teleosemantic account, what makes something a signal is its functional relations with other things. If a single part of the world has two sets of functional relations with other things, each of which makes it a signal with a particular content, it seems to me more natural to see it as two signals, one with one content and one with another, but this is really just a terminological matter.

that in normal circumstances, a K state three hours earlier is necessary for an M_1 state to arise at sunrise and for the leaves to open but the sender must produce a further signal, an M_1 state, in order for the leaves to open. Moreover, an M_1 state is, in normal circumstances sufficient to open the leaves: if, as a result of aberrant chemical goings on, K arises two hours before sunrise but M_1 still arises at sunrise, the leaves also open at sunrise. My general claim is that a signal cannot have imperative content if, in normal circumstances, the sender has to send another signal later to elicit a response from the receiver. There is no response to the first signal, from the receiver, that constitutes the first signal's satisfaction conditions.

A comparable case is a clockwork chess clock in which the flag falls when the minute hand reaches 12 on the clock face, indicating that the player's time has expired. Barring unusual mechanical goings on, the hand will only reach 12 when time has expired if it reaches the nine o'clock position with 15 min to go — but if there are such goings on and the hand reaches 12 even though it did not reach nine with 15 min to go, the flag will still fall.

K states, then, are not imperative signals but, like M_1, they are indicative signals. When we are explaining how the clock-controlled genes perform their functions, we must mention the whole of the regular mapping between chemical states and times in the daily cycle, including the mapping between K and the time in the cycle with which it usually coincides. If we just said that when state M_1 arises at sunrise, the clock-controlled genes are expressed, the adaxial cells elongate and the leaves open, we would have described *what* the clock-controlled genes are supposed to do but not *how* they do it.

On most receiver-based theories, the content of an indicative signal is what it maps onto that we must refer to in explaining how the signal helps the receiver perform its functions.[5] In our case, an explanation of how the clock-controlled genes perform their function must characterize the times in the daily cycle onto which the chemical states of the clock map in terms of their temporal relations with important points in the cycle, particularly sunrise. The human clock time is irrelevant. Moreover, an explanation must characterize those temporal relations in *forward-looking* terms. The fact that K is supposed to arise nine hours after sunset need not figure in an explanation of how the clock-controlled genes perform their functions but such an explanation must mention the fact that K happens three hours *before* sunrise. The function of the clock's chemical states is not to mark the passage of time since the last sunset: doing that has not helped the plant's ancestors survive and reproduce. Their function is to coordinate the expression of the clock-controlled genes with the *next* sunrise. They do does this by arising at the right 'forward-looking time' in the light-dark cycle. On a receiver-based view then, K is an indicative signal that the sun will rise in three hours' time.

A requirement for correlational information?

Shea (2007) argues that a satisfactory teleosemantic theory should ensure that the accuracy of a signal explains why the receiver prospers but that a purely receiver-based theory does not do so. One of the reasons the accuracy of a signal helps the receiver respond appropriately to environmental conditions is that accurate signals bear correlational information about those conditions but Shea notes that a pure receiver-based theory does not include this requirement. He therefore requires that a signal bear correlational information about the relevant environmental conditions — on his account, the evolutionary success conditions, specific to the type of signal, of the behaviour of the receiver prompted by such signals — as well as meeting the functional requirements of a receiver-based theory.

There is a lot more that could be said here (e.g. Millikan 2007) but even if we adopt Shea's stronger requirements, we find that at least M_1 states of the clock are signals with specific content. Whatever plausible candidate we may accept for the evolutionary success conditions of the behaviour prompted by M_1 — sunrise is the obvious choice — there is a strong temporal correlation between M_1 states and those conditions.

Triggering and non-triggering states

We have so far supposed that some chemical states trigger the opening of the leaves and others do not, but the states of the cell are not so neatly divided into triggering and non-triggering. The expression of the clock-controlled genes happens over time, as does the elongation of the cells that effects the opening. In this more realistic scenario, each chemical state retains its status as an indicative signal, but more chemical states are imperative signals. Consider a chemical state M_2 which is supposed to arise when the leaves of our plant are half open. In this case, it is a function of the clock-controlled genes to produce half open leaves in response to M_2.

Sender-based theories

'Low church' teleosemantic theories are sender-based: 'a sensory representation, RED, has the indicative content that there is red if the *RED producing system* has the function to produce REDs in response to red' (Neander 2013, my italics).

Neander's theory is confined to sensory representations though she believes it can work as a foundation for a theory of more sophisticated representational systems. Circadian clocks do not produce sensory representations — although the photoreceptor cells that provide input into the entrainment mechanism (see Sect. Resetting the clock — entrainment) probably do — so we need to find a plausible way of extending Neander's idea to this somewhat different case.

One approach would be to apply the formulation given above directly and say that a representation R, whether sensory or not, has the indicative content C if the R producing system has the function to produce Rs in response to Cs. It is clear that it is not the function of the clock genes to respond to any immediate state of affairs in the environment: in our cress case, it is the function of the clock genes to produce an

M_1 state at sunrise even if the plant remains in darkness when the sun is rising and a K state regardless of what is going on outside (see Sect. Biological background). On this approach, then, Ks have no indicative content.

Still, we might extend the notion of response beyond responses to immediate states of affairs. The entrainment mechanism (see Sect. Resetting the clock — entrainment below) means that the clock is set by reference to past sunrises.[6] If the sun rises before M_1 arises in a cell, the clock is set forward: it is a function of the clock genes to respond to the relationship between the sunrise, registered by photoreceptors in the leaves, and the chemical state of the clock at that point. The clock genes can only have a response function if it is their function to respond to past states of affairs — they clearly cannot respond to future states of affairs — so, to be more specific, it is the function of the clock genes to produce various chemical states in response to the relationship between the previous sunrise and the state of the clock at that point. On this view — if the chemical states of the clock can have purely indicative contents (see Sect. Imperative and indicative signals above) — the content of a state like K might be something like, 'The sun rose 21 hours ago'. In any case, it seems that sender-based theories like Neander's cannot attribute any kind of future-directed content to non-triggering states like K.

More sophisticated cases

Resetting the clock — entrainment

The signalling performed by the circadian clock can be more sophisticated than in the basic cress example.

Entrainment is the resetting of the clock to match environmental cycles (Barak et al. 2000). If a burst of light is administered after the peak of the daily cycle to an organism that has been kept in constant darkness, the overt rhythm is shifted ahead. If it is administered before the peak, the rhythm is shifted back. In a natural setting, seasonal changes in day length progressively adjust the clock. If the organism registers strong light at the point in time when the chemical state of the clock is supposed to coincide with sunrise ('subjective sunrise'), the clock's chemical cycle is advanced. If it registers the same light at subjective sunset, the cycle is delayed (Roenneberg and Klerman 2019).

Entrainment is a universal feature of circadian timekeeping, whether the environmental synchronizer is light or food or temperature. Even relatively simple organisms like cyanobacteria display this capacity (Li et al. 2020).

Depending on how the clock is entrained, the same chemical state is supposed to map onto different points in the daily cycle. In a natural setting, the same chemical state might be supposed to arise two or three or four hours before sunrise, depending on the season. The clock in each plant is therefore capable of using the same chemical state as a signal of different points in the light-dark cycle.

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[6] Sensory input into the entrainment mechanism also registers changes in light at sunset but this makes little difference to the argument, so I will speak only about sunrises.

This adds a very considerable degree of flexibility to the clock's representational capacities. Particular chemical states are repurposed to meet prevailing environmental conditions. An analogous artefact would be a clock that runs faster or slower so as to ensure that the hands reach 12 o'clock both at sunrise and sunset even though the length of day and night change over time.

Clock regulation of anticipatory behaviour

In the cress example, the leaves are supposed to open at sunrise and their opening is supposed to help the plant deal with sunrise. In other cases, though, the overt rhythm is supposed to appear before the circumstances with which it is supposed to help the organism deal. That is, the clock allows the organism to anticipate conditions in the external environment.

The clearest examples involve the entrainment of the clock to food rather than sunlight. Food can work as a synchronizer in bees, fish, marsupials, birds and various mammals (Stephan and Friedrich 2002). In rats and mice, for example, rhythms of food anticipatory behaviour, like approaching a food bin or pressing a lever, persist for several days if food is withheld. They do not emerge if the feeding interval is not close to 24 h and they respond to shifts of mealtime by gradual rather than immediate resetting (Blancas et al. 2014), so we can be fairly sure that an endogenous circadian cycle is in operation.

These are more sophisticated cases than the leaves of the cress plant. Consider the production of digestive enzymes in rats. On a receiver-based theory, the imperative content of a chemical state that is supposed to trigger enzyme production — call it M_2 — is something like, 'Produce enzymes, clock-controlled genes.' But unlike the cress case, the indicative content looks forward to feeding time. The function of the clock-controlled genes in relevant cells is to synchronize the availability of enzymes with the availability of food. Consequently, to explain how an M_2 state helps the clock-controlled genes perform their function we must mention the fact that feeding time usually comes at a particular point in the future. The indicative content of M_2 is something like, 'Food will be arriving in half an hour.'

As in the cress case, a non-triggering state like K lacks imperative force but still constitutes an indicative signal. An explanation of how the clock enables the clock-controlled genes to perform their function must mention the fact that K maps onto the point in the light-dark cycle when the anticipatory behaviour is supposed to occur. So if K is supposed to arise two hours before the clock-controlled genes are supposed to start producing enzymes, its content is something like, 'The clock-controlled genes will activate in two hours' time', because we must mention that mapping in explaining how K helps the clock-controlled genes perform their function.

Does K also signal the next feeding time? That is, when we are explaining how K helps the clock-controlled genes perform their function, must we mention the fact that K maps onto feeding time? I think we do. If we just said, 'K helps the clock-controlled genes perform their function by arising half an hour before they are supposed to start producing enzymes', we are omitting the key fact that the function of the clock-controlled genes is to start producing enzymes *half an hour before feeding time*'. Their function is not just to produce enzymes but to do so at a particular time

before feeding time. If this is right, K also has the indicative content, 'It will be feeding time in two and a half hours.'

Timekeeping and learning

In the cases we have considered so far, synchronization between an organism's behaviour and external conditions is achieved through entrainment of the clock. There are, however, cases where the circadian clock seems to feature in associative learning.

Honeybees can learn when flowers secrete nectar, returning to the flowers at the same time on consecutive days and continuing to do so for several days after the flowers are removed (Moore 2001). The foraging rhythm continues under conditions of constant light with a period close to 24 h. It is entrained to changes in the light-dark cycle. Like other circadian rhythms, it will fail if the light-dark cycle is much shorter or longer than 24 h. So it seems very likely that it relies on an endogenous circadian clock.

But this is not the whole story. If you put food out at a particular place and time of day, even for a couple of days, forager bees will return to the place at that time on later days. This change in behaviour is too quick to be the product of entrainment so it seems that there must be some kind of learning going on. We have not unraveled the mechanism at a cellular or molecular level, but since entrainment of a circadian clock is an unlikely explanation, the bee appears to be recording the time of day (according to the circadian clock) at which food is available and this record must be used later to regulate behaviour. We do know that the recording mechanism has a one-day period: the bees will go to the feeding station every day, even if food has only been available every second day (Gallistel 1990). We also know that the bees come early, before the time that food has been available on training days, possibly using the same mechanism behind the anticipatory behaviour discussed in Sect. Clock regulation of anticipatory behaviour. Similar phenomena appear in birds — if a kestrel is successful in hunting in a particular area at a particular time of day, it is more likely to return to hunt there at that time on the following day (Rijnsdorp et al. 1981).

The point here is not that bees and kestrels have learning mechanisms but that the circadian clock interacts with other mechanisms to guide sophisticated and flexible behaviour. It makes information about future states of affairs available to learning mechanisms that use this information to regulate behaviour. In these cases, the clock acquires some of the functional flexibility of an artefactual clock: it is not merely a switch that triggers an overt rhythm at a fixed time of day.

It is hard to see how functions involved in these more sophisticated cases could be derived entirely from natural selection. The mechanism that guides the bee to the location at the right time acquires its specific functions not only from natural selection but also from more flexible learning mechanisms.
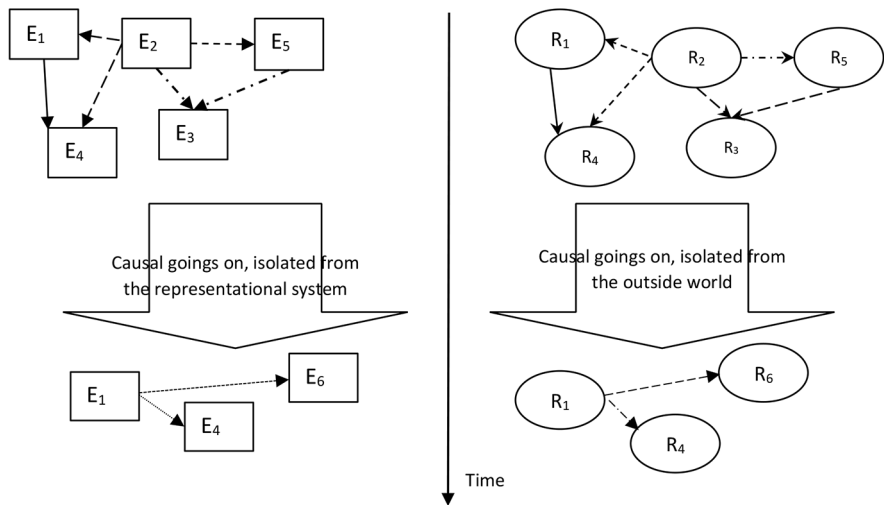
E₁ E₂ E₅
E₄ E₃

R₁ R₂ R₅
R₄ R₃

Causal goings on, isolated from the representational system

Causal goings on, isolated from the outside world

E₁ E₆ E₄

R₁ R₆ R₄

Time

Fig. 3 Signals causally isolated from states of affairs Note: In the left panel, Es are entities in the world, arrows are relations between them. In the right panel, Rs are representational vehicles, corresponding to entities, arrows are relations between them, corresponding to the relations in the left panel.

Broader implications

The indicative-imperative distinction is basic

Millikan (2004) emphasizes the pushmi-pullyu nature of signals internal to an individual organism, i.e. that they are both imperative and indicative at the same time:

> How and why did perception-action cycles, which seem fully to characterize the cognitive character of the simplest animals, slowly give way to … more articulate and differentiated representations such as human beliefs, which are merely descriptive, and human desires, which are merely directive. ….

The circadian clock both tracks the external world (producing indicative signals) and, from time to time, produces pushmi-pullyu signals which are indicative but also imperative, causing receiver systems to execute overt rhythms. The tracking function of the clock exhibits a 'tower bridge' structure (Swoyer 1991) in which, for periods of time, the representing system is causally isolated from the represented system (Fig. 3). Clearly, the functions of the clock go beyond perception-action cycles. The distinction between pushmi-pullyu and purely indicative signals is not a later development in more sophisticated animals but a feature of ancient systems in simple creatures.

We can also be confident that there are no entirely pushmi-pullyu animals. Some animals, e.g. dogs, have more sophisticated, decoupled representational capacities than others, e.g. nematodes, and probably some organisms rely mainly on pushmi-pullyu representations to guide their behaviour. Every animal, however, has a circa-

dian clock that tracks goings-on in the outside world without direct sensory input and produces both pushmi-pullyu and purely indicative tokens.

Probably, the most basic kind of signals are pushmi-pullyu signals if 'basic' means functionally unrelated to other signals but it is at least unclear that this is the case if 'basic' means (a) coming first in evolutionary history or (b) generated by the simplest biological systems.

a. Circadian clocks arose early in evolutionary history, probably in the most primitive cyanobacteria as much as 3.5 billion years ago (Dvornyk et al. 2003). Probably, the first neurons — which are the home of most representational phenomena in the non-human biological world (at least the ones philosophers have mostly been interested in) — appeared maybe 550 million years ago.

b. By comparison with nervous systems, the circadian clocks are quite simple. At the molecular level, of course, there is a lot going on but still, the core of the circadian clock is a handful of genes in a single cell. This is orders of magnitude less complicated than eyes and brains.

Assessing the clock's representational capacities

It would not do to overstate the sophistication of the signalling that the clock performs. It is clearly a simple system compared with things like human natural languages or the cognitive systems of some animal species. Is it so simple that it is not representational at all? I will not try to set out a complete theory of representation that distinguishes fully intentional systems from simpler systems, but there are a few dimensions which have received a great deal of attention in the literature and which it seems natural to see as relevant to the representational status of a biological system.

1. *The range of behaviour the representational tokens help to control*. In the simplest systems, one kind of token is produced in response to one kind of external state of affairs and one reaction is generated in response to the token In more sophisticated systems, a representational token can play a role in many different behaviours. For example, rats have some kind of map of their environment encoded in their hippocampus — we know something about how this works on a cellular level — which guides many different behaviours (Moser et al. 2008; Shea 2018). Among humans, Anna's mental representations of the fruit shop guide a very wide range of behaviour: getting to the shop, giving others instructions for reaching it, planning meals, and so on. The circadian clock is quite limited in this respect. In most organisms it controls a number of different overt rhythms but each of the rhythms is rigidly coupled to the state of the clock. The signals are not used to generate different behaviour in different circumstances. Now (a) the response may itself be very complicated (for example, at a particular point in the year an endogenous annual clock prompts birds to migrate half-way around the world) and (b) as we have seen with the bees, the clock can interact with other systems to vary the time of day at which the receiver system responds, but even in these cases the function of the clock itself is just to trigger the response at the right time.

2. *Decoupling of token and state of affairs*. The idea here is that full representational status requires that tokens can be decoupled — in space, in time and causally — from the states of affairs that they represent (Clark and Toribio 1994; Rowlands 2006; Kiverstein and Rietveld 2018). Like any clock, the circadian clock runs all the time, continually producing indicative tokens, regardless of what is going on in the outside world, so there is a degree of decoupling in play. However, the entrainment mechanism constantly adjusts the clock to bring it into synchronization with the world, so the degree of decoupling is strictly limited. When Anna is thinking about the fruit shop, she can think about Genghis Khan visiting the shop, about the shop being a front for a foreign intelligence service etc. Her representations of the shop can be entirely decoupled from the actual world. So on this dimension, the circadian clock displays a measure of sophistication, though less than fully intentional systems.

3. *Interaction between tokens in controlling behaviour*. The idea is that in more sophisticated representational systems, tokens interact in guiding behaviour (Burge 2010; Schulte 2015). For example, in influencing Anna's behaviour, her representations of the fruit shop interact with representations of many other objects and states of affairs: the bus stop, the time of day, the traffic on the road to the fruit shop and so on. In the basic cress case, the chemical states of the circadian clock do not interact with other tokens. Entrainment, however, involves interaction between the chemical states of the clock and sensory input from the phytochrome receptors in the plant's leaves, which register sunlight (Chamovitz 2019). This input is, arguably, representational — at least, it is as representational as the raw activation patterns on the human retina. When the plant registers sunrise, the indicative content of the M_1 state, and this is out of synchronization with its internal clock, it adjusts the internal state of the clock to fit the external state of the world. So there is some interaction of tokens in the circadian clock case, though quite limited in scope and function.

4. *Whether tokens are stored for later use*. Anna can store a representation of an episode at the fruit shop and retrieve it later for combination with other representational tokens but the circadian clock does not produce representations of past events. In the cress case, tokens are not stored: the clock-controlled genes simply respond to the chemical state of the cell as they arise. But in learning cases (Sect. Timekeeping and learning), the clock's interactions with other systems involve the storage of tokens that represent particular points in the daily cycle. Of course, the central oscillator of the clock does not do this on its own, but as part of a larger system.

5. *Whether tokens are symbolic*. Defining symbolic representation is a tricky business (Planer and Godfrey-Smith 2020) but one characteristic generally insisted on is that the relationship between the symbol and its content be in some sense arbitrary. We use SOS as a symbol for emergency, but we could use BLB etc. In terms of game theory, we see a stable set of correspondences between signals, states of the world and actions of a receiver system, but there are other stable sets of correspondences that could have arisen (Skyrms 2010). By contrast with symbols, Peirce (1906) characterized indexes as being 'really and in [their] individual existence connected with the individual object' (see also Maynard-Smith

(2000) and Sterelny (2000)). The mapping between the clock's states and the points in the light-dark cycle make the states indexes, not symbols: given the laws of chemistry, the states must be as they are if they are to cause the right responses in the clock-controlled genes.

6. *Whether simple tokens can be composed into more complex arrangements with different contents.* Not only do Anna's representations of various objects and properties in the world interact in guiding her behaviour but they do so compositionally. Through neuronal processes that we do not yet fully understand, she can believe that the fruit shop is close to the lake and that the fruit shop is close to the butcher shop etc. The chemical states of the clock do not display the same flexible kind of compositionality that we find in natural languages or human thought. The re-use of tokens noted in (4) above looks a little like composition but, whatever physical form composition may take, the chemical states of the clock do not seem to combine with other signals to form larger contentful wholes.

7. *Explanatory purchase.* The thought here is that a system should not count as representational if describing it in representational terms serves no explanatory purpose. Sterelny (1995) says:

> The suppression of ovulation in subordinate female naked mole-rats is chemically mediated. These chemicals merely function to suppress ovulation: I see no explanatory point in supposing they have the imperative content "Thou Shalt Not Ovulate!".

Burge (2010), Shea (2018) and others make the same point. I agree that if we understand in detail the selective functions, molecular genetics and cellular chemistry of a particular sender-signal-receiver system within the cell, we probably do not gain much additional insight by attributing representational properties to it. Nevertheless, doing so still makes sense if attributing basic representational properties to simple systems is part of a broader theory that works well for the more complex and less well-understood cases to which we really do want to attribute representational properties. Whether teleosemantics is such a theory is on open question: maybe it is untenable for some independent reason, e.g. ineradicable indeterminacy of content. On a teleosemantic view, however, it seems best to say that:

    a. simpler sender-signal-receiver systems like the circadian clock possess basic representational attributes; but

    b. because we understand the clock at a functional level and, largely, at a molecular level, those attributes have relatively little explanatory purchase.

In summary then, the circadian clock is fairly sophisticated in relation to the range of behaviour its tokens help to control and the extent to which token and state of affairs are decoupled from one another. In relation to the storage of tokens for later use and interaction between tokens in controlling behaviour, the basic clock case shows little sophistication, though in many animals the clock interacts with other systems so

as to display these characteristics. Because we understand the clock at a functional level and (largely) at a molecular level, its representational attributes have limited explanatory power. Simple tokens cannot be composed into more complex arrangements with different contents and the clock tokens are not symbolic, so the clock is unsophisticated in these respects.

After this stock take, it is natural to ask whether the circadian clock is sophisticated enough to make its signals fully fledged representations. The contested borderline between representational and non-representational systems is often taken to be that between perceptual and sensory systems. For example, Schulte (2015) writes, '… I propose that we accept Burge's claim that perception "marks the lower border of representation" … — not only for the sake of the argument, but also because it is quite plausible in itself. Under this assumption, the border between representational and non-representational states is identical with the border between genuine perceptions and merely sensory states …' This border has been the focus of the debate about examples like magnetotactic bacteria (Rescorla 2013), vasopressin moving from the hypothalamus to the kidneys (Schulte 2015), E. coli tumbling to avoid toxic chemicals (Shea 2018), photoreceptors in Euglena (Burge 2010), the thalamus generating a particular firing pattern when there is a dark spot in the visual field (Artiga 2016) and the scarlet gilia changing from red to white in June (Dretske 2004).

The circadian clock obliges theorists to consider a case where:

- the core of the chemical mechanism can be described in functional and molecular terms. While not every component of the system in mouse-ear cress, for example, has been described down to the molecular level, the central mechanism has been. This suggests that there is little explanatory gain to be had from attributing representational properties to the clock or its components; but
- the purportedly signalling states are decoupled from the environmental conditions they may be signalling. Indeed, this is the whole adaptive point of the clock: the plant does not have to rely on environmental cues to trigger of opening of its leaves. Sensory input is crucial to the operation of the entrainment mechanism but the clock itself is not; and
- the tracking and triggering functions of the clock argue for a distinction between imperative and indicative signals (Sect. Imperative and indicative signals).

People who think that representational status is determined by a number of different dimensions like those considered above (e.g. Neander 2017, Rowlands 2017), must consider how to trade off explanatory power, which is quite limited in this case, against decoupling and the imperative/indicative distinction, which are more sophisticated characteristics. Even if you think that a single characteristic — perhaps serious explanatory power (e.g. Sterelny 1995) — is necessary for a system to count as a representational system, so that the circadian clock is excluded, the clock case at least brings your theoretical commitments into sharp relief.

Implications for theories of genetic representation?

There has been considerable debate in the literature about what (if anything) genes, conceived of as coding regions of the genome, represent. The circadian clock case supports the view that gene expression, rather than genes themselves, can have representational capacities.

One thought is that some genes represent the phenotypes with which they are associated. Many biologists take this view, thinking of the genotype as a prescriptive representation of the phenotype with which it is supposed to be (and usually is) associated, i.e. as a blueprint or recipe for the phenotype of the adult organism (DeLisi 1988; Nijhout 1990; Burglin 2006). So, for example, a particular pattern of hox genes might be thought of as prescriptively representing the body plan that individuals with that pattern are supposed to exhibit. This may seem plausible but it is hard to fit it into a sender-signal-receiver theory of representation. The main problem is that it is hard to identify a single coherent receiver whose function it is to respond to the gene pattern by producing an individual with the usual phenotype. The set of non-genetic developmental resources needed to produce a viable individual is large, complicated and interconnected in any given case and varies widely from individual to individual, depending on the environment that the individual is in. A particular pattern of genes could perhaps be seen as a kind of prescriptive representation on a more permissive theory, but not on a sender-signal-receiver theory.

A more modest thought is that a gene represents the string of amino acids which is supposed to be assembled into a protein at the ribosomes when the gene is expressed, according to the 'genetic code'. On a receiver-based theory, it is plausible to see the gene (when expressed) as a sender, the mRNA transcribed from the gene as an imperative signal and the ribosome (perhaps with some associated genetic machinery) as a receiver. Since the function of the gene (when expressed), is to trigger the synthesis of the corresponding protein by the ribosome, we can see that protein structure as the content of the imperative signal.

Where gene expression is an adaptive reaction to immediate chemical conditions in the cell, it is also plausible to see the mRNA as an indicative signal of the relevant chemical conditions as well as an imperative signal of the protein that the ribosome is supposed to synthesize. One example among many is the *lac* genes which are expressed in response to the presence of lactose in prokaryotic cells (Hartwell et al. 2000).

Circadian clocks are a more sophisticated gene expression case. They offer no support for a teleosemantic interpretation of genes taken in isolation. As I argue in Sect. The base case, however, it is entirely plausible to see gene expression in the circadian clock as sending signals of future conditions in the outside world.

Conclusion

On receiver-based teleosemantic theories, but not on sender-based theories, the circadian clock produces signals of future states of affairs, both imperative signals, which tell clock-controlled genes to switch on overt biological rhythms, and indicative sig-

nals which track the time in the light-dark cycle by reference to key future events. These results have a number of implications for the way we see signalling and representation in the biological world.

Pushmi-pullyu representations, which are imperative and indicative at the same time, are sometimes thought of as the most basic kind of signal but the circadian clock, which arose very early in evolutionary history, which operates through gene expression not cellular connections, and which appears in creatures as simple as cyanobacteria, produces both pushmi-pullyu and purely indicative signals.

The clock is not a fully intentional system, but it displays a measure of sophistication in a number of different respects: it is fairly sophisticated in relation to the range of behaviour its tokens help to control and the extent to which token and content are decoupled both temporally and causally. In many animals tokens are stored for later use and then interact with other systems to enable the animal to learn when in the light-dark cycle to engage in particular forms of behaviour. When we consider what systems should count as representational, the clock obliges us to address unique trade-offs between sophistication in some respects and simplicity in others. In relation to genetic representation, the clock cases offer no support for the view that genes in themselves have representational capacities but they do support the view that gene expression can do so.

Declarations

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