Representation Without Informative Signalling

Gerardo Viera

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Abstract

Various writers have attempted to use the sender-receiver formalism to account for the representational capacities of biological systems. This paper has two goals. First, I argue that the sender-receiver approach to representation cannot be complete. The mammalian circadian system represents the time of day, yet it does not control circadian behaviours by producing signals with time of day content. Informative signalling need not be the basis of our most basic representational capacities. Second, I argue that representational capacities are primarily about control, and only when specific conditions obtain does this control require informative signalling.

1 Introduction

What makes a biological system a representational system? An increasingly common answer in the philosophical literature is that representational capacities arise in the biological world as a result of signalling behaviours that guide animal behaviour (Artiga [2016]; Dretske [1981]; Ganson [2018]; Godfrey-Smith [2014]; Martínez & Klein [2016]; Millikan [2004]). In more recent years, researchers within this program have begun to use the sender-receiver formalism developed by Brian Skyrms ([2009], [2010]) as a way to formally model these signalling behaviours and to better understand how representational capacities arise in biological systems.

This paper has two aims. First, to show that the sender-receiver framework cannot account for some basic representational capacities in biological systems. Second, to show that the emphasis on signals as the primary bearers of content has been misguided. Representations are fundamentally about control, and control need not be exerted through meaningful signalling.

The paper goes as follows: Section 2 lays out the sender-receiver framework as it has been developed by Skyrms and others. Section 3 distinguishes transmission from the mere possession of information. Section 4 describes the mammalian circadian system and argues that this system coordinates animal behaviours with the time of day without transmitting time of day information to downstream systems. Section 5 argues that the mammalian circadian system is a genuinely representational system with time of day as its content. Therefore, we have a basic representational capacity not analysable via the sender-receiver framework. Section 6 articulates the relation between control and communication.

2 The sender-receiver framework

Before we see the details of the sender-receiver framework, it is useful to situate our discussion within a larger context to avoid a specific confusion. The goal of this paper is not to argue that there is something fundamentally wrong with the sender-receiver formalism. In so far as it is a formalism, it is

a tool for understanding a range of signalling phenomena. The target of this paper are those views that use the sender-receiver formalism to account for how representational capacities arise in biological systems.

Largely within the *teleosemantic tradition*, researchers in recent years have taken the insights of Millikan ([1984]) that representational capacities are a form of signalling within individual organisms and have thought that the formalism of the sender-receiver framework explains how simple and complex representational capacities can arise in biological systems. The ultimate aim of this research program is not necessarily to develop a particular formalism. Rather, its aim is the naturalization of content. To explain how representational mental states, often appealed to in the cognitive sciences and characterized in terms of their content, fit within the biological world.

While these researchers are typically cautious, and do not claim that the sender-receiver framework will provide an account of all mental representations, they often claim that the framework accounts for the sensory, motor, and affective capacities that coordinate animal behaviours with the environment (Artiga [2016], [forthcoming]; Ganson [2018], [forthcoming]; Godfrey-Smith [2014]; Martínez & Artiga [forthcoming]; Martínez & Klein [2016]; Planer & Godfrey-Smith [forthcoming]; Shea et al. [2018]). Godfrey-Smith ([2014]) goes further and argues that memory can also be understood in terms of the framework.

It is this approach to the naturalization project that is the target. Throughout the paper, when I refer to the sender-receiver theorist, I am referring to those working within this naturalization project. The aim of this paper is to show that there are basic representational capacities that cannot be explained by the sender-receiver formalism.

Skyrms' sender-receiver framework is best seen as an extension of two projects – Lewis' signalling game analysis of conventional meaning (Lewis [1969]) and Dretske's information theoretic approach to mental representation (Dretske [1981], [1997]), which were both designed to account for content involving phenomena.

Lewisian signalling games begin with two perfectly rational, rule-following, agents with shared interests (such that outcomes that benefit the one benefit the other).[1] The *sender* is able to observe some aspect of the world and can only act by producing a *signal*. The *receiver* can only observe the signals produced by the sender and acts on the world in a way that affects the outcomes of the sender and receiver. Through a rational decision process, the sender and receiver alter their observation-signal and signal-act rules until they find a combination of rules that optimizes their outcomes. When no unilateral changes in sender or receiver rules brings about better results the pair are said to be in *equilibrium*. Lewis claims that at these equilibria we have all the resources needed to understand the conventional meaning of signals within a game. The sender rules let us know what in the world the signals are tracking, and the receiver rules let us know what these signals *mean* to the receiver (for instance whether the receiver treats distinct signal types equivalently or not). Through this interaction senders and receivers can coordinate their activities despite receivers lacking the epistemic access to the world possessed by the sender.

Skyrms' sender-receiver framework involves two advances to Lewis' signalling games. First, in Lewis' signalling games, senders and receivers were sophisticated rational agents that would arrive at their rules through similarly sophisticated and rational means. Skyrms argued that we can understand the process of rule selection as arising through *dumb* processes like natural selection and individual trial-and-error learning. The sender and receiver need not possess any sophisticated capacities. All that is needed is some ability to adapt their behaviour to inputs and some preference function that guides the

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[1] Not all developments of Lewisian signaling games rely on shared interests. However, for our purposes we can ignore that issue.

adoption of different rules. This allows for the sender-receiver framework to provide an account of how intentional actions can arise in biological systems without presupposing intentional sophistication on behalf of the individuals involved.

The second major shift from Lewis to Skyrms involves appealing to information theory to determine the meaning of the signals. Lewis' analysis focused on the sender and receiver roles but did not describe the means by which information could be transmitted between the two agents. Information theory, however, provided the tools to understand how information (or meaning, properly understood) could be transmitted via a communication channel. The key idea was that the state of one system could carry information about the state of another, and that this information could provide a basis for the meaning of the signals mediating the sender-receiver interactions. To use the informal characterization from Dretske ([1981]), a system or signal,[2] *s*, carries information about another system, *t*, provided that the probability of *t* being a certain way, say, *t's being F*, is increased given that *s* is a certain way, say *s's being G*.[3] For example, honey bees will produce a specific buzzing sound to alert other bees to the presence of predators at a food source (Kietzman & Visscher [2015]; Nieh [2010]). This buzzing carries information about the presence of a predator, since the probability of a predator being present, conditional on the bee's buzzing, is greater than if the bee were not buzzing. Understood in this way, for a system to carry information about another is just for there to be the correct association between property instantiations.

One apparent difficulty for straightforward information-theoretic analyses of intentionality is that any given signal often carries information about a range of states of the world. A bee's buzzing carries information about the presence of predators, but it also carries information about the ambient temperature and the health of the bee (since if the ambient temperature is too low, or the bee is ill, the buzzing would be less likely to be produced). Yet, our attributions of content, or meaning, to signals is often less indeterminate than this – signals often indicate specific ways the world could be, and not just various probabilities about how the world is – and this determinate content allows the content to be assessed for truth of accuracy. To account for this, Skyrms distinguishes between the *informational content* of a signal, which is a simple conjunction of all of the shifts in the probabilities of how different aspects of the world may be given a signal, from *propositional content*.[4] According to Skyrms, the propositional content of a signal is a disjunction of the states of affairs that are not ruled out by the signal. For a signal to have the propositional content, *a predator is present*, is just for the signal to reduce the probability of there being no predator to zero. It is this propositional content that is clearly amenable to representational notions like truth or accuracy.

By bringing together information-theory and the signalling game framework, sender-receiver theories are able to overcome two shortcomings that these theories have in isolation. First, information alone cannot account for representation since information is everywhere. A piece of toast by the road carries information about human activity, since the presence of toast increases the probability that people were nearby. However, we would not normally attribute content or meaning to a piece of toast. The toast does not play the right role to be a representation. The sender-receiver framework says that information bearing states are representational (or have meaning) when they coordinate sender and receiver behaviours. Second, sender-receiver dynamics alone only characterize the causal interactions between

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[2] In many formulations, 'signal' picks out whatever carries information. In this paper, I will use 'signal' to refer to the causal means by which senders and receivers interact.

[3] There are more formal analyses of this relation, however, nothing crucial is added by the formalism.

[4] The notion of propositional content that Skyrms has in mind is that of sets of worlds or situations, and not something's having a discursive or language-like format. This notion of propositional content is less determinate than what many philosophers of language have in mind. The propositional content of the bee buzzing includes not just that a predator is present but also that the bee is not dead (etc.). Thank you to a referee for pointing this out.

systems but do not specify any intentional or semantic properties of this interaction. Instead, it is through information theory that these causal mechanisms come to *be about* the world around them.

While the sender-receiver framework was initially developed to understand how initially meaningless symbols acquire meaning in the coordination of action, it is through its application to intra-individual coordination that the model has been applied to phenomena like neural and mental representation. Sensory systems, for instance, are causally sensitive to the environment and communicate the state of the environment to downstream systems by the signals they produce.

Another problem that arises for using the sender-receiver framework, or any information-theoretic analysis of representation, is accounting for the possibility of misrepresentation. We typically take signals to be capable of misleading their consumers. Naturalistic theories of meaning should account for this. To see why this is a problem, let us follow a line of reasoning raised by Jonathan Birch ([2014]). For the sake of simplicity, let us follow Skyrms and adopt a frequentist notion of objective probability.[5] Consider the bee buzzing again. A (type of) buzzing, *d*, is supposed to signal that there is a predator nearby. For the signal to have this determinate content, it must be the case that the signal reduces the probability of there being no predator to zero. In other words, on a frequentist interpretation of probability, it must be the case that *d* never co-occurs with a situation in which no predator is present. However, there are cases in which the bee misrepresents (or mis-signals) the presence of a predator. In this case, *d* would occur in a situation where no predator is present. However, we now have a clear contradiction. For *d* to misrepresent the presence of a predator, *d* must occur in the absence of predator, but it also must never occur in the absence of a predator (that is, it must mean predator). Misrepresentation seems impossible.

A standard fix to this problem available to all information-theoretic approaches is to appeal to natural functions as a way of specifying correct operating conditions under which the meaning of a signal or representation is determined (Dretske [1991]; Neander [2017]). Misrepresentation is possible, since under proper operating conditions, specified by the function of the signalling system, the representation would accurately describe the world. Misrepresentation arises when these proper operating conditions are violated. What has emerged over the years is that specifying these functions is a notoriously difficult task (Godfrey-Smith [1989]; Neander [2017]).

Nevertheless, several authors have argued that the sender-receiver framework has the resources needed to provide an account of misrepresentation. According to Birch ([2014]), we evaluate a signals content not by what it correlates with in our world, but what it would correlate with in a nearby possible world in which the signals produced by a sender stand in a one-to-one relationship with the intended class of properties in the world. According to others (Ganson [2018]; Shea et al. [2018]), signals acquire a content, and thereby the ability to misrepresent, in virtue of acquiring a function within a signalling game. We look to what state of affairs in the world explained why a certain sender-receiver pattern was established, and then we take those states of affairs to be the content of the signal in subsequent use.

The important thing to take from this section is the role of signalling in the sender-receiver framework. Representational capacities arise out of the signalling behaviours that coordinate actions between senders that have epistemic access to the world and receivers that lack that epistemic access. Signals coordinate receiver actions with the world by causally influencing receivers in ways that corresponds with the information about the world those signals carry. Signals represent by effecting this coordination.

3 Possessing and transmitting information

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[5] We need not make this assumption, but it simplifies the discussion. For more see (Birch [2014]; Godfrey-Smith [2013]).

Central to the sender-receiver framework is the idea that signals influence receiver actions (Artiga [forthcoming]; Bergstrom et al. [2020]). The information that is transmitted by signals is meant to explain how receivers are influenced in ways that coordinates their actions with the world. It is because the signal carries information about a state of affairs in the world that the receiver can coordinate their actions with regards to that state of affairs. In this section, I will make explicit the distinction between possessing and transmitting information. Nothing here should be controversial.

The definition of mutual information from the last section specifies what it is for a system to carry information about something else. All that is required is the correct relationship between property instantiations. A brain region may carry information about the presence of a tumour in virtue of its colour, since certain types of cancer cause nearby brain tissues to turn blue (Lee et al. [2013]). That same region may carry information about objects in the environment in virtue of its spiking patterns. The brain region carries or possesses both pieces of information. However, the cancer information is not transmitted to other brain regions because the colour of brain tissue exerts no direct causal influence on other neural systems. However, given how information about objects is encoded in the brain, this information is transmittable, since spiking activity does have causal influence on recipient neural systems. That is, due to biological contingencies, information about objects can be transmitted between brain regions, while information about tumours, carried by brain tissue being blue, is not. To transmit information requires that the information encoding properties of a signal be capable of causally influencing receivers.

For the informational content of a signal to explain why a receiver behaves the way they do, the receiver must be capable of discriminating between those signals that carry this information from those that do not.[6] That is, the information must be transmitted.

4 Circadian control systems

The goal of this section is to show that the mammalian circadian system provides animals with information about, and coordinates their behaviours with, the time of day, but does not produce outputs that transmit this information to receiver systems. In the next section, I will argue that the circadian system represents the time of day.

Organisms across the biological world exhibit patterns of behaviours with roughly 24-hour periods. These *circadian behaviours* were originally thought to derive from environmental cues with 24-hour cycles. When Jean Jacques d'Ortous de Marain observed the 24-hour cycle in the opening and closing of *mimosa pudica* leaves he thought this pattern was driven by the influence of light. However, in 1729 he published a study showing that these circadian behaviours persisted under constant lighting conditions. Whatever was driving these behaviours seemed to be internal to the organism.[7]

Subsequent studies with organisms across the biological world, from cyanobacteria to complex vertebrates, have shown that a wide range of circadian behaviours persist in *free running conditions* where individuals are kept isolated from external cues that could inform them about the time of day.[8] It is widely accepted that the central component of the mammalian circadian system is located in a region of the hypothalamus called the *suprachiasmatic nucleus* (SCN) (Weaver [1998]).

The localization of the SCN as the central component of the circadian system came through a series of studies. Animals with damaged SCNs lose the vast majority of their circadian behaviours (Weaver, 1998).[9] For instance, SCN-lesioned mice and hamsters kept in free running conditions exhibit irregular

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[6] The claim is not that receivers are sensitive to information per se. They are sensitive to information encoding properties.
[7] For the history of circadian research see (Sollars & Pickard [2015]).
[8] See (Bano-Otalora & Piggins [2017]; Bechtel [2011]; Bell-Pedersen et al. [2005]; Welsh et al. [2010]).
[9] Some food related rhythms are preserved after SCN lesioning (Marchant & Mistlberger [1997]).

feeding and sleeping patterns relative to control populations that have either undergone no surgery or have undergone sham surgeries that involve similarly invasive procedures yet leave them with intact SCNs (DeCoursey et al. [2000]; Schwartz & Zimmerman [1991]). In another study (Maruyama et al. [2007]), rats which were trained to expect heat stress at a certain time of day showed anticipatory behaviours where they would lower their body temperature in preparation for the expected heat stress at the correct time of day. Half of this population was then subjected to SCN lesioning. The SCN-damaged rats persisted in showing heat stress anticipatory behaviours albeit at the wrong time of day (their body temperature regulation became arhythmic). In all, various studies show that many circadian patterns in overt behaviour and homeostatic control depend on a functioning SCN.

In the 1970's researcher began to uncover the molecular basis of the circadian clock. While many details remain unknown, quite a bit is known about the intracellular and intercellular circadian mechanisms. The intracellular story is common, in its basic form, across the animal kingdom. Here is a simplified model of the core molecular clock (paraphrased from (Viera [2020])).[10] The intracellular rhythms of circadian clock cells are underpinned by endogenously driven transcription / translation feedback loops that give rise to electrical oscillations with approximately 24-hour periods. The feedback system is roughly divided into positive and negative components. The proteins BMAL1 and CLOCK combine within the cell to initiate the transcription of various genes, including *Per* and *Cry*. As *Per* and *Cry* are expressed and the concentrations of the proteins PER and CRY increase which ultimately inhibits the ability for BMAL1 and CLOCK to initiate the transcription of *Per* and *Cry*. This back and forth, with BMAL1 and CLOCK as the positive component, and PER and CRY as the negative component, gives rise to 24-hour oscillations in gene expression and electrical activity within individual SCN neurons.

The intracellular story explains the circadian patterns found within individual SCN cells. However, individual SCN cells kept in isolation quickly show erratic behaviour, for example phase drifting as the feedback loops are sensitive to disturbances (Bano-Otalora & Piggins [2017]; Webb et al. [2009]; Yamaguchi et al. [2003]). It is at the system level that the SCN begins to show robust circadian patterns. Through a series of different mechanisms, involving synaptic connections, the local dispersal of regulatory molecules and the high prevalence of gap-junctions, SCN cells regulate one another (Colwell [2000]; Hastings et al. [2018]; Liu et al. [2007]; Pilorz et al. [2020]). Individual SCN cells cannot account for stable circadian behaviours. Rather, it is at the system level that the SCN constitutes a reliable timekeeping mechanism. This system level, intercellular, story will be the focus of the rest of this section.

The SCN was originally thought of as a single oscillator entrained by the local day / night cycle, since the average firing rate of the SCN as a whole shows a 24-hour cycle. However, that simple model has over the years been replaced by models that attribute increasingly complex internal structure to the SCN.

The SCN can be divided into two gross anatomical areas, the core and the shell. The dominant inputs to the core are from the melanopsin visual channel, which serves as the dominant calibrating force in the mammalian circadian system[11], and it mostly projects to the SCN shell. The shell has reciprocal connections with the core as well as SCN-external sites that control specific behaviours / activities (Abrahamson & Moore [2001]; Brancaccio et al. [2014]; Evans et al. [2015]; Welsh et al. [2010]). The shell and core were initially thought of as two independent oscillators with the same period but with the core reaching its peak slightly before the shell. However, even this picture has been shown to be false.

Within both the shell and the core there are distinct phase-shifted oscillatory networks that interact to stabilize circadian outputs (Hastings et al. [2018]; Pilorz et al. [2020]; Yan et al. [2007]). Individual

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[10] For further details see (Bano-Otalora & Piggins [2017]; Bechtel [2011]; Buhr & Takahashi [2013]; Gachon et al. [2004]; Lowrey & Takahashi [2011]; Viera [2020]).

[11] See (Freedman et al. [1999]; Schibler et al. [2003]; Stephan [2002]) for details of SCN calibration.

cells join together to form small local modules, these modules interact with neighbouring modules, and their interactions give rise to the larger scale oscillatory behaviours of the SCN (Evans et al. [2013]; Yoshikawa et al. [2021]). One way of understanding the interaction between these individual cells, localized modules, and more global networks is in terms of the network properties of the SCN placing constraints on the intracellular clock mechanisms. It is the intracellular clock mechanism that drives the activity of the cell, but the local network properties restrict the variability of activity within nearby cells, forcing synchronization within modules and desynchronization between modules (Bechtel [2017]; Evans et al. [2013]; Hastings et al. [2018]).

Importantly, neither the shell nor the core function independently of the other. The core and shell influence one another with the core initiating activity in the shell and the shell playing a role in the deactivation of the core, resulting in an overall 24-hour rhythm to SCN activity as a whole. Therefore, no single region of the SCN can be isolated as *the* clock mechanism. Rather, it is the activity of the SCN as a whole, composed of various interacting oscillatory and regulatory mechanisms, that provides the organism with a mechanism capable of grounding the circadian rhythms observed in overt behaviour and homeostatic regulation (Evans et al. [2013], [2015]; Hastings et al. [2018]; Herzog et al. [2017]; Kalsbeek, Perreau-Lenz, et al. [2006]; Meijer et al. [2010]; Pilorz et al. [2020]; Schaap et al. [2003]; Yan et al. [2007]).

How then does the SCN control circadian behaviours[12]? A simple, albeit false, story is that the SCN operates similar to how GPS networks calibrate clocks around the world. GPS networks output a signal to all receiver systems that transmits time of day information (the signal changes covary with the time of day and receiver systems are sensitive to these signal changes). The simple story of SCN outputs would be that the SCN sends a signal to receiver sites that transmits information about (in other words, appropriately covaries with) the time of day. However, this simple story is false.

SCN outputs come in two forms (Kalsbeek et al. [2006]). Some come in the form of diffusion or humoral factors. Evidence for this sort of output came in a series of experiments in which SCN-lesioned hamsters, that showed no circadian rhythmicity, would have some circadian patterns re-established through the implantation of donor SCN tissues that were encased in a semi-permeable membrane (Silver et al. [1996]). The membranes would allow for smaller molecules to pass through but would not allow for axon growth. Therefore, the re-established circadian patterns could not be the product of neuron-to-neuron transmission.

The second form of SCN output are neural projections from the SCN shell to specific SCN-external targets (Kalsbeek, Palm, et al. [2006]; Kalsbeek, Perreau-Lenz, et al. [2006]; Meijer et al. [2010]). These outputs, like the diffusion outputs, are produced by specific regions of the SCN shell. As these subregions of the SCN shell reach their peak activations, they produce a fixed output that initiates activity at their receiver sites (Kalsbeek, Palm, et al. [2006]). These outputs are not general purpose. They consist of projections from specific output regions of the SCN to activity-specific receiver systems (Evans et al. [2015]; Kalsbeek, Palm, et al. [2006]; Kalsbeek, Perreau-Lenz, et al. [2006]). Furthermore, the causal properties of these signals do not change depending on when they are produced. Whenever these subregions reach their "on" phase, they emit a specific packet of neurotransmitters to their receiver systems, and then the receiver initiate a fixed response (Kalsbeek, Palm, et al. [2006]). For instance, the SCN output region controlling melatonin production will produce the same combination of GABAergic and glutamatergic outputs whenever it reaches its "on" phase, and a fixed homeostatic activity is initiated in response.

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[12] Several philosophers have discussed how the circadian system carries time of day information (Bechtel [2011]; Viera [2020]). Neither author, however, discusses what the outputs of the circadian system conveys to downstream systems. Bechtel ([2011]) is concerned with articulating a role for representational explanations in dynamical systems. Viera ([2020]) is concerned with an architectural claim about whether we have sensory systems for time.

While the shell was originally thought of as simply an output component of the SCN, the shell, including these output regions is implicated in the operation of the SCN as a whole, through reciprocal interactions with the core (Evans et al. [2013]; Yan et al. [2007]). The output regions of the SCN cannot be isolated from the timekeeping mechanism since their activity partly constitutes the timekeeping capacity of the SCN as a whole.

If an animal's needs and environment are stable, then their SCN will produce specific outputs at the same time everyday to coordinate their actions with this stable environment. Therefore, the specific SCN outputs would transmit information about time of day since they would appropriately correlate with specific times and receiver systems are sensitive to these outputs. Putting the point in epistemic terms, observing the SCN outputs would allow us to know what time it is.

However, animals do not live in fixed environments. As seasons pass, or animals migrate, day / night patterns change. Food can be restricted to different times of the day. Novel stresses might also be encountered. In all these cases, animals must adapt their behaviour to meet the timing of their environment. This coordination is not achieved by changing *what* the SCN outputs. What is released stays the same. Rather, this coordination is achieved by adjusting *when* the SCN produces its outputs (Riede et al., 2017). The dynamics of the SCN adjust so that the SCN output regions reach their "on" phases at the correct moment in the day (Kalsbeek, Palm, et al. [2006]; Meijer et al. [2010]; Riede et al. [2017]).

As a result of this flexibility, SCN outputs do not transmit unambiguous time of day information. Any given SCN output, for instance signals that control melatonin production, body temperature regulation, etc., can co-occur with multiple times of day. Depending on the analysis of the probabilities involved, SCN outputs will at best carry ambiguous, or disjunctive, information about various times of day. However, the adaptiveness of any circadian behaviour is not explained by the behaviour occurring *at some point* during the day. Rather, the adaptiveness is due to these behaviours occurring at specific times of day. The informational content of the signals produced by the SCN are not adequate for accounting for the success of the sender-receiver coordination.

While the SCN outputs do not carry, and therefore cannot transmit, time of day information, the SCN as a whole nevertheless does. Despite the local shifts as to when SCN output regions reach their "on" phases, the SCN as a whole exhibits a stable 24-hour rhythm throughout these local changes (Hafner et al. [2012]; Meijer et al. [2010]). As mentioned above, the details of this process are still largely unknown, but through various means individual SCN cells constrain the activity of their neighbours, thereby leading to synchronized modules, that in turn influence other networks, and which, in conjunction to external calibrating influences, ultimately gives rise to the global behaviour of the SCN (Evans et al. [2013]; Hafner et al. [2012]; Yamaguchi et al. [2003]; Yoshikawa et al. [2021]). Therefore, there is a loss of information between the states of the SCN as a whole and its outputs. Information about time of day does not flow beyond the SCN. In the rest of the section, we will consider five attempts to preserve the idea that circadian systems involve the transmission of time of day information.

OBJECTION #1: One could object that token SCN outputs necessarily carry time of day information, since they necessarily have the indexical property of *having been produced at a specific time* which perfectly co-varies with a time of day. However, whether a signal has that property or not has no causal influence on receiver systems, and therefore, any information carried by that property instantiation cannot be transmitted by the signal. Similar points arise for other historical properties of token SCN outputs. A token signal possessing the property of *having been produced by an appropriately calibrated SCN* might carry information about the time of day, but this historical property has no causal influence on receiver actions. This history is screened off from the causal properties of the output.

OBJECTION #2: Another objection is that the analysis so far has treated SCN outputs as *simple* signals. However, as is the case in many signalling systems, a single ambiguous signal may be disambiguated

in conjunction with some contextual signal. Perhaps SCN signalling is like this. In isolation, a given SCN output is ambiguous with regards to time of day, but receivers may also receive an additional contextual signal that disambiguates this time of day signal. While this objection is correct, in that if there were such a contextual signal, we may uncover time of day signals in the operation of the SCN, yet, as far as we know there is no such contextual signal to which receiver systems are sensitive. Not even internal states of the receivers will do, since these are not tied to specific times of day, but rather, to the preparedness to perform certain actions (see below and next section).

OBJECTION #3: A fourth objection might account for SCN outputs having time of day content by initially assigning them imperative contents. SCN outputs most closely co-vary with the specific actions they initiate. SCN outputs might be understood as commands. They may be action specific, "Produce melatonin!", or they may be general, "Go!". The adaptive values of such signals will be tied to whether the world is appropriate for the animal's engaging in these activities. The command, "Produce Melatonin!", is adaptive just in case the conditions for sleep are satisfied, so it can be understood as also signalling "the conditions for sleep are satisfied". There is an interplay, then, between a signal's imperative contents and a corresponding descriptive content. [13] However, this connection between imperative contents and descriptive contents will not get us time of day content. Since these commands are action specific, and they can be issued at different times of day, there is no link between the issuing of a command and its being a certain time of day. Rather, the descriptive contents that we would derive are action specific. Of course, one could try to take this result as forcing us to abandon the idea that the SCN represents time of day, however, in the next section I will argue that the SCN represents time of day, so this option will be closed.

OBJECTION #4: In order to apply the sender-receiver framework to a system we first need to determine what the relevant senders, receivers, and signals might be. This objection is that the analysis so far has incorrectly assigned sender or receiver roles. Could the relevant signalling be occurring entirely within the SCN?

Could we consider the SCN core as a sender that transmits time of day information to the shell? Conceiving of the core as the sender and the shell as the receiver does not salvage the idea that time of day information is transmitted. Models of the interconnectivity within the SCN point to an interplay between the shell and core that allows for a reliable timekeeping mechanism (Herzog et al. [2017]; Pilorz et al. [2020]). The core itself is not the clock. The core itself does not have epistemic or informational access to the time of day without the shell. It is the SCN as a whole that plays that role. The core alone was not the relevant sender in the establishment of circadian behaviours, it was the SCN as a whole. Furthermore, given the ongoing reciprocal interaction between the shell and core, these mediating signals likely do not appropriately co-vary with the time of day in order to carry time of day information. That information, again, is found at the level of the entire SCN.

A variant of this objection is that we should take the SCN as a whole to be the sender and the output subregions of the SCN as the receiver. Since the SCN as a whole carries time of day information, the SCN as a whole could be interpreted as sending signals with time of day content to these output subregions. Since signalling is a causal notion, this objection requires that the SCN as a whole can causally influence its parts.[14]

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[13] An interplay of this sort is found in (Millikan [1995]). Thank you to a referee for pointing this out.

[14] If this causal relationship is understood in terms of a leveled ontology, then we run into a debate within the mechanisms literature. Many have argued that interlevel causal relationships are impossible. According to some, the worry arises due to the nature of causation. Causes are necessarily distinct from their effects, yet a mechanism engaged in some activity is not a distinct event from the activity of the lower-level entities that constitute that mechanism. Therefore, there cannot be interlevel causation within a mechanism since these levels are not appropriately distinct (Craver & Bechtel [2007]; Glennan [2010]). According to others, the nature of the constitution relation and its reliance on Woodwardian interventionism renders interlevel causation impossible

An ontologically neutral way of understanding the mechanistic structure of the SCN is to consider it as a *flat mechanism* (Bechtel [2017]; Eronen [2013]). Apparent cases of top-down causation within a mechanism are explained away as intra-level causal relationships between elements that constitute the mechanism. On this approach, we can think of the constitution of the mechanism in graph-theoretic terms. Individual SCN cells act of nodes within the network. Each cell exhibits oscillatory behaviour driven by the internal molecular feedback look described above. These cells form localized modules in which the cells within those modules are synchronized. Nodes within a module are highly interconnected and have sparse connections to nodes in other modules. The SCN output regions are modules specified at this intermediate scale of organization. Nearby modules are not synchronized, and as their distance increases, their average phase shift also increases (Yoshikawa et al. [2021]). These modules are then, somehow, orchestrated in such a way that gives rise to the overall oscillatory behaviour of the SCN as a whole.

The suggestion, then, would be to take the output module as the receiver and take the rest of the overall mechanism, the assortment of different modules, to be the relevant sender.[15] Since the mechanism as a whole carries information about time of day, then could not the causal influence of the rest of the mechanism on the output region signal time of day?

While many of the details of how SCN modules interact are still unknown, we do know that this interaction seems to be local (Evans et al. [2013]). Individual cells have to be in close spatial proximity to synchronize. Through computational modelling, this synchronization seems to be a function of the density of interconnections between individual cells (Yoshikawa et al. [2021]). How then are phase relations maintained across modules? While the details are not worked out, it is known that VIP and GABA$_A$ work together to synchronize and desynchronize regions of the SCN. Importantly, VIP and GABA$_A$ do not seem to have fixed influences on synchrony. Rather, if cells & modules interact with these transmitters during particular parts of their daily cycles, then these transmitters will aid or inhibit synchronization (Evans et al. [2013]; Hastings et al. [2018]).

With those facts in hand, we can see that the behaviour of the output systems can depend on the overall timekeeping capacity (or overall state) of the SCN, without the need for time of day information to be signalled within the SCN. One way to think of this is in terms of the global network properties of the SCN constraining local operations.[16] Considered in isolation, any given cell or module can exhibit a high degree of variability in its activity patterns. However, the global network properties of the SCN limit this variability, without determining local oscillatory properties, in the same way that the shape of a vessel places constraints on the movement of molecules inside of it (Juarrero [2009]). If the SCN no longer tracked time of day, then the relevant constraints on the operation of the constituent modules would be removed, and they would begin to drift or behave arrhythmically. Yet, the global constraints filter down into increasingly local constraints enacted by VIP and GABA$_A$ release. These molecules can be released at different times of day by any given module, and it is through their interaction with the internal state of the module that they constrain (within certain limits) the intrinsic oscillation of the module (Bechtel [2017]). The action of individual modules is sensitive to the overall timekeeping

since you could never intervene on the mechanism or its part without also intervening on the other level (Baumgartner & Gebharter [2016]; Gebharter [2017]; Romero [2015]). Other worries concern the epiphenomenal nature of the higher-level mechanism due to causal exclusion worries (Kim [2005]). In contrast, some have argued that if we reconceive of the constitution relation and provide an account of diachronic levels, then we can salvage a notion of inter-level causation (Kaiser & Krickel [2017]; Krickel [2017]; Leuridan & Lodewyckx [2020]). To avoid these worries I will put this objection in terms that do not presuppose a leveled ontology and instead adopt a flat conception of mechanisms (Bechtel [2017]; Eronen [2013]).

[15] The output region is being excluded from the sender since this would result in problematic self-causing loop.

[16] It is a question whether constraints in neuroscience should be understood as causal factors (Ross [forthcoming]).

behaviour of the SCN, since it constrains the pattern of activity throughout the SCN, but this need not involve within SCN time of day signalling.[17]

One final variant of this objection is to take the influences on the output region as an ambiguous signal that is disambiguated by the internal state of the SCN output region. However, if this is the strategy, then we lose the distinction between signal and receiver since the contextual signal within the receiver is just the receiver's activity. It is unclear how this could be a sender-receiver scenario if there is no epistemic / informational asymmetry to be overcome.

We can apply the sender-receiver framework to the SCN's internal structure, and there is interesting work to be done here to better understand how SCN-internal signalling gives rise to the network properties of the SCN, but this need not involve time of day signalling.

OBJECTION #5: Finally, could the SCN outputs be interpreted as misrepresenting the time of day? In the analyses of misrepresentation described above, the content of a signal is tied to those state of affairs that the signal has the function of indicating. However, since the SCN outputs are not tied to times of day, but instead to behaviours, the signals would seem to have action-specific contents. Furthermore, rampant misrepresentation is often taken to be maladaptive. But the flexibility of the SCN outputs is exactly what allows for adaptive coordination with the environment. The outputs of the SCN do not seem to be misleading their receivers.

The section should not be read as a criticism of the sender-receiver framework. The goal of this section has been to apply the sender-receiver framework and note that the SCN does not produce signals that carry time of day information. In the next section, I will argue that the SCN represents time of day. Therefore, there will be basic representational capacities not captured by the sender-receiver framework.

5 Representing time of day

This section's goal is to establish that the SCN represents the time of day. Given the paper's dialectic, if this conclusion were argued for on the basis of an alternative theory of content, then the conclusion would beg the question against the sender-receiver approach to representation. Instead, the argument must occur on common-ground shared with the sender-receiver theorist. To build this common ground, we will focus on what Ramsey ([2007]) calls *the job description* of mental representations. Any adequate theory of mental representation must specify what role representations play in our explanations of psychological phenomena. It is here where we find our common ground.

While no answer to the job description question is universally accepted, several attempts exist in the literature (Fodor [1980]; Neander [2017]; Ramsey [2007]; Rupert [2018]; Shea [2018]; Sprevak [2011]). Despite their differences these answers share a common core. Representations are entities that act as *proximal surrogates* or *stand-ins* for aspects of the world that are not directly available to cognitive systems. Their standing in for specific aspects of the world, their having content, is closely tied to explaining the role those representations have within the cognitive system. At the core of the sender-receiver approach to mental representation is the conjecture that signals, not senders or receivers, are what act as stand-ins for states of the distal world.

By the sender-receiver theorist's own lights, the SCN itself is a representational system representing the time of day. However, it is the states of the SCN itself, not its output signals, that play the appropriate stand-in role. Therefore, we would have a representational capacity that does not fit the sender-receiver analysis.

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[17] The reasoning here ultimately depends on future empirical investigation. However, the point is that time of day signaling is not needed for this interaction.

Recall the coordination problem that sender-receiver systems overcome. Senders have epistemic access to the world but can only act by producing signals. Receivers lack the relevant epistemic access but can act on the world. The sender controls the receiver by producing signals that cue receiver responses that are appropriately coordinated with the world. According to the sender-receiver theorist, the informational content of the signal explains how receiver actions are coordinated with the world and how sender-receiver strategies are stabilized.[18] Representations, then, are just those aspects of the sender-receiver system that play a role in stabilizing sender-receiver dynamics in virtue of their *standing in* for the relevant state of the world. It is this role in coordinating sender-receiver activities that Godfrey-Smith ([2014]) has acknowledged as being one of the central insights of the sender-receiver framework. As we will see, however, it is not just signals that can play this coordinating role.

Compare two explanations for circadian behaviours. Alligators might appear at a location around the same time every day to feed on fish scraps left by incoming fishing boats. This could be explained by appealing to an internal timekeeping mechanism. However, in some cases no timekeeping mechanisms are involved. The alligators may have associated the sound of incoming boats with food. Since the boats are on a regular schedule the alligators' behaviour will exhibit a regular schedule. Since the boats arrive at the same time every day, then the alligator auditory responses to the boats will carry information about the sound sources but also information about the time of day (since the auditory responses covary with both). However, the time of day information plays no role in stabilizing alligator behaviours. If the boats fail to appear, or sound differently, the alligator behaviour will not be triggered. If the boats begin to appear at a different time of day, then the alligator feeding behaviour would shift to that time of day. The success of the alligator behaviour is due to their auditory responses tracking the boats and not the time of day. Time of day information is, as it were, accidental.

However, as noted above, many circadian behaviours persist in free running conditions. Something internal to the organism has to be coordinating animal behaviours with the right time of day. The SCN plays this role in mammals. The rhythms of the SCN allow the SCN to carry information about time and the SCNs output allows the organism to control *when* it engages in certain activities. The SCN plays the role of a sender in the sender-receiver framework since it has behaviourally relevant information that downstream systems lack. However, this does not show that the SCN is a representational system. What is needed is to show that these states of the SCN stand in for the time of day, in that their carrying this information stabilizes the sender-receiver strategies. If that is shown, then by the sender-receiver theorist's own lights, the SCN is representational.

Like the auditory responses of the alligator, states of the SCN, and states of its subregions, carry information about aspects of the world other than time. For instance, states of the subregion controlling body temperature regulation carry information about the likelihood of heat stresses in the environment (as in the Maruyama et al. study). Similar claims can be made of the SCN as a whole. In a study by DeCoursey et al. ([2000]), SCN-lesioned chipmunks and SCN-intact chipmunks were released into the wild. The SCN-lesioned chipmunks were arrhythmic and as a result of being active at night were killed by predatory weasels at a much higher rate than the SCN-intact chipmunks. The states of the SCN-intact chipmunks, therefore, carried information about weasel activity (since the states co-varied with weasel activity). Similar claims can be made about SCN subregions. If we focus on individual receiver behaviours and ask what information carried by the SCN stabilizes that receiver's responses, then we will be able to point to action-specific information. Why is body temperature regulation adaptive *now*? Time of day is only accidental. What matters is whether there will be a heat stress. Information about time is not needed. Focusing on individual cases renders time of day information accidental.

The situation changes when we notice the artificiality of focusing on the adaptiveness of individual circadian behaviours. The SCN as a whole functions as a reliable means of coordinating a range of

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[18] See (Ganson [2018]; Shea et al. [2018]) for accounts that specify content by appeal to functions as opposed to information.

activities with the time of day (Herzog et al. [2017]; Meijer et al. [2010]; Pilorz et al. [2020]). It is the very same SCN rhythm, grounded in the interaction of its many parts, that controls how various circadian behaviours are coordinated with the time of day. If we want to know what the SCN is doing, then we need to consider its role in governing this range of behaviours, not individual behaviours.[19]

Does the SCN's carrying of information about heat stress, predator behaviour, food availability, or any other specific activity, explain why other activities controlled by the SCN are adaptively coordinated with the environment? No information about weasels, for instance, explains the success of an animal controlling its body temperature (except insofar as this plays a role in weasel-related activities). If weasels are not present in the environment, say they are wiped out by an invasive species, then whether or not the SCN is properly tracking weasel activity says nothing about whether other behaviours can properly be coordinated with the environment. Similar points can be made with regards to each action-specific environmental condition that the SCN carries information about. Those action-specific states of the world do not help us understand how other SCN controlled behaviours are adaptively coordinated with the environment. The same point can be made by considering what happens to behaviours when the SCN undergoes a global phase shift (perhaps as the result of controlled light exposure) (Canal & Piggins [2006]; Renner [1960]). In these cases, if a single behaviour is shifted so that it is performed earlier in the day, then other circadian behaviours will undergo a similar phase shift. These shifts are global in character. Just as time of day information did not explain the alligator behaviour in the prior example, action-specific information does not explain circadian behaviours.

It is the SCN's ability to keep track of time that explains the adaptive coordination of circadian behaviours. The SCN governs *when* actions should occur. While we could answer the question, "when should I sleep" with "when weasels are active", we could not use this to guide action if there are no weasels or if we lacked informational access to weasel activity. Instead, the SCN has informational access to the time of day and this information governs when certain SCN outputs are produced. The global state of the SCN stands in for time of day since it is this content that best explains circadian behaviour.

We have landed in a peculiar situation. The SCN carries information about time of day, however, as I argued earlier, this information is not transmitted to receiver systems. Time of day information does not flow through the SCN to its receiver systems. How then does the information about time of day in the SCN have any influence on receiver systems? Why is the information not inert? To see how information carried by the SCN, but which is not transmitted, influences receiver behaviours, let us consider the following scenario: A parent needs to get their children to do certain tasks at specific times of day, for instance, get ready for school, soccer, walk the dog, etc. These children, for whatever reason, are not able to keep track of time – they are either too young or absent-minded. Instead, it is the parent's task to keep track of time and coordinate the children's actions. There are two ways that the parent might achieve this coordination.

In scenario 1, *the broadcasting scenario*, the parent periodically announces to their family what time it is. At 7:30AM, they yell "It's 7:30!", at 2:30PM, they yell "It's 2:30!", etc. In this scenario, the parent coordinates their children's behaviours with the time of day by sending signals to their children that carry time of day content. It is up to the children to utilize these signals, in combination with an understanding of when they need to perform actions, to then perform the correct action. If the child can do this, then the parent's signalling actions will achieve the right outcomes.

In scenario 2, *the conductor scenario*, the parent does not announce the time of day. Instead, they simply tell their kids to do certain tasks at the appropriate time of day. At 7:30AM they tell their children, "school!", at 2:30PM they say, "soccer!", etc. The parent says nothing about the time of day (perhaps

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[19] Notice that this point is not generalizable to the brain as a whole. Localized damage to the brain often leads to specific impairments. Damage to the SCN leads to global circadian deficits.

soccer practice times vary from day to day as well, so the calls carry no precise information about time of day). The children also do not need to know what tasks to perform at what time of day (or perform inferences over the tasks they need to perform and the current time of day). Rather, the signals function to initiate certain actions. By keeping track of time and issuing their commands at the correct time of day the parents are able to successfully coordinate their children's behaviours.[20]

Both scenarios overcome the type of coordination problem that the sender-receiver framework is meant to. The parent has epistemic access to the time of day. The children do not. And the parent coordinates the children's behaviours with the time of day. While only scenario 1 involved the transmission of time of day information both scenarios have the same results. Yet even in scenario 2, the conductor scenario, we can see that time of day information still plays a role in the coordination of the children's behaviours.

The parent in the conductor scenario coordinated their children's activities not by issuing commands that communicated time of day, but instead, by altering *when* those commands were issued. It was not temporal content carried by the signals that did the work, rather, it was the temporal properties of the signals themselves.[21] If the parent could not keep track of time, then they would not be able to issue their commands at the correct time, and therefore, the behavioural coordination would be impossible. Information is used by the sender system, but not transmitted. If the information were absent the receiver behaviours would not be coordinated with the environment, and no sender-receiver behaviours would stabilize.[22]

The SCN controls downstream activities in way that is similar to the conductor scenario. It coordinates receiver actions with the time of day by controlling when its outputs are produced. If the SCN were unable to keep track of time, then it would not be able to properly produce its outputs at the correct time, and the relevant behaviours would not be adaptively coordinated with the environment. Furthermore, given that the SCN coordinates the timing of various different systems, it does not derive its usefulness in the system as a result of any action-specific information. It is the information it carries about time that explains the role that the SCN has in the overall system. Misrepresentation occurs not because the SCN sends false signals, but rather, when the SCN fails to keep track of time. Receiver behaviours would be produced in response to faulty signals just as though the system were tracking time, since it is the tracking of time that stabilized the SCN's signalling behaviour and the receiver responses. Receivers make use of time of day information carried by the SCN by being recipients of outputs produced by a properly calibrated SCN.

According to the sender-receiver theorist, the states of the SCN play a representational role. SCN states act as stand ins for an aspect of the world, time of day, that receiver systems do not have access to. It is in virtue of standing in for these states that we explain why senders and receivers act in the way they do to produce adaptive behaviours. The sender-receiver theorist was mistaken in claiming that meaningful signalling was the only way of grounding basic representational capacities. Information can be made use of without communicating that information and senders (or their states) can be bearers of representational content.

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[20] There is a disanalogy between this case and the SCN. The parent utilizes a watch that is distinct from mechanisms that are utilized to issue the command. Therefore, if it were not for the time of day signal from the watch the parent would fail to produce their commands at the correct time. However, within the SCN there is no distinction between the clock and the output mechanism. The output mechanisms partly constitute the clock. The important similarity is that in both cases, a system can coordinate the activities of another with the time of day without issuing signals with time of day content.

[21] A similar point is made by Krebs and Dawkins ([1984]). Content free signals can drive behavior. Their formal properties can suffice. While Dawkins and Krebs take this to show that content plays no role in these scenarios, the circadian case is one in which information plays an explanatory role.

[22] It is awkward to say that the parent is a representation. In this way, the analogy is only illustrative since the case for the SCN is less awkward.

6 Controlling without communicating

The SCN coordinates receiver behaviours without transmitting time of day signals to its receiver systems. We also have reasons for thinking the states of the SCN represent time. Therefore, we have a representational capacity of the very type sender-receiver theorists took their framework to account for, which does not fit the framework.[23]

If this conclusion is correct, then we seem to run into another problem. The scientific term, 'representational system' would seem to pick out two distinct types of system – signal-based representations (those amenable to the sender-receiver analysis) and sender-based representations (those described here). Representations, as a kind, would be split. However, we can avoid this conclusion by noting that there is a unified characterization of representational capacities, in terms of control, that captures both signal-based representations and sender-based representations.

At the core of the sender-receiver framework was the notion of control (Godfrey-Smith [2014]). Senders control receiver actions by providing them with signals that allow them to perform actions that are properly coordinated with the world. In the simplest case, like the one found in the case of the SCN, receiver systems are simple in the sense that each receiver produces a single response.[24] The sender need not choose which signal to send, since the receiver has a fixed response. However, if the receiver has more than a single action available to them, and those actions are appropriate in difference circumstances, then the signals produced by the sender must allow the receiver to choose the appropriate action from their repertoire. In this case, information about the state of the world must make it to the receiver since the signals must track these states of the world. When the receivers are sufficiently complex, then the appropriate control of receiver behaviour requires a sufficiently complex repertoire of signals. In this scenario, control requires meaningful signalling. If, however, the receivers are simpler, then meaningful signalling is not needed. Furthermore, since it is the informational content of the signals that is playing the relevant coordinating role, then we have reasons for assigning representational content to the signals themselves, and not the sender states. The signals act as the relevant stand ins.

It is control on the basis of information in the context of epistemic and practical asymmetries that is fundamental to understanding representations in biological systems. In this way, sender-based and signalling-based representational capacities are sub-types of the same scientific kind. Informative signalling arises out of this more fundamental notion when the receiver is sufficiently complex. The sender-receiver framework provides us with insight into the nature of representation.[25]

Author Department: Department of Philosophy

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[23] A sender-receiver theorist could deny that the circadian system is representational, but the onus would be on them to explain why without begging the question.

[24] These are similar to what Barrett and Skyrms ([2017]) called cue-reading games, however, in our case, the sender role is more complex.

[25] The position developed here is similar to that developed by Shea (2018). There are various ways for a system to have the appropriate informational and functional properties needed to count as representational.

Author Institution: University of Sheffield

Author City, Country: Sheffield, UK

Author Email: g.viera@sheffield.ac.uk

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