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Representing Time of Day in Circadian Clocks

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Positing representations and operations on them as a way of explaining behavior was one of the major innovations of the cognitive revolution. Neuroscience and biology more generally also employ representations in explaining how organisms function and coordinate their behavior with the world around them. In discussions of the nature of representation, theorists commonly differentiate between the vehicles of representation and their content—what they denote. Many contentious debates in cognitive science, such as those pitting neural network models against symbol processing accounts, have focused on the types of *vehicles* proposed for mental representation and whether they have the appropriate structure to succeed in bearing their contents. Philosophers, in contrast, have focused their debates on *content* and the particular way in which vehicles might bear content—that is, the process of representing rather than the format of representations. I will offer a novel answer to the question of how it is that a representation has content by focusing on the architecture of representation. My proposal is that representations occur in a particular type of mechanism—one in which a control system regulates a plant—and that we can gain traction on cognitive systems of representation by considering how this works in physical systems more generally.

Questions of representation, especially with respect to the content of mental representations, have a long and rather inconclusive history in philosophy. The simplest construal of content will be sufficient for my purposes here, namely, that the content of a representation is what it refers to, typically something in the external world. More challenging is the question of how representations come to have content. Philosophical accounts have tended to approach the problem in one of two ways. The first approach, seeking to capture the idea that representations carry information about what produced them, focuses on the role of the referent in generating the occurrence of the representation (Dretske, 1981). One challenge is that representations can misrepresent by being about something other than what caused their occurrence. This led Brentano (1874) to suggest that intentionality (the relation between a representation and its content) is not a proper relation; others, though, have proposed a variety of solutions that preserve treating representing as involving a relation to a content. The second approach focuses on the consumer of the representation—the entity or system that uses the representation to secure information about its referent. The challenge for this approach is specifying what the system is treating as the content. A major proponent, Millikan (1984), appeals to natural selection to settle this question: the representation has a particular content because it was selected for its success in representing that content. Such an appeal to natural selection to ground representations has been challenged by Fodor (1990), who proposed his own alternative, and active debate continues among advocates of these various ways of explaining how representations have content.

In this paper I will not enter into the details of this debate, but advance an alternative account that situates both the focus on information and that on the consumer in a context that is actually

motivated, ironically, by theorists who present themselves as rejecting appeals to representations in understanding the mind. Advocating a dynamical approach to cognitive science, van Gelder (1995) argued that, just like a much simpler dynamical system—the steam engine governor designed by James Watt—mental systems perform their tasks without representations. I concur with van Gelder that the Watt governor is a more productive model for understanding cognitive systems than is the digital computer widely invoked by theorists advancing representational accounts of the mind. But I will further argue that, properly understood, the Watt governor employs representations. The Watt governor is a control system, and like any other control system must employ representations to perform its task. A control system is part of a larger system and is specialized to regulate the behavior of other parts of that system. Often the part performing the control function is called the *controller* and the parts it controls the *plant*. The controller has internal operations that, when the system is functioning correctly, carry information about parts of the plant or entities or processes external to the plant that affect it. This information, whether it misrepresents or accurately represents actual states or activities, is used by the controller to regulate the plant's behavior.[1]

My main objective is to illustrate the value of thinking of representations and their content from this perspective. Rather than starting with representations as they might figure in cognitive accounts of activities such as reasoning or memory, though, I will focus on representations as described in neuroscience (and biology more generally), where we can more readily gain traction in accounting for their content. Neuroscientists have long characterized the brain processes they study as representational, but have left implicit the reasons for bringing in talk of representations. In the first section I note highlights of research on the primate visual system and show that the assumed framework is that of Dretske, according to which a neural process represents the stimulus that caused it. Neuroscientists are well aware, though, that neural processes may misrepresent stimuli; for example, in cases of illusions they characterize the mind as representing what the organism takes to exist in the world (vs. what actually exists). The framework of control theory provides a way of understanding this practice, so in the second section I take up the challenge posed by the dynamicists by showing how control systems require representations, albeit ones understood dynamically. In the remaining sections, I illustrate the control theory approach to understanding representations by focusing on a specific example: the circadian clocks by which organisms represent both time of day and the length of daylight (the photoperiod). Circadian clocks are physiological oscillators with a period of approximately 24 hours localized within individual cells (although often involving coordinated interactions among those cells). Research has revealed not only the basic mechanisms operating within cells as circadian clocks, but also has begun to shed light on how they can be entrained by time and length of day and can be used by other systems within the organism to regulate behavior that depends upon time and length of day. I will not in this paper be able to extend the account into more cognitive domains, but presume that if an account succeeds in explaining how neural processes such as those involved in controlling circadian behavior have content, it can be

[1] An advantage of this approach over that of Millikan is that it obviates any need to appeal to the history of the system to evaluate what are representations. If a system has a controller within it, the operations that carry information in that controller are representations, regardless of whether such processes were the product of selection at some point in the past. That is, even if a controller evolved via drift or some other non-selectionist process, its internal states count as representations. Whether something is a representation is a question about the role it plays within a system (does it figure in control processes?), not about its history.

extended to the processes the brain employs when engaged in tasks that are more clearly cognitive such as problem solving and making evaluative judgments.[2]

1. The Widespread Use of Representations in Neuroscience

In the 19th century, researchers began trying to localize responsibility for control of motor and sensory processing in the brain. Gall (1812) was an early pioneer, but his contemporaries severely challenged both his criteria for localization (correlations between the size of brain regions and behavioral propensities) and his implementation (using skull protrusions as a proxy for the size of a brain region, and positing correlations impressionistically rather than quantitatively). This led researchers in subsequent decades to be skittish about advancing similar claims. Broca's (1861) linkage of acquired speech impairments to lesions in an area of left prefrontal cortex—later known as Broca's area—rejuvenated the project of localizing control of specific behaviors or mental abilities in particular regions of the brain. This was opposed by Wernicke (1874), who focused instead on connections between primary sensory and motor areas in explaining normal and pathological conditions. But even proponents of this associationist approach, such as Hughlings Jackson (1884), spoke of the brain as representing and re-representing features of the world.

Localizationist research gave rise to the positing of representations in the brain as researchers began to identify specific brain regions responsible for particular kinds of sensory processing or motor control. Vision researchers, for example, initially simply sought the locus where visual information was processed in the brain. Relying on both lesion studies and electrical stimulation, Ferrier (1876) argued for a locus in the angular gyrus, whereas Munk (1881) defended a locus in the occipital lobe that had earlier been distinguished by its pattern of striation and would later be known as the striate cortex. A variety of investigatory strategies soon settled the issue in favor of striate cortex. As techniques were refined, though, researchers began to investigate which parts of striate cortex responded to which parts of the visual field, treating it as embodying a map of the visual field. Henschen (1893) offered the first account of such a map, although ironically his proposal reversed the pattern of projection supported in subsequent research by Inouye (1909) and Holmes (1918).

The characterization of areas of cortex as possessing a map of the visual world clearly adopts a representational perspective, and the quest to specify maps became a major pursuit of neuroscientists in the 20th century. With the development of single cell recording techniques, investigators such as Talbot and Marshall (1941) began to focus on individual neurons. Following a strategy used in the retina and LGN by Kuffler (1953), Hubel and Wiesel (1962, 1968) investigated what features of a sensory stimulus would drive cells in striate cortex. Their

[2] Vogeley and Bartels, this volume, advocate a functional role account of representation, contending that it best fits the practice of cognitive neuroscience research. I would argue that a functional role account is not an alternative to the control theoretic framework I offer here, or even to accounts that emphasize just the causal processes generating representations or their consumption, but rather is appropriate in analyzing control systems, such as cognitive systems, in which multiple representations are deployed in complex relations to each other so as to regulate the plant. In such situations a major task in the analysis is to understand how the various representations relate to each other. However, if the whole system of representations is not grounded in causal connections to what is represented and is not employed in regulating behavior, then it is not clear why the different roles within a system serve a representational function.

discovery that simple visual features (oriented lines, stationary or moving in a particular direction) would elicit responses from specific cells in striate cortex, and that cells that responded to different features of a given stimulus were organized together within a column, led them to propose that information represented in one set of cells was further processed in others:

> We may tentatively look upon each column as a functional unit of cortex, within which simple fields are elaborated and then in turn synthesized into complex fields. The large variety of simple and complex fields to be found in a single column suggests that the connexions between cells in a column are highly specific (Hubel & Wiesel, 1962, p. 144)

They also observed that this processing of oriented lines is "a very elementary stage in the handling of complex forms" and identified as a question for the future "how this information is used at later stages in the visual path" (Hubel & Wiesel, 1968, p. 242).

Hubel, Wiesel, and others soon discovered that these later stages involved additional maps in occipital, temporal, and parietal cortex. Combining information from earlier stages in different ways, neurons in these areas analyzed visual stimuli in terms of such features as color, shape, direction of motion, and identity of objects (see Bechtel, 2008, for details of this history). A similar history led to the identification of motor (Leyton & Sherrington, 1917) and somatosensory (Penfield & Boldrey, 1937) maps as well as tonotopic maps in auditory processing areas (Woolsey & Walzl, 1942).[3] The advent of tools such as fMRI later fostered the discovery of maps in more anterior brain areas, notably those involved in attentional and working memory tasks (Sereno, 2001; Hagler & Sereno, 2006).

In this section I have described how neuroscientists seek to identify representations, especially maps, in the brain. Typically they do not elaborate on foundational issues, such as what it means to be a representation, what kinds of neural data license what kinds of inferences regarding representations, and the implications of these inferences and of representation talk more generally. Despite their reticence, it is fairly clear that neuroscientists' approach is guided by the assumption Dretske articulated, according to which a process is presumed to carry information about its causes. Thus, techniques such as single cell recording and fMRI proceed by presenting stimuli (experimenter-designed causes) to the organism and recording of the resulting activity in the brain. Neural maps are inferred from the correspondences found between the topology of the sensory field and that in the resulting map. Seldom as explicit as in Hubel and Wiesel's papers, but sometimes implicit, is a thorough-going analysis of how certain downstream brain areas act as consumers of these maps, typically by deriving from them more specialized maps, but sometimes instead using them to determine behavioral responses. In one of the most impressive studies pinning down a representational function in the brain, Britten, Shadlen, Newsome, and Movshon (1992) established the role of MT in representing motion by combined three kinds of data: (a) deficits in perceiving motion after lesions to MT; (b) single cell recording from MT during the presentation of motion stimuli; and (c) microstimulation of MT designed to bias a monkeys' response to perceiving ambiguous motion displays. In their single-cell recording experiments the researchers were relying on the causal relation to the stimulus, while in appealing to the monkey's perceptual responses the researchers were targeting the consumer of this information.

[3] As in the case of vision, the discovery of one map was soon followed by additional maps. A second somatosensory map was identified by Woolsey (1943), and multiple auditory areas were discovered by Merzenich and Brugge (1973).

2. Dynamicists' Objections to Representations and the Control Theory Framework

Beginning in the 1990s, cognitive scientists' and neuroscientists' practice of ascribing representations has been challenged by theorists advocating dynamical systems accounts of cognitive activity. Sometimes these criticisms have focused on representations involving specific types of vehicles, notably the language-like representations employed in symbolic theories. But often the critics have targeted anything that might be construed as a representation. Van Gelder addressed his challenge to "pretty much any reasonable characterization, based around a core idea of some state of a system which, by virtue of some general representational scheme, stands in for some further state of affairs, thereby enabling the system to behave appropriately with respect to that state of affairs" (van Gelder, 1995, p. 351). The maps advanced by neuroscientists clearly fall within the scope of his challenge. To point the way towards accounting for cognition without appealing to representations, van Gelder presented the centrifugal governor that James Watt devised for the steam engine, which van Gelder maintains is "preferable to the Turing machine as a landmark for models of cognition" (p. 381).

The governor is designed to regulate the flow of steam powering an engine such that the engine maintains as constant a speed as possible despite intermittent variability in load (e.g., from commercial sewing machines driven by the engine). Its key components are a spindle and two attached arms, each hinged with a heavy ball at the end. The left side of Figure 1 shows how one end of the governor is linked to the throttle valve used to modulate the supply of steam to the engine cylinder and the other end is directly connected to a flywheel or equivalent device. (This vintage diagram omits the rest of the engine, including the cylinder, the piston, and the output shaft and belt that drive the flywheel. Absent this primary mechanism, there would be nothing for the governor to govern.) At each moment the current engine speed is translated via the flywheel to the spindle and its attached arms. When the engine and hence the spindle speed up, centrifugal force drives the balls outwards, which increases the angle of the spindle arms, which lowers the arm of the linkage mechanism, which is attached to the valve such that it partly closes. With less steam being supplied, the engine slows down. Conversely, when the engine slows down (due to this regulatory effect, fluctuations in the supply of steam, increased resistance in the machinery, etc.) there is less centrifugal force. This lowers the balls, which decreases the angle of the spindle arms, which raises the linkage arm, which partly opens the valve, which increases the flow of steam, which speeds up the engine. There is, thus, a tight feedback loop that regulates the primary operation (steam-driven engine activity) with only a slight time lag.[4]

[4] For a very illuminating discussion of the Watt governor, including its history and how, in some uses, it produces problematic oscillations, and the strategies engineers employed to cope with these, see Denny (2002).

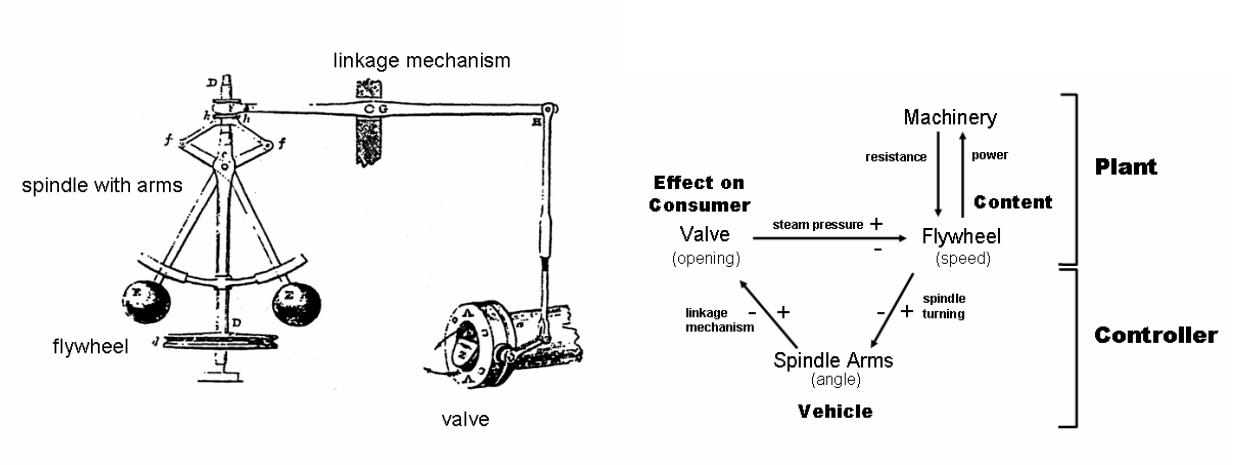

Figure 1. On the left, Watt's governor for the steam engine (adapted from Farley, 1827); on the right, a schematic diagram showing how a representational system (vehicle linked to content and consumer) is realized in the control system architecture.

Van Gelder contended that the governor operates without representations and can be taken as a simple model for how a cognitive system could likewise function without representations. He offered several arguments for rejecting as "misleading" "a common and initially quite attractive intuition to the effect that the angle at which the arms are swinging is a representation of the current speed of the engine, and it is because the arms are related in this way to engine speed that the governor is able to control that speed" (p. 351). Here I will consider just the first of these arguments, as doing so will help show why the "quite attractive intuition" is in fact correct (I have addressed his other arguments in Bechtel, 1998). In this argument van Gelder contended that there is no explanatory utility in construing the angle of the arms in representational terms; rather, a pair of differential equations suffice to account for the operation of the governor: one relating the acceleration in the angle of the arms to the engine speed and current angle (eq. 1 below) and another relating the engine speed to the angle of the arms. To answer van Gelder I will argue that (a) a mechanistic analysis of the behavior of the governor is informative and dovetails with the dynamical analysis and (b) that mechanistic analysis of the governor requires a representational account of the arm angles: they *stand in for* the speed of the engine and can effectively regulate the valve opening *because* they do so.

A mechanistic analysis identifies parts of a system and the operations they perform, and shows how they are organized so as to generate the phenomenon to be explained (Bechtel & Abrahamsen, 2005). The parts of this governor include the flywheel, spindle arms, and the linkage mechanism connected to the valve. As shown on the right side of Figure 1, each component operates on a different engineering principle and hence performs a specific operation that contributes to the ability of the governor to keep the engine operating at a constant speed. This exemplifies the tasks in a mechanistic analysis: specifying each part and its operation and connecting each operation to the functioning of the whole system. The diagram makes it clear *why* Watt inserted the spindle arms: it is *because* the spindle arms rise and fall in response to the speed of the flywheel (and the engine more generally) and their angle can be used by the linkage mechanism such that the valve will open and close appropriately. Without the spindle arms and their appropriate linkage mechanism, the valve has no access to information about engine speed. Watt included them in the governor to encode that information in a format that the valve-opening

mechanism could employ. This analysis illustrates a general point about representations: someone (a designer or evolution) has gone to the trouble of representing a state of affairs in a particular vehicle because that vehicle is suited for use by the consumer of that information.

While accepting the potential legitimacy of appeals to representation within this explanatory framework, Chemero (2000) challenged whether they do sufficient work.[5] In particular, he contended that when it comes to explaining how the Watt governor actually operates to regulate the behavior of the steam engine, one turns not to an account of its representational content, but to the dynamical equations that characterize its operations. To answer this objection, it is necessary to show how the dynamical equations that describe the Watt governor actually describe the representational content that the representational vehicles, the angle arms, provide to the consumer, the throttle valve, which then uses that content to appropriately adjust itself.[6] Nielsen (2010) shows that this is the case.

Nielsen's analysis starts with one of the two differential equations presented by van Gelder as jointly characterizing the operation of the governor, and argued by Chemero to provide a sufficient explanation of how the governor works. This equation, on its own, specifies the acceleration of the angle of the arms at time *t* given a particular engine speed:

(1) $$\frac{d^2\varphi}{dt^2} = (n\omega)^2 \cos\varphi \sin\varphi - \frac{g}{l}\sin\varphi - r\frac{d\varphi}{dt}$$

In this equation φ is the angle of the arms; ω is engine speed; and n, g, l, and r are parameters reflecting the gearing, gravity, length of the arms, and friction at the hinges respectively. To change the focus to how engine speed is represented in the behavior of the arms, Nielsen solves for ω:

(2) $$\omega = \frac{\sqrt{\dfrac{\dfrac{d^2\varphi}{dt^2} + \dfrac{g}{l}\sin\varphi + r\dfrac{d\varphi}{dt}}{\cos\varphi\sin\varphi}}}{n}$$

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[5] Chemero (2000, p. 627) offered the following formal characterization of the role for representations, which agrees with the informal characterization I offered: "A feature R0 of a system S will be counted as a Representation for S if and only if:

> (R1) R0 stands between a representation producer P and a representation consumer C that have been standardized to fit one another.
>
> (R2) R0 has as its proper function to adapt the representation consumer C to some aspect A0 of the environment, in particular by leading S to behave appropriately with respect to A0, even when A0 is not the case.
>
> (R3) There are (in addition to R0) transformations of R0, R1...Rn, that have as their function to adapt the representation consumer C to corresponding transformations of A0, A1... An.

[6] One of van Gelder's objections to treating the Watt governor representationally was that at best the angle arms misrepresent the speed of the flywheel because they are always slightly lagging behind it. My strategy in 1998 was to appeal to Millikan's contention that something can represent even if it rarely or even never covaries with what it represents. Nielsen provides a much better response—the claim that the angle arms misrepresent the velocity of the flywheel stems from focusing only on the angle φ, not on the dynamic behavior of the angle arms, which includes their rate of change and acceleration.

This reveals that engine speed at any point in time, *t*, is precisely represented by appropriate parameters and three variables characterizing the behavior of the angle arms at time *t*: φ, the current angle, $\frac{d\varphi}{dt}$, the rate of change in the angle, and $\frac{d^2\varphi}{dt^2}$, its acceleration.

There are limitations to Nielsen's analysis, since it captures only how engine speed is represented at a moment. Without the coupling of equation (1) with a second equation characterizing the effect of the governor on the engine speed, the dynamic relation between ω and φ is not incorporated. It nonetheless illustrates the strategy of dynamic mechanistic analysis (Bechtel & Abrahamsen, in press), insofar as it establishes a correspondence between variables in dynamic equations and properties of parts and operations of a mechanism and thereby coordinates what are often separate types of accounts into an especially revealing, integrated account. It also draws attention to an important aspect of the representational analysis of the Watt governor: in order to understand the representational content of the vehicle (the angle of the arms) it is necessary to view the vehicle dynamically—analyzing how the angle is changing—not just statically, as would be the case if only the current angle were considered. As Nielsen notes, the angle of the arms alone is ambiguous as the same angle will appear when the arms are rising and when they are falling, but in one case the valve will respond by closing to some degree whereas in the other it responds by opening to some degree. The velocity resolves this ambiguity: when the angle is increasing, the valve closes, whereas when it is decreasing, the valve opens.[7]

Nielsen's analysis provides a compelling answer to Chemero's challenge; the dynamical analysis of the governor is in fact characterizing the representational content of the representational vehicle in the mechanism. But this response may fall victim to another objection to identifying representations in the Watt governor: the claim that characterizing a component of the mechanism as a representation is useful to the person trying to understand the operation of the mechanism, but that the mechanism itself has no actual representations (Haselager, de Groot, & van Rappard, 2003). The mechanism comprises only the parts and operations that produce its own behavior. To counter this objection it is fruitful to focus on what type of mechanism the Watt governor is. A governor or controller is that part of a mechanism (or submechanism, if it has multiple parts) that regulates the operation of other part(s)—i.e., one or more of those comprising the plant—by rendering them responsive to conditions internal or external to the plant. To regulate the plant the controller must be appropriately connected to it.[8] To make the plant responsive to conditions internal or external to it, the controller must carry information about them. This account of the controller turns out to employ precisely the two relations I previously described as crucial to representations. In the Watt governor, the changing angle of the arms is the vehicle and that vehicle is related both to the content of the representation (engine

[7] The situation is far more complex when, as happened when steam engines became more powerful, the governor generates perpetual oscillations around the target value. In the original case Watt confronted, the oscillations were rapidly dampened when perturbed only slightly from equilibrium, and so the focus of the analysis is on the equilibrium values,

[8] During many stages in its operation, representations in the controller may be detached from the current state of the plant. Many controllers use emulators to represent the plant when information from the plant is not directly available (Grush, 2004). The circadian oscillator presented below in fact is often detached from the environmental cues that could inform it about time of day. However, if there is never an active coupling by which the operations in the governor are affected by operations in the plant, then the governor should not be credited with representing the plant.

speed) and the consumer of the representation (the throttle valve). In general, if it were not for these two relations, controllers would not have been designed by engineers for machines and would not have evolved in organisms.

This suggests the hypothesis that the locus of representations is within control systems, and hence that representation cannot be understood apart from an understanding of control systems. Moreover, gaining such understanding involves exploration not only of the mechanical control systems conceived by engineers but also the far more ancient and widespread control systems in the biological world. The prevalence and importance of biological control systems can be recognized by considering the basic conditions in which organisms live. They are systems far from thermodynamic equilibrium with their environment and must, if they are to maintain their identity, recruit matter and energy from their environment and deploy it to build and repair themselves (Ruiz-Mirazo, Peretó, & Moreno, 2004). A basic component of all living systems is a boundary membrane, a semi-permeable boundary whose permeability can be modulated by the organism itself. Organisms also require operations for extracting energy from the materials that cross the membrane into the organism and utilization of this energy and matter to synthesize new parts, including the boundary membrane.[9] Continuous building and repair are essential operations in living mechanisms, as they must counter the basic tendency toward equilibrium exhibited by any system that is out of equilibrium with its environment (i.e., increased *entropy*—a general tendency throughout the physical world, including but not limited to organisms). It is conceivable that an organism could exist in which these ongoing operations are all adequately coupled to each other, such that it could survive and reproduce without any specialized regulatory system modulating and coordinating their dynamics. But such a mechanism would be extremely vulnerable, as it would be dependent upon its environment for provision of exactly the matter and energy it requires and for removal of its waste products precisely when necessary.

All known organisms, except perhaps for sulfur bacteria, must cope with variable environmental conditions and for this reason need to be flexible in deploying their component mechanisms. They therefore include control systems that serve to up- or down-regulate specific operations within the organism and to couple different operations so that they can be deployed in a coordinated manner. Such control need not be centralized and often involves signaling pathways through which the detection of internal or external circumstances directly triggers or shuts down the performance of an operation. Chemical signaling is common in single-celled organisms; in multi-celled organisms it is supplemented by neurons—cells specialized for faster and more directed communication via action potentials down axons. With the evolution of central ganglia and later of brains, ever more complex control systems appeared.

Control systems constitute the natural locus for representations, and the task of a control system is to acquire information that affects the plant being controlled and employ the information to regulate the plant. Even the control systems employed in chemotaxis in bacteria are quite complex, involved parallel enzyme-mediated reactions, and to understand these it is necessary to focus on the information individual reactions are carrying and how the reaction pathways are

[9] Metabolism and construction of a membrane are two components of Gánti's (2003) conception of a chemoton, the simplest hypothetical physical system he could conceive that would exhibit the basic features of life. The third component is a control system, which he proposed could take the form of a component for constructing polymers whose length could then regulate other functions.

linked. This is even more true when, in the cortex of mammals, multiple specialized brain areas process representations with different but related contents. The individual areas involve highly connected neurons that perform particular information processing operations, but these also need to be coordinated, which is achieved through a few long-range connections between areas dominated by local connections (Strogatz, 2001; van Leeuwen, 2007).

In the following section I will focus on one fundamental representational activity that, as far as we can tell, figures in the regulation of behavior of most organisms, namely, the representation of time and length of day. Before turning to that, though, I summarize the lessons I draw from reconsidering van Gelder's arguments. First, the introduction of the Watt governor as a kind of prototype for the design of cognitive systems was a happy choice. We should view the mind/brain as a controller (or, better, a collection of controllers) regulating an already active biological system. Accordingly, we should employ tools and perspectives from control theory in characterizing the design and functioning of the mind/brain. Second, as van Gelder suggested, the activities of the mind/brain may best be described in differential equations. Further, the tools of dynamical systems theory and complexity theory may generate some of the most informative accounts of the functioning of the mind/brain as a control system. But, third, doing so does not entail rejecting the characterization of brain activity in representational terms. Indeed, it is only by identifying their representational vehicles and understanding the content they carry that we understand how brains function as control systems. In pursuing this inquiry, our understanding of what representations are and how they are employed may radically change. One such change has already been noted: that it may be important to focus not on representational states but representational processes since some of the crucial information involves not the instantaneous state of a system but rather rates of change or acceleration of operations in that system.

3. A Dynamical System for Representing Time of Day

A wide range of physiological and behavioral activities of organisms are linked to particular periods of earth's 24-hour day: fruit flies eclose from pupae at dawn (Pittendrigh, 1960-1961), cyanobacteria fix nitrogen at night (Golden, Ishiura, Johnson, & Kondo, 1997), chipmunks forage at times best suited to avoid predators (DeCoursey, Walker, & Smith, 2000), and humans exhibit their quickest reaction times shortly after midday. In these and numerous other cases, physiological and behavioral activities remain keyed to time of day even in the absence of all external cues such as daylight or temperature changes. That is, the timing of activities is under substantial endogenous control: organisms represent time of day through some internal process and use it to regulate their activities. One of the clearest examples is that animal species (both invertebrate and vertebrate) have preferred times to sleep. Even if an animal is deprived of sleep during this period and thereby suffers a sleep deficit, it will tend to delay its subsequent sleep to the preferred time.[10]

Researchers commonly refer to the mechanism responsible for daily timekeeping as a clock. Since, in the absence of external cues, most organisms maintain a highly reliable cycle with a period of approximately but not exactly 24 hours, it is called a *circadian* (*circa* = about + *dies* =

[10] Time periods for sleep are regulated independently from the amount of sleep required. Organisms deprived of sleep will compensate with increased intensity and duration in subsequent sleep episodes, a phenomenon known as *sleep homeostasis* (Saper, Cano, & Scammell, 2005).

day) clock. The assumption that there exists *a* clock reflects a common research heuristic: when a system performs some activity, assume one part of the system is responsible for it. This assumption, which Richardson and I (Bechtel & Richardson, 1993) labeled *direct* or *simple localization*, is fallible in that the activity may actually result from the coordinated operation of many components, not just (or even including) the one initially identified. Even though there are now good reasons to challenge the assumption of a single clock,[11] it paid off handsomely in animal research as researchers were able to localize the presumed clock in particular parts of organisms' brains. In mammals this was the suprachiasmatic nucleus (SCN) of the hypothalamus, a structure residing just above the optic chiasm where the nerve projections from the two eyes come together before resegregating en route to the thalamus. Several lines of evidence support the claim that the SCN is the central clock: lesioning the SCN renders mammals arrhythmic (Moore & Eichler, 1972), transplanting a donor SCN into animals whose own SCN has been removed restores rhythmic behavior (Ralph, Foster, Davis, & Menaker, 1990), and many neurons in SCN explants maintained in culture generate circadian rhythms (Welsh, Logothetis, Meister, & Reppert, 1995).

The SCN indeed is the mammalian central clock, but this direct localization was only the first step towards a far more complex account. A key part of the mechanism is in fact molecular and intracellular: its primary parts and operations have been identified and are now known to be replicated not only within individual neurons in the SCN but also, as peripheral clocks, in somatic cells of the liver and other organs. The first clue towards a molecular decomposition of the central clock came from research on fruit flies (*Drosophila*) in which Konopka and Benzer (1971) succeeded in generating mutants that exhibited shortened or lengthened circadian rhythms or became arrhythmic. They named the gene that had been altered to this effect *period* (*per*). The development of cloning techniques in the 1980s enabled Rosbash and his collaborators to identify *per*'s mRNA transcript and the resulting protein, PER. Hardin, Hall, and Rosbash (1990) established that concentrations of both *per* mRNA and PER exhibited circadian rhythms, with the peaks and valleys in PER concentration following those of *per* mRNA by about eight hours. Further, they determined that these oscillations were shortened, lengthened, or absent in mutants of the types first generated by Konopka and Benzer. Based on these results, Hardin et al. proposed a feedback mechanism in which, once PER has been synthesized in the cytoplasm, it is transported back into the nucleus where, in some way not understood at the time, it inhibits expression of the gene *per* and hence its own further synthesis (Figure 2). Assuming this account of the mechanism (it later turned out to be more complex), here is an intuitive understanding of how it would generate oscillations. When concentrations of PER in the nucleus are low, gene expression proceeds normally, leading to a gradual buildup of PER in the cytoplasm towards its peak concentration there. This buildup would be countered by breakdown over time of PER molecules; some, however, are first transported into the nucleus, where their concentration peaks approximately 8 hours after that of *per* mRNA. This inhibits further transcription of *per*, which leads to a gradual reduction of PER in the cytoplasm. But on this account, another operation also

[11] Typically, across many fields of science, when a direct localization is hypothesized it turns out to be correct only to a first approximation. In the case of circadian timekeeping, the same basic mechanism is present in many cells distributed through the animal's body. These cells maintain oscillations, but fail to synchronize without input from the SCN. Within the SCN individual cells vary considerably in their periodicity so that the regular oscillatory pattern exhibited in behavior depends upon the integration of individual cells' behavior into stable collective behavior via intra-SCN synchronization.

plays a role in producing oscillations in concentrations: as in the cytoplasm, the PER molecules in the nucleus break down over time. As its nuclear concentration declined, PER's inhibitory effect on *per* declines as well. Consequently, transcription and translation gradually return to their maximum rate, and PER levels in the cytoplasm recover. This negative feedback loop would repeat indefinitely; and assuming that the various operations proceed at appropriate rates, the resulting oscillations in concentrations of the molecules can be envisaged as taking approximately 24 hours.[12]

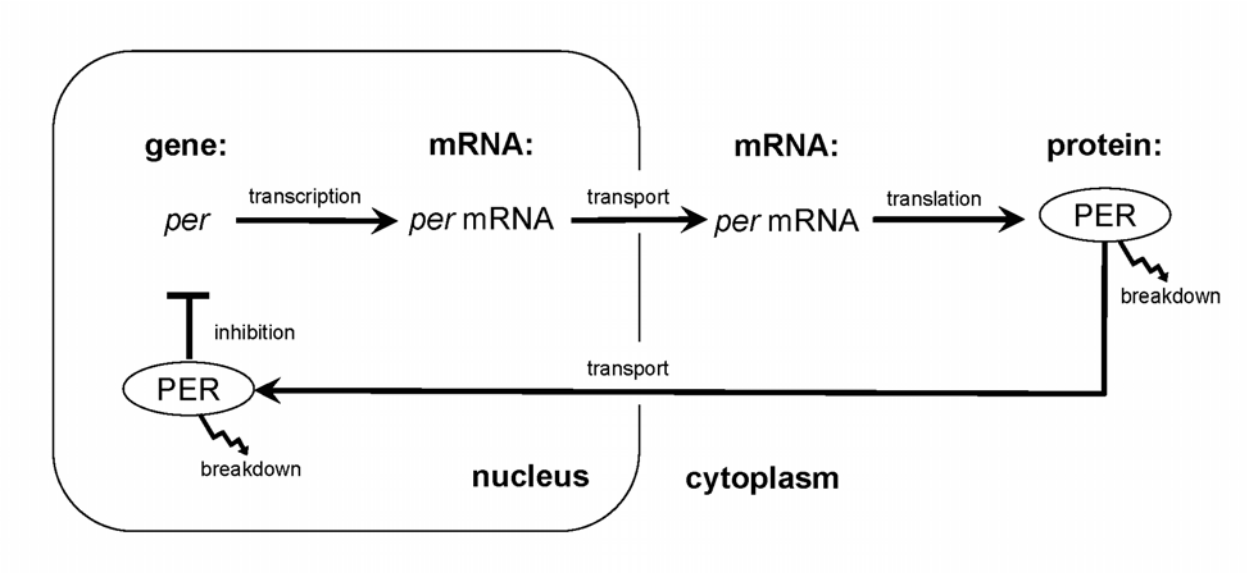

Figure 2. Hardin, Hall, and Rosbash's (1990) proposed feedback mechanism for generating circadian oscillations in fruit flies.

Arriving at this proposed mechanistic explanation drew on the strategies common to most biological research: *simple localization* of the overall mechanism (for mammals, in the SCN); *decomposition* of that mechanism into its parts (*per*, *per* mRNA, PER) and their operations (transcription, transport, translation, inhibition, and breakdown); and *recomposition* of the component parts and operations into a complex mechanism capable of producing the phenomenon of interest (see Bechtel & Abrahamsen, 2009). As the first such proposal it was a landmark that guided future research; but as one would expect, it was incomplete in numerous respects. The ensuing two decades of research have yielded a much more complete mechanistic account of circadian clocks. One gap was recognized almost immediately—since PER has no DNA binding region, PER molecules could not directly act on the *per* gene to inhibit transcription of additional PER molecules. Following the same research strategy that had successfully identified *per* in fruit flies, Vitaterna et al. (1994) sought and found in mice a gene that they named *Clock* (for *circadian locomotor output cycles kaput*). When the mutant gene was heterozygous, it resulted in a lengthened period; when homozygous, it resulted in loss of circadian rhythms within two weeks. When the group succeeded in cloning *Clock* two years later, they correctly predicted "that this candidate gene encodes a novel member of the bHLH-

[12] Such intuitive reasoning is fallible. The initial oscillations in such a mechanism potentially could dampen as the concentrations approach a steady state. To show that such a mechanism would in fact sustain oscillations requires mathematical modeling; Goldbeter (1995b) developed such a model and, using biologically plausible parameter values, achieved oscillatory behavior.

PAS domain family of transcription factors" (King et al., 1997, p. 645). Such a transcription factor would enable binding to a site known as an E-box on the promoter of another gene such as *per*. Shortly thereafter Darlington et al. (1998) found a homolog of *Clock* in fruit flies and, conversely, Sun et al. (1997) demonstrated the existence of a mammalian homolog of *per*. This established a basic parallel between the clock mechanisms of fruit flies and mammals. (There were also many differences of detail; for example, it was soon found that mammals have three homologues to *per,* at least two of which (*mPer1* and *mPer2*) code for clock proteins.) In fruit flies, Gekakis (1998) hypothesized that PER in some way alters the ability of CLOCK to bind with the E-box on the *per* promoter. Other research in the 1990s and beyond revealed additional complexities in the clock mechanism. There were corresponding findings for fruit flies, but focusing here just on mammals, it was found that both proteins function by forming dimers (compounds) with other proteins (PER with CRY and CLOCK with BMAL1). Another complexity is the discovery of a second, positive feedback loop in which the dimer formed by CLOCK and BMAL1 also binds to the E-Box on the promoter of RORα, which in turn binds to the RORE-box on the promoter of BMAL1, so that BMAL1 stimulates production of more of itself. Figure 3 shows the current conception of the organization of the mammalian clock mechanism.

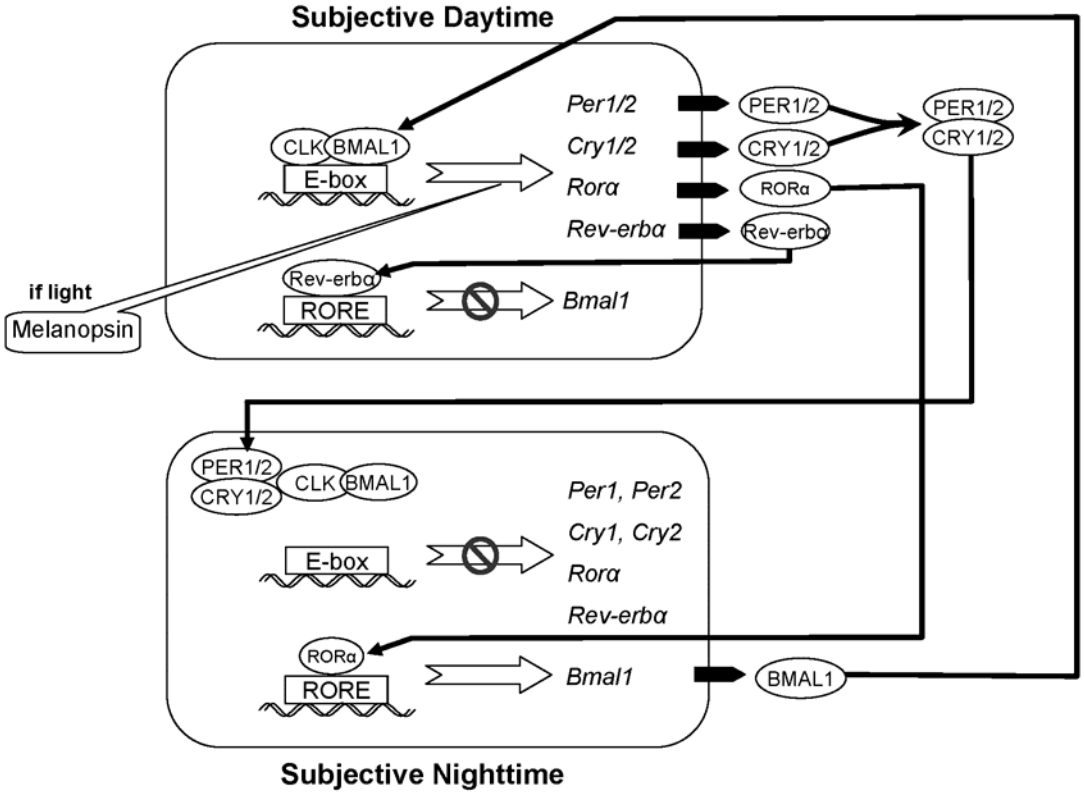

Figure 3. The basic components of the mammalian circadian oscillator. During subjective day, the CLK:BMAL1 dimer binds to the E-box promoter on the *Per1*, *Per2*, *Cry1*, *Cry2*, *RORα and Rev-erbα* genes, activating expression of these genes. During subjective night, the PER:CRY dimers interact with the CLK:BMAL1 dimers, removing them from the E-boxes and hence inhibiting gene expression. The *Bmal1* gene has the opposite cycle, inhibited during subjective day but activated during subjective night. The large open arrows indicate whether gene expression is activated or inhibited. The smaller filled arrows represent the combined operations of gene expression that are shown individually in Figure 2 (transcription, transport, and translation into the appropriate protein).

I have focused on how molecular operations within individual SCN generate a 24-hour oscillation in concentrations of mRNA transcripts and proteins. In the next section I will address how these operations carry information about time of day and are used by the organism because they do so, thereby establishing that they represent time of time. Before doing so, though, I should note that while uncovering this intracellular mechanism was absolutely crucial, investigations targeting a higher level of organization have helped flesh out how 24-hour oscillations are maintained (for further discussion, see Bechtel & Abrahamsen, 2009). These investigations, with an intercellular rather than intracellular focus, examined the SCN as a network of neurons that could influence one another's behavior. Consider what happened when Welsh, Logothetis, Meister, and Reppert (1995) dispersed neurons from the SCN of mice on multielectrode grids. They produced the first demonstration that individual SCN cells exhibit regular oscillations in their rates of neural activity. But they also noted an important unexpected finding: considerable variability across cells in their period of oscillation, ranging from 21.25 hours to 26.25 hours with a SD of 1.25 hours. This was in stark contrast to the low variability exhibited whole organisms on behavioral measures; for example, individual mice are very regular in the time of day at which they attain peaks in their wheel running and other activities. Moreover, when Herzog, Aton, Numano, Sakaki, and Tei (2004) maintained the pattern of neural connectivity in slices they found much less variability. This suggested that oscillations in neural activity somehow become synchronized when neurons are organized into a network within the SCN. The same laboratory soon produced evidence pointing to vasoactive intestinal peptide (VIP) as the synchronizing agent, and considerable research subsequently has been devoted to the process and pattern of synchronization (Welsh, Takahashi, & Kay, 2010). Other research has established that even when the period of increased activity is well-synchronized across neurons in SGN, individual neurons differ in the time at which activity peaks; also, these times are more widely dispersed on days with longer photoperiods than on days with shorter photoperiods (Schaap et al., 2003; vanderLeest et al., 2007). The result is that on days with short photoperiods, the amplitude of the waveform generated by electrical activity over the whole SCN is greater, providing a possible encoding of photoperiod that could be used to regulate activities that must be performed on shorter or longer days over the course of the year.

4. Responding to Referents and Informing Consumers

In the previous section I sketched the research that in the past two decades has revealed the mechanisms which endogenously generate circadian oscillations within SCN cells—as revealed in both gene expression and electrical activity—and synchronize oscillations between SCN cells as well. This does not yet establish that these oscillations satisfy the control-theoretic account of representation I presented in section 2. Many other oscillatory processes have been found in organisms, some of which perform important regulatory functions while others apparently do not (Goldbeter, 1995a; Buzsáki, 2006). Because most do not carry information about external cyclic phenomena, there is no compelling reason to think of them as representing temporal processes outside themselves. In order to show, on the control theory account, that circadian oscillations in the SCN constitutes a clock—that they represent time of day—they must be shown to carry information about time of day (the referent of the representation). Further, the fact that they carry information about time of day must figure in how the activity in the SCN is consumed. The

activities elsewhere in the organism that are affected by the oscillations in the SCN must be ones that need information about time of day to be performed effectively.

Considerable progress has been made in identifying the processes by which the SCN oscillations are normally linked to actual time of day, although they can be maintained even under constant conditions in which they receive no information about time of day. There are several sources of information from which an organism can gain information about time of day—light, ambient temperature, food availability, and physical activity all are effective under appropriate circumstances—but the onset and offset of daylight is the most effective for entraining circadian oscillators. In mammals there is a direct neural pathway—the hypothalamic tract—from the retina of the eye to the SCN. It was the discovery of this pathway that initially led Moore and Lenn (1972) [13] to focus on the SCN as a candidate locus for the clock. At the molecular level, almost immediately after the discovery of the mammalian homologues of *per*, Shigeyoshi et al (1997) determined that exposure to light induced expression of *mPer1* in SCN cells; subsequent research showed that *mPer2* was similarly affected, but not *mPer3* (Zylka, Shearman, Weaver, & Reppert, 1998). This research established that light exposure has causal effects in the SCN, but did not reveal the mediating mechanism. The determination that organisms in which rods and cones are destroyed can still entrain to light, while those without eyes cannot, pointed to the existence of an additional type of photosensitive cell in the eye. Working with the frog *Xenopus laevis*, Provencio, Jiang, De Grip, Hayes, & Rollag (1998) discovered a new member of the opsin family, melanopsin, in melanophores (melanin pigment containing cells). Subsequently they determined that melanopsin is present in the mammalian inner retina (Provencio, Rollag, & Castrucci, 2002), which helped resolve the puzzle and established melanopsin at the input end of the pathway.[14]

The task was then to fill in the intermediate steps by which information about light is transmitted to the SCN. Crosio, Cermakian, Allis, and Sassone-Corsi (2000) showed that increased transcription of *mPer1* and *mPer2* resulted from chromatin remodeling (a process that alters the manner in which DNA wraps around histones and thereby affects whether the enzymes required for transcription can attach to the DNA). Soon thereafter Travnickova-Bendova, Cermakian, Reppert, and Sassone-Corsi (2002) offered evidence that the final pathway involves a cAMP response element (CRE) phosphorylating a CRE-binding protein (CREB), which binds to promoter sites on *mPer1* and *mPer2* to initiate transcription. A role was also established for PACAP (pituitary adenylate cyclase activating peptide), a neurotransmitter active in the retinohypothalamic tract during subjective day. At the input end, Hannibal, Hindersson, Knudsen, Georg, and Fahrenkrug (2002) established that in mammals melanopsin is found in the same inner retinal ganglion cells as PACAP. Moreover, PACAP receptors were identified on SCN cells, and a signaling pathway within SCN neurons was proposed whereby PACAP binding initiates the sequence culminating in CRE phosphorylating CREB Thus, in less than five years researchers had identified the main components and achieved a coherent account of how light

[13] Moore was initially searching for the visual pathway that controlled pineal biosynthetic activities.

[14] The discovery that mice mutants lacking melanopsin can still entrain to bright light, albeit with less responsiveness than wild types to pulses of light, indicated that the dismissal of rods and cones as playing a role in entrainment had been premature (Panda et al., 2003; Hattar et al., 2003). Dkhissi-Benyahya, Gronfier, De Vanssay, Flamant, & Cooper (2007) demonstrated that a mid-wavelength opsin (peak sensitivity above 530 nm) found in cones was the likely agent of entrainment via cones. Hatori et al. (2008) showed that the entrainment produced from the cones is mediated by the melanopsin-expressing retinal ganglion cells.

entrains the mammalian clock.[15] This establishes that the circadian oscillations of PER and other clock proteins in the SCN cells carry information about time of day since they are typically entrained to the day-night cycle on the planet (the referent). The fact that entrainment only occurs at certain times of day and that when entrainment is impaired, oscillations continue, does not jeopardize the claim that the content of the representation is time of day, for that is what the consumer components of the organism (the plant) require information about in order to time their own operations in order for them to be effective.

Turning to the consumer side, there is overwhelming evidence that oscillations in protein concentrations within the SCN are used to coordinate the timing of various mammalian activities, although many of the details of how they do so remain obscure. Part of the challenge is the extraordinary range of physiological and behavioral activities that exhibit circadian regulation. These include sleep, cardiovascular activity, endocrine levels, body temperature, renal activity, gastro-intestinal tract activity, hepatic metabolism, and motor activities. These various activities all exhibit circadian oscillations, but differ in the time at which they initiate and peak. Accordingly, they differ in the way they utilize the SCN oscillator in controlling these activities.

The mechanisms involved in many of these activities are not well understood, making it difficult to establish the detailed connections between the protein oscillations in SCN cells and the regulation of these activities. It is, however, clear that circadian oscillations in these activities are regulated by the SCN. The pioneering studies identifying the SCN as the locus of the central clock, showed that lesions to the SCN in rats eliminated circadian control of adrenal corticosterone (Moore & Eichler, 1972) and of drinking and locomotion (Stephan & Zucker, 1972). Transplant studies in the 1980s on lesioned rats that had been rendered arrhythmic established that transplanting SCN tissue from intact rats into the third ventricle could restore circadian motor activity, but not endocrine oscillations (Drucker-Colin, Aguilar-Roblero, Garcia-Hernandez, Fernandez-Cancino, & Rattoni, 1984; Sawaki, Nihonmatsu, & Kawamura, 1984; Lehman et al., 1987). If the donor tissue is from a mutant with a different circadian period, circadian behavior in the host will reflect that of the donor (Ralph, Foster, Davis, & Menaker, 1990).

These lesion and transplant studies provide compelling evidence that oscillations in the SCN are used elsewhere in the body as a source of information about time of day so as to coordinate behaviors. A clue to how this is accomplished emerged along with the discovery of mammalian clock genes *Clock* and *mPer1* and *mPer2*, as they were found to cycle not just in the SCN but in organs throughout the body (King et al., 1997; Sun et al., 1997).[16] Balsalobre, Damiola, and

[15] A further aspect of entrainment is that light is effective in resetting the circadian oscillator only during the night, and it is most effective immediately after subjective dusk and before subjective dawn. Light delivered during the middle of the subjective night can so disrupt circadian oscillations as to render the organism arrhythmic, an effect first hypothesized by Winfree (1970) and confirmed in subsequent research (Honma & Honma, 1999). Research on the mechanism has now suggested why light at different times is responded to differently (Pulivarthy et al., 2007).

[16] Rhythmic expression of clock genes was first identified in fruit flies both in the central nervous system, especially the visual system, and in the digestive track (Siwicki, Eastman, Petersen, Rosbash, & Hall, 1988). The development of techniques for fusing the luciferase gene *luc* to the *per* gene facilitated the creation of transgenic flies in which bioluminescence accompanies *per* expression. This enabled Plautz, Kaneko, Hall, and Kay (1997) to demonstrate *per* oscillations in dissociated head, thorax, and abdomen tissue from flies. With *per* driven green fluorescent protein

Schibler (1998) demonstrated that with serum shock they could induce circadian oscillations in rat fibroblast tissue kept in culture for more than 25 years and concluded:

> On the basis of our results with fibroblasts and hepatoma cells, it appears that peripheral tissues contain a clock capable of measuring time with impressive precision. One can thus hypothesize that many circadian outputs might be controlled by peripheral clocks, which may themselves be synchronized by the central clock (p. 934).

Subsequently, peripheral clocks have been shown to regulate the rhythmic generation of numerous transcription factors such as *Dbp*, *Hlf*, and *Tef* (Gachon, Olela, Schaad, Descombes, & Schibler, 2006), and *E4bp4*, which oscillates out of phase with the others and competes for their binding sites on regulated genes (Mitsui, Yamaguchi, Matsuo, Ishida, & Okamura, 2001). These transcription factors provide circadian regulation of clock controlled genes. Researchers have found that in any given tissue approximately 10% of genes exhibit a circadian pattern of expression, with the specific genes showing such a pattern varying by tissue type (Storch et al., 2002; Panda et al., 2002).

Peripheral clocks thus appear to play an important mediating role in the consumption of the SCN oscillations. The understanding of the way in which peripheral clocks are dependent on the SCN has undergone major revision in recent years. When peripheral clocks were first identified in the late 1990s, it was assumed that they dampened after a few cycles of oscillation without inputs from the SCN (Yamazaki et al., 2000). This led researchers to view the SCN as the master clock and peripheral clocks as slaves (Akhtar et al., 2002). There had long been behavioral evidence, however, suggesting the existence of sustained circadian oscillators outside the SCN. Shortly after the discovery of the role of the SCN in most circadian behavior, several researchers determined that SCN lesioned rats that are fed at regular but restricted times anticipate their mealtime (Stephan, Swann, & Sisk, 1979). The fact that the food anticipatory behavior (locomotor activity and body temperature changes) free runs during periods of food deprivation and shows a transient effect as the organism adjusts to phase shifts in feeding times indicates that it is governed by a circadian clock distinct from that in the SCN (Davidson & Stephan, 1999). Even with the SCN intact, gene expression in the liver, kidney, heart, and other tissues can be altered by changes in feeding time while leaving the phase of gene expression in the SCN unaffected (Damiola et al., 2000).[17]

Nonetheless, the assumption that peripheral clocks could not sustain oscillation unless they received input from the SCN or Zeitgebers (environmental time cues such as light) persisted until Yoo et al. (2004), using a luciferase reporter that enabled tracking oscillations of *per* transcription in individual cells, showed that liver and lung explants can maintain rhythmicity for at least 20 cycles. They concluded that the appearance of dampening was due to the fact that individual oscillators were no longer synchronized and so, at a population level, the oscillations

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(GFP) they found oscillations in the probiscus, antennae, legs, and wings. All these oscillators were able to entrain anew when the photoperiod was advanced or retarded.

[17] The effect of eating on the phase of the liver oscillator may be mediated by the increase in NAD^+ levels (levels are decreased in muscle and fat tissue), likely as a result of fat synthesis. The effect of NAD^+ on circadian oscillations may in part be direct, as the ratio of NADH to NAD^+ (or NADPH to $NADP^+$) can affect the binding of the CLOCK:BMAL1 or CLOCK:NPAS2 to DNA (Rutter, Reick, Wu, & McKnight, 2001). But there is also evidence that it is mediated by SIRT1 (Sirtuin 1), an NAD^+-dependent histone deacetylase that binds with CLOCK:BMAL1 and promotes the deacetylation and degradation of PER2 (Asher et al., 2008; Nakahata et al., 2008).

in individual cells cancelled out. This prompted Davidson, Yamazaki, and Menaker (2004) to propose the orchestra conductor metaphor as preferable to the slave master metaphor:

> He [the conductor] uses a baton rather than a whip because musicians (peripheral oscillators) are independent interpreters in their own right and must be coaxed, not driven. The aesthetic quality of the performance (fitness) depends heavily on how successfully the flow of information (coupling) regulates synchrony among the performers (p. 119).

The conductor metaphor captures the representational perspective I am advancing here. Insofar as the SCN is the conductor, it is producing representations that peripheral clocks (orchestra players) employ in regulating physiological systems (their instruments). In the framework I have been developing, the conductor is the central controller, the orchestra players are controllers in peripheral systems, and the instruments are the plants that are regulated.

Evidence thus strongly suggests that the SCN's representation of time of day is consumed by peripheral oscillators and by this means their timekeeping is coordinated with that of the SCN. The details of how information is transmitted are not yet known, but some steps in the process have been identified. The SCN is itself divided into two major regions, the core and shell. The core sends projections to the shell and also to the lateral parasubventricular zone ($_{L}$SPV) of the hypothalamus, while the shell sends outputs to the paraventricular nucleus of the thalamus (PVT), the paraventricular nucleus of the hypothalamus (PVN), the medial subparaventricular zone ($_{M}$SPV), the preoptic area (POA), and the dorsomedial hypothalamic nucleus (DMH). These areas in turn send projections to many other regions of the body. However, the SCN is not solely dependent on neuronal output. In transplant experiments in hamsters, even when the donor SCN was encased in a semipermeable polymeric capsule and so developed no neuronal connections, the donor could promote rhythmic behavior (Silver, LeSauter, Tresco, & Lehman, 1996). This suggests an important role for hormonal outputs from the SCN. Several peptides exhibit circadian oscillations and are thought likely to be regulated by central clock components: AVP (vasopressin), PK2 (prokineticin-2), TGFα (transforming growth factor-α), and a cardiotrophin-like cytokine (Antle & Silver, 2005; Kalsbeek et al., 2006). TGFα inhibits locomotor activity by acting on receptors in the hypothalamic subparaventricular zone (SPZ), which also is a major relay station for SCN neuronal efferents (Kramer et al., 2001). PK2 also suppresses locomotor activity, but not by affecting the SPZ. There thus appear to be multiple pathways by which information from the SCN is transmitted to its various consumers. This is fitting given that the various consumers differ in the preferred time of day for their activities.

Existing accounts of how the SCN oscillators are entrained by light, how they orchestrate oscillations in peripheral oscillators, and how these oscillators can be entrained by Zeitgebers other than light are still incomplete, but there is little reason to be dubious that such connections exist. We can be confident that the SCN has appropriate connections to information about time of day and to consumers of such information, and hence can be credited with *representing* that information for mammals.

5. Conclusion: Representations as Components of Control Systems

The embrace of representations in the cognitive and neural sciences has been challenged by advocates of a contentiously narrow dynamical systems approach. In this paper I have pursued

how a different stance—dynamic mechanistic explanation—can bring together the dynamical and representationalist perspectives rather than set them in opposition. I showed that even the Watt governor, which van Gelder advanced as a paradigm case of dynamics without representation, exemplifies this hybrid approach, by which representations invariably arise in the functioning of any dynamical system that incorporates a control system. Within this perspective I have explored both how dynamical processes within controllers carry information about the plant and its environment, and on how the plant consumes this information, but my main concern has been the implications of construing control systems themselves as the loci of representations. In particular, given a control system, one does not need to speculate further about how selection might have favored the representational system—it is sufficient to understand how representations arise within the controller and are used to coordinate behavior.

In suggesting that control systems provide a novel and informative framework in which to understand representations, I not only showed how representations arise in the Watt governor, but examined a biological case—the circadian clock that represents time and length of day. Circadian clocks utilize intracellular oscillatory processes to maintain an endogenous timing signal. In all but bacteria, the oscillation occurs when proteins synthesized from a few particular genes feed back in an inhibitory manner on that same process of gene expression. This internal oscillation is entrained by Zeitgebers such as light so as to align its phase with the day-night cycle in the world. Moreover, it is used in varying ways to regulate physiological and behavioral activities of the organism. From within a control theory perspective, the common objection to the notion of representation—that this is purely a convenience to theorists—gains little traction. A control system, such as the SCN, can regulate an organism's behavior only if it represents the relevant information about the plant (the rest of the organism's brain and body) and the conditions impinging on it and uses this information (dynamically varying representations) in directing the plant. If it does not encode the relevant information, the controller is unable to perform its function in the organism.

On the account I am advancing, representations have their home within, and are essential to, a particular type of mechanism—a control system. A simple feedback mechanism such as the Watt governor is the simplest exemplar. More elaborate mechanisms, such as the circadian clock, can represent dynamic information even when no current input from the referent is available (they are what Grush has characterized as emulators). Other neural and cognitive systems make more elaborate use of representations, and extending this basic account to these contexts in which more elaborate mechanisms are involved will require considerable additional work (see Barsalou, 1999, for an account of concepts grounded in basic sensory motor processes that offers a promising route for doing so).[18] An advantage of having begun with a representational system which appears to be present in all five kingdoms of living organisms—the circadian clock—is that it compellingly illustrates that the challenge of linking representational vehicles to their content need not be daunting if we focus on the right kind of mechanism—a control system linked to a plant.

[18] In cognitive control systems multiple representations are processed in the same system, and a major challenge in understanding such systems is to understand how these relations relate to one another. In this context, focusing on the functional role of representations, as discussed in Vogeley and Bartels paper in this volume, is critical. As discussed in note 2 above, this is not incompatible with the control theoretical perspective advanced here.

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