Principles of Minimal Cognition
Casting Cognition as Sensorimotor Coordination

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Abstract
Within the cognitive sciences, cognition tends to be interpreted from an anthropocentric perspective, involving a stringent set of human capabilities. Instead, we suggest that cognition is better explicated as a much more general biological phenomenon, allowing the lower bound of cognition to extend much further down the phylogenetic scale. We argue that elementary forms of cognition can already be witnessed in prokaryotes possessing a functional sensorimotor analogue of the nervous system. Building on a case-study of the *Escherichia coli* bacterium and its sensorimotor system, the TCST-system, we home in on the characteristics of minimal cognition, and distinguish it from more basic forms of ontogenetic adaptation. On our view, minimal cognition requires an embodiment consisting of a sensorimotor coupling mechanism that subsumes an autopoietic organization; this forms the basis of the growing consensus that the core of cognition revolves around sensorimotor coupling. We discuss the relevance of our interpretation of minimal cognition for the study of cognition in general.

Keywords: Minimal cognition, *Escherichia coli*, bacteria, sensorimotor coupling, TCST-system, situated cognition.

1 Introduction

What is cognition? Although cognition is one of the core concepts in the behavioral and cognitive sciences, there is no single, generally accepted answer. In fact, explicit conceptual interpretations are usually the subject of controversy (e.g. Brooks, 1999; Dennett, 1996; Clark, 1997). Nevertheless, there does seem to be a strong consensus that cognition involves processes such as perception, thinking, memory, and action. Since there is also a widespread conviction that cognition is best exemplified by human beings, cognition and the processes that are associated with it usually are interpreted from an anthropocentric perspective. Typically human cognition then becomes the yardstick by which the abilities of other animals are to be measured. From that perspective, cognition is tantamount to characteristically human-like capabilities such as reasoning, problem-solving and symbolization. These processes have to be present to a significant degree before one can speak of a bona fide cognizer (Gould & Gould, 1998). Internal, representation-handling processes are considered to be the source of these particular thinking skills, and it is a matter of painstaking research to establish whether, and if so, which other creatures also exhibit these refined capabilities (see for example Heinrich, 2000; Smirnova, Lazareva & Zorina, 2003). Cognition is a scarce commodity in this view.

In this anthropocentric interpretation of cognition, organisms whose behavior does not unequivocally involve human-style-reasoning subsequently remain outside the cognitive domain. As a result, the behavior of such organisms is still often argued to be predominantly composed of inflexible, hard-wired reactions to environmental stimuli (e.g. Dennett, 1984; 1996; Gould & Gould, 1998; Sterelny, 2001); behaviors that are not very interesting from a cognitive perspective (see also Godfrey-Smith, 2001; Shettleworth, 1998). Dennett (1984) and Hofstadter (1985), for example, talk about

"sphexisms" in this context, drawing the term from an anecdote in which a digger wasp of the *Sphex* genus[i] was manipulated so that it remained stuck in an iterative, automatic behavioral loop; endlessly repeating its own inbuilt, behavioral responses. In other words, anthropocentric interpretations of cognition depict a rough dichotomy between intelligent cognizers, and inflexible, mechanic-like organisms merely capable of reflexive/instinctive behaviors.

However, there are important practical and theoretical drawbacks to such a dichotomy, and to anthropocentric interpretations of cognition in general. First, this putative dichotomy does not stroke with the underlying intricacies that make so-called 'non-cognitive' organisms tick, as it simply fails to provide a realistic account of the behavioral complexities that can be found in non-human organisms (Brooks, 1999; Keijzer, 2001; Menzel, Brembs & Giurfa, *in preparation*; Roth & Wullimann, 2001). When investigated in their own right, the mechanisms and processes required to generate these presumably non-cognitive behaviors are found to be very complex and extraordinarily difficult to replicate in robots (Prescott, Redgrave & Gurney, 1999).

Second, the dichotomy does not cope with any differentiation within the so-called non-cognitive organisms. There are huge gaps between the behavioral capabilities of for instance nematodes and octopi, or between sharks and squirrel monkeys, all of which are - definitely to plausibly - considered 'non-cognitive' from an anthropocentric perspective. The assumption that the behavior of these 'lower' organisms is entirely composed of reflexes, instinct and/or hardwired reactions does not help to articulate how such very different behavioral capabilities come about.

Third, when one turns to the basic processes of cognition, and leaves aside their anthropocentric interpretation, it is clear that these processes, such as perception, memory, and action are dispersed extremely widely across and even beyond the animal kingdom. It is now even plausibly defended that these exemplar features of cognition are already present in invertebrates, and even bacteria (di Primio, Müller & Lengeler, 2000; Greenspan & van Swinderen, 2004; Lengeler, Müller & di Primio, 2000; Menzel, Brembs & Giurfa, *in preparation*, Müller, di Primio, & Lengeler, 2001).

Given all these considerations, it becomes evident that the time is ripe for a more systematic and in-depth perusal of the question *What is cognition?*, which is precisely what we propose in the following[ii]. How to proceed with this task? Davidson made a relevant remark:

> *"We have many vocabularies for describing nature when we regard it as mindless, and we have a mentalistic vocabulary for describing thought and intentional action: what we lack is a way of describing what is in between. This is particularly evident when we speak of the "intentions" and "desires" of simple animals; we have no better way to explain what they do." (Davidson, 1999, p.11)*

In line with this remark, we think that the notion of cognition ought and can be developed to fill in this gap between the mindful and the mindless. As an example, Godfrey-Smith (2001, p.234) recently argued that cognition in the first place evolved to enable organisms to control their own behavior, allowing them to cope with environmental complexity. On his view, cognition "shades off" into basic biological processes such as metabolism. Being sympathetic with this latter perspective, we believe that a proper interpretation of cognition should aim to be more specific about this "shading off", and allow for a better differentiation between the wide array of cognitive capabilities that can be found in nature. For this purpose, we will focus on the notion of *minimal cognition*, and try to articulate the minimal requirements for the generation of cognitive phenomena.

In recent years, the question as to what defines the lowest bounds of cognition is increasingly debated on (e.g. Beer, 2003; Keijzer, 2003; Lyon, *in preparation*; Moreno, Umerez & Ibañez, 1997; Moreno & Etxeberria, 2005). Within the field of embodied and situated cognition, many researchers have chosen insect-like organisms as a starting point (Beer, 2003; Brooks, 1999). However, this seems to be a rather arbitrary starting point, and indeed, a small minority of researchers has pursued the notion of minimal cognition by looking at prokaryotes, the simplest organisms in existence (e.g. Bitboll & Luigi, *in preparation*; Lengeler *et al.*, 2000; Lyon, *in preparation*; di Primio *et al.*, 2000). In this paper, we will follow the latter line and focus on bacteria in order to home in on minimal cognition, and inquire what the implications of minimal cognition can be for the notion of cognition

itself and the study of cognition in general. By adopting a biogenic approach (Lyon, *in preparation*), biology rather than the human case becomes the starting point for our investigating of minimal cognition. From this perspective, it makes sense to ask for the earliest manifestations of cognition as well as the various intermediate kinds of cognition that fill in the gap between the 'mindful' and the 'mindless'.

This paper has the following structure. First, we briefly sketch the relevant ideas of Maturana and Varela (Maturana, 2002; Maturana & Varela, 1980, 1988). They made an important initial contribution to this fledgling field by arguing that life and cognition are equivalent. In connection with these ideas, we discuss theoretical work by Moreno, Etxeberria and several collaborators, who argue that nervous systems are a necessary condition for cognition. In contrast, we argue that the most elementary forms of cognition can already be witnessed in prokaryotes possessing what is in some regards a molecular sensorimotor analogue of the nervous system. In the ensuing section, we provide a case-study of *Escherichia coli* bacterium and focus on its molecular sensorimotor, or TCST-system to come to our account of minimal cognition, and distinguish it from more basic forms of ontogenetic adaptation. In our view, minimal cognition requires an embodiment consisting of a sensorimotor coupling mechanism that subsumes a basic metabolic/autopoietic network; grounding the increasingly popular idea that cognition revolves around sensorimotor coupling. We end with a resume of what we think are the implications of this interpretation of minimal cognition for the study of cognition.

2 Previous Views on Minimal Cognition

In this section, we discuss two existing views on minimal cognition. We start with a brief outline of Maturana and Varela's (e.g. 1980, 1988) autopoietic theory which, besides providing a theory of life, delivers an original perspective on what defines cognition[iii] (see also, Beer, 2004; Bitbol & Luigi, *in preparation*; Luisi, 2003; Lyon, 2004). Next, we introduce the work of Moreno and collaborators regarding their ideas on what sets cognition apart from life.

2.1 Cognition as Life Itself

The term 'autopoiesis', coined by Maturana and Varela (1980), is a concept that denotes an abstraction of the self-producing processes that take place in all living systems (Maturana & Varela, 1980; 1988). An autopoietic system is an intricate, recursive network of self-organizing processes that is capable of maintaining its own organization despite environmental perturbations, acting as an invariant, bounded unity in space and time (Varela, 1992). In autopoietic theory, even minimal living systems, the simplest autopoietic organizations, are regarded as autonomic 'identities' that are categorically distinct from non-living organizations (Maturana, 2002). In these roots of autonomy also lies the very essence of cognition, at least according to autopoietic theory. Maturana and Varela (1980; 1988) consider all life to be inherently cognitive for two closely related reasons: Firstly, autopoietic organizations are, up to a certain point, capable of "responding appropriately" to their ever-changing surroundings (Maturana, 2002). That is, they are capable of interacting with, and adapting to the environment in which they are embedded, by means of self-producing their own organization. Secondly, at the same time, autopoietic systems are able to uphold their organization in spite of these adaptive changes. Maturana and Varela therefore hold that all autopoietic systems are inherently 'cognitive'. On this view, life and cognition are not necessarily taken to be strictly equivalent, but rather as closely related phenomena that share essential characteristics (for elaboration see: Heschl, 1990; Stewart, 1996).

Other authors, including Moreno (Moreno *et al.*, 1997, p.112) have pointed out that there are serious drawbacks to positing such a strong link between the notions of life and cognition. As di Primio *et al*. (2000) recently phrased it: "Seeing cognition everywhere is virtually equivalent to seeing it nowhere in particular." Differently put, by equating cognition with autonomy or autopoiesis, the concept 'cognition' becomes redundant: The problem of explaining cognitive behavior is merely shifted to the problem of explaining life or autopoiesis. This is by itself not very elucidating, especially if we want to come to an understanding of the differences between minimal life and minimal cognition, or between minimal cognition and the more advanced cases of cognition. To put it crudely, it seems important to differentiate between the cognitive processes of the rabbit and those of the carrot.

The idea of equating life with cognition therefore appears to lack the explanatory power that is required to distinguish different forms and aspects of cognition in general.

By casting the relation between cognition and life more loosely, for example by drawing cognitive phenomena as a particular subset of living systems, it becomes possible to maintain a strong link between cognition and life, while at the same time developing a more specific articulation of cognition. Moreno and collaborators, who also criticized the conflation of cognition with life, have already developed such a more limited articulation of cognition. In the following, we will discuss this work and use it as an important stepping stone for developing our own proposal, which is centered on sensorimotor coordination.

2.2 Nervous systems and the Cognitive Domain

Moreno and collaborators (e.g. Moreno, Merelo & Etxeberria, 1992; Etxeberria, Merelo, & Moreno, 1994; Moreno, Umerez, & Ibañez,, 1997; Barandiaran, *this issue*; Moreno & Etxeberria, 2005) consider the cognitive domain to be a clearly bounded sub-domain of the biological domain. In their view, the biological domain is characterized by the basic metabolic reactions that are already present in minimal life forms, and extending to metabolism-based behaviors, or what they term "metabolic agency". For example, Moreno *et al*. (1997) claim that sensorimotor behavior in organisms without nervous systems is still an intrinsic part of metabolic functions, which lack the proper organizational requirements that allow organisms without nervous systems to initiate more than mere metabolic reactions: "*flagellum movements involved in oriented locomotion in certain types of bacteria can be equivalently characterized as modifications in metabolic paths*" (*Ibid*., p.112).

On their view, minimal cognition requires a more complex type of embodiment, enabling so-called 'meta-metabolic functions' that transcend metabolism-based processes by sustaining what Moreno and collaborators call an "independent domain of patterns". To generate these metabolism-independent patterns, organisms require a fast-paced, dynamically de-coupled sensorimotor mechanism. This so-called 'dynamic de-coupling' of sensorimotor patterns is argued to mediate a fast sensorimotor information flow, insulated from the intervention of slower metabolic processes (Moreno & Etxeberria, 2005, p.168).

Moreno and collaborators hold that nervous systems allow for the dynamic de-coupling of sensorimotor patterns, thereby providing organisms with an internal, autonomous sensorimotor domain. The nervous system is depicted as a meta-organization within a general metabolic organization, which supports a form of meta-control over metabolic-like processes through sensorimotor patterns. At least on this view, nervous systems clearly mark the divide between the biological and the cognitive domain. As Moreno *et al*., (1997) argue: "*... the nervous system is the material support of the cognitive phenomenology as an autonomous level with regard to the rest of the biological domain. Cognition appears as a consequence of the emergence of the nervous system.* (p.116)

Recently, however, the contention that nervous systems are essential for the generation of cognitive behavior has been questioned by Lengeler *et al*. (2000), di Primio *et al*. (2000) and Müller *et al*. (2001), who convincingly demonstrated that the evolution of nervous systems was not so much a watershed in the evolution of cognition, but rather an augmentation and amplification of abilities that exist already in unicellular organisms (see also Bitboll & Luigi, *in preparation*; Lyon, *in preparation*, Taylor, 2004). Müller *et al*. (2001) list some of the minimal cognitive capacities that can be found in modern-day prokaryotes, such as indirect and modifiable stimulus-response couplings, memory, adaptation, and even cooperation, thereby satisfying even Neisser's (1967) well-known textbook definition of cognition, namely, "all the processes by which sensory input is transformed, reduced, elaborated, stored, recovered and used".

Although bacteria obviously possess no nervous system, most do embody a molecular sensorimotor mechanism that closely resembles some of the functional sensorimotor features of nervous systems. The discovery of the two-component signal transduction (TCST) system, a molecular sensorimotor system in bacteria, has significantly altered the way in which the complexity of bacterial behavior is viewed by modern-day microbiologists. Taylor (2004) explains why the discovery of the TCST system was such a landmark finding:

"….because it represented the first elucidation of a molecular mechanism for [physiological] adaptation and memory. The discovery also gave some neurophysicists apoplexy because they believed that a nervous system was needed for adaptation and they could not conceive of a complete sensory system in a single bacterium". (p.3671)

Although the sensorimotor organization of the TCST system is ultimately dependent on and sustained by metabolic activity, the sensorimotor organization is organizationally autonomous. Functionally similar to the nervous system, the TCST system gives rise to sensorimotor patterns that transcend purely metabolism related functions (Alexandre & Zhulin, 2001; Taylor & Zhulin, 1998). Given these findings, we believe that a better understanding of minimal cognition can be obtained by looking closer at bacterial behavior.

3 Case Study: The *Escherichia coli* Bacterium

In this case study, we concentrate on chemotaxis behavior in the *E. coli* bacterium, and the workings of its TCST system, a molecular sensorimotor mechanism, which is made up of two 'branches' or pathways, one for perception and one for adaptation. By means of temporal comparison, bacteria are able to detect subtle changes in gradients of chemicals, so that they can travel gradients of attractant and repellant chemicals; a behavior termed 'chemotaxis' (e.g. Koshland, 1980; Boyd & Simon, 1982).
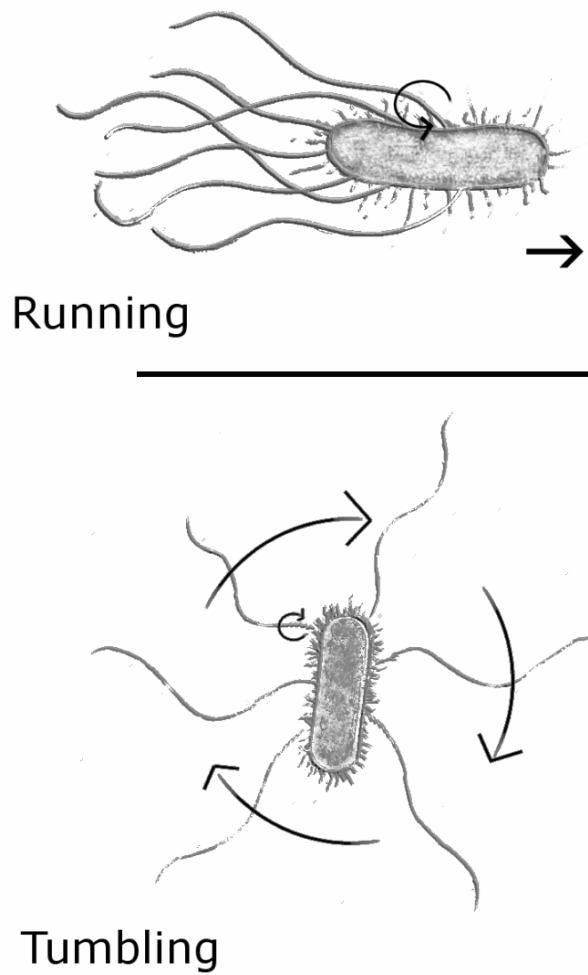

Figure 1. Running and tumbling behavior in *E. Coli*.

3.1 Chemotaxis Behavior in *Escherichia coli*

It is well known that phototaxis can be generated by placing two light sensors at the front of an autonomous vehicle, which drives toward the light by maintaining an equal level of stimulation at both sensors (e.g. Braintenberg, 1984). Due to size constraints, however, evolution has favored temporal detection mechanisms over spatial ones at the bacterial level (Dusenbery, 1998). *E. coli* possesses a total of five types of transmembrane proteins that function as receptors, four of which handle the transmembrane signaling for the TCST system[iv] (Berg, 2000). Each bacterium possesses an estimated total of 8000 of such on/off receptors, each equipped with multiple binding sites, and sensitive to a wide range of extra-cellular concentrations of chemicals. When attractants or repellents dock at these receptors, a signal is carried throughout the bacterium by means of phosphosignaling, ultimately inducing a behavioral change, to run or to tumble (Figure 1).

In a neutral solution, *E. coli*'s behavior resembles a 3D random-walk consisting of periodic patterns of running and tumbling behaviors. When its six or so flagella, semi-rigid, propeller-like structures, rotate counterclockwise, the so-called 'run-modus' is engaged. The flagella then rotate in an organized fashion, thereby providing the bacterium with a powerful torque that may last up to a few seconds (Berg, 2000). During the brief tumbling modus, which lasts on average about 0.1 seconds, the flagella rotate clock-wise, causing the bacterium to move erratically, randomly reorienting it on average 60° from its original direction (Lengeler & Postma, 1999).

When a chemical gradient of attractants is present in the solution in which the bacteria are dispersed, they engage in a hill-climbing strategy to ultimately achieve positive net migration towards the attractant. By altering the frequency of tumbling behaviors, the 3D random walk of the bacterium becomes biased in such a manner that it steadily steers towards an optimal chemical environment (Berg, 2000): When the bacterium detects a higher concentration of attractants, tumbling frequencies decrease, resulting in longer consecutive runs towards an attractant or away from a repellent. In contrast, when encountering a lower concentration of attractants, or a higher concentration of repellents, its tumbling frequencies increase, so that it is more likely to move into another direction.

3.2 Two-Component Signal Transduction Systems (TCST)

The TCST system, or two-component signal transduction (TCST) system is a molecular sensorimotor mechanism that also acts as a molecular form of memory required for chemotaxis (Bourret, Charon, Stock & West, 2002). The TCST system is made up out of two separate but interacting 'branches' or signalling pathways: one that mediates perception, the phosphotransferase or perception pathway, and one that mediates adaptation by providing feedback on the bacterium's receptors, the methylation pathway. The dynamics of the fast-paced perception pathway, which operates at the level of milliseconds, and those of the slower methylation pathway, which functions on the level of seconds, up to minutes, give rise to intricate feedback cycles between the two pathways (Falke *et al*., 1997; Lengeler & Postma, 1999). Due to the interaction of both pathways on different time scales, the methylation level of the receptors is 'compared' to the level of attractor and repellent occupancy at the receptors (Berg, 2000). We first focus on some of the protein complexes and their interactions, which are involved in the signal transduction of the TCST system in *E. coli* before we adress some of the dynamic principles that gouvern the workings of this sensorimotor system.

The general set-up of a TCST system consists of (1) receptors, (2) a transmitter, the protein histidine kinase (CheA) (3) and a response regulator, the protein aspartate kinase (CheY). The latter regulates the direction of the flagella (Koretke, Lupas, Warren, Rosenberg & Brown, 2000; Lengeler & Postma, 1999).
The phosphotransferase pathway is driven by phosphorylation of the histidine and aspartate residues by ATP: CheA (histidine kinase) acts as the phospho-donor and CheY (response regulator) operates as the phospho-receiver (Figure 2).

High levels of repellent chemicals at the bacterial receptors cause CheA, the histidine protein kinase, to auto-phosphorylate, creating a phosphate-derivative of the CheA protein (CheA-P), subsequently leading to the phosophorilation of the response regulator (CheY-P) and the methylation enzyme CheB-P (Figure 2). By becoming phosphorylized, the response regulator (CheY-P) is able to bind with the flagellar switch protein, thereby increasing the probability that the flagellum switches its rotation, inducing tumbling behavior. CheY-P is often said to act as a 'tumbling signal' within the

bacterium, as it regulates the overall tumbling-frequency (Boyd & Simon, 1982; Armitage, 1999). Whereas in normal conditions the CheY-P concentration is maintained on such a level that random alternations between running and tumbling behavior occur, high levels of attractants at the receptors cause a significant drop in CheY-P levels. This causes the chemoreceptors to become less active, subsequently leading to lower tumbling frequencies and prolonged swimming behavior (Manson *et al.*, 1998).
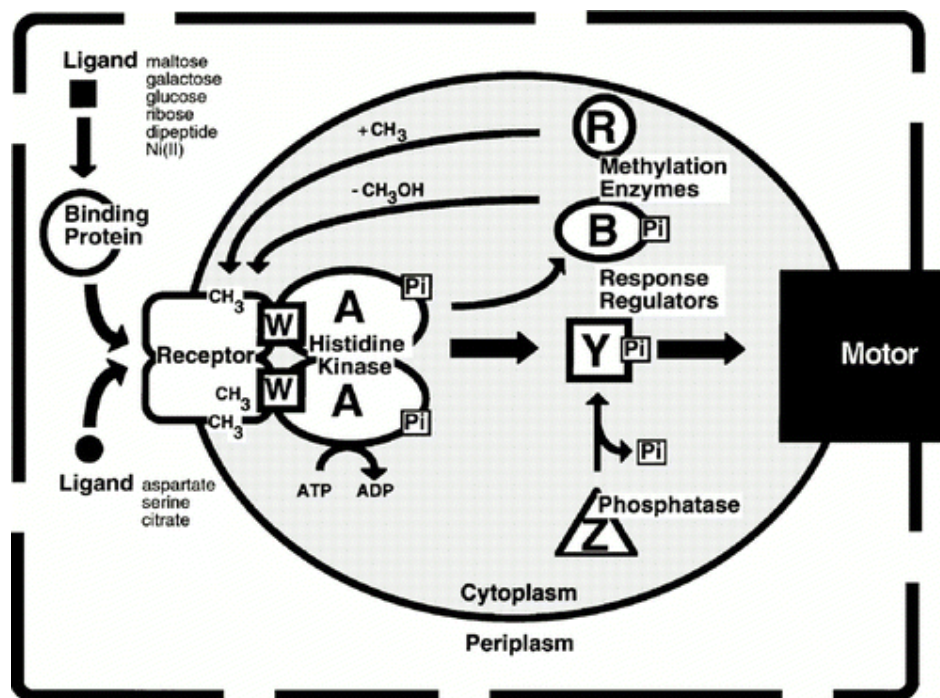

Figure 2. Schematic representation of the protein complexes and their interactions in the TCST system of the *Escherichia coli* bacterium (taken from Falke *et al.*, 1997, used with permission of the first author).

The second pathway in the TCST system, the methylation pathway, regulates the adaptation of *E. coli's* receptors. The concentration of methylgroups at the receptors provides the bacterium with information about previous environmental conditions: When the methylation levels at the receptors sites are high, it reflects that attractant concentrations were high a few seconds ago (Armitage, 1992). When the receptors are occupied by attractants, the protein CheR 'methylates' the receptors; next, CheB-P, a methylesterase, removes the remaining methyl groups from the receptors (Figure 2). The methylation/de-methylation process neutralizes the receptors, and resets them to their null-configuration (Armitage, 1999). The continuous process of methylation and de-methylation of the receptors underlies the bacterium's sensitivity to the relative concentration of chemical compounds rather than to their absolute value (Garraty & Ordal, 1995), and also allows it to remain in an optimum environment once it has arrived there by going back to default running and tumbling frequencies (Boyd & Simon, 1982).

The TCST system can also be interpreted as a signal detection/response regulation system that processes environmental inputs and internal feedback to achieve perfect adpatation. As Tyson, Chen and Novak (2003) frame it in their discussion of the mathematical modelling of the dynamics of these cellular signaling/response relations*:*

"By supplementing the simple linear response element with a second signalling pathway, we can create a response mechanism that exhibits perfect adaptation to the signal. Perfect adaptation means that although the signalling pathway exhibits a transient response to changes in signal strenght, its steady state response R is independent of S. Such behavior is typical of chemotactic systems, which respond to an abrubt change in attractants or repellents, but then adapt to a constant level of the signals. Our own sense of smell operates this way." (p. 223).

In other terms, the transient feedback that is sustained by the slow-paced methylation pathway provides *E. coli* with a dynamic, molecular form of memory which allows it to perform what has been dubbed as "robust integral feedback control". That is, by filtering out external noise and internal variations, and enhancing tiny variations in populated receptor density, the output of the system becomes independent of the input level in steady-state, enabling perfect adaptation to a stimulus (Yi, Huang, Simon & Doyle, 2000).

4. Minimal Cognition as Sensorimotor Coordination

How does the discussion of *E. coli's* chemotactic behavior help to make a clear case concerning the minimal forms of cognition? The context for asking this question was work from Moreno and coworkers who set cognition clearly in the context of living organizations, as argued for by Maturana and Varela, but who also claimed that the cognitive domain should be distinguished as a special case from the general biological domain. In their view, cognition arises when biological systems transcend mere metabolism-dependent functions. For this purpose, they say, a nervous system is required, which provides a structurally autonomous sensorimotor subsystem that can be used to initiate and guide sensorimotor behaviors decoupled from metabolic processes. We think that our *E. coli* example helps to improve upon this biological account in two important ways.

First, it presents a strong case against the intuitively appealing idea that nervous systems are necessary for cognition, and that nervous systems should serve as the proper starting point for a theory on cognition (e.g. di Primio *et al*., 2000; Lengeler *et al*., 2000; Lyon, 2005). The best reason for making a strong linkage between the nervous system and cognition is that it seems so obviously true. All creatures that are obviously cognitive—such as humans and maybe apes—have big brains and thus the connection seems logical. Why the nervous system? Tissue characteristics are an unlikely candidate as this would cast brain stuff as a sort of magical substance that made the difference. A much more likely candidate would be the performance of a particular function by the nervous system, but then one would have to specify this function, and argue that such a function cannot be performed by other structural organizations, such as a bacterial TCST-system.

Second, the example suggests a more basic, more general and conceptually clearer starting point for minimal cognition: sensorimotor coordination. We will argue that sensorimotor behavior is intrinsically different from metabolic processes and thus a very suitable starting point for a solid account of minimal cognition. In the following, we will first develop and discuss these two improvements of a biological account of minimal cognition. Subsequently, we will draw a link with situated cognition, and argue that our way of casting cognition falls nicely within this paradigm; grounding the growing consensus that the core of cognition revolves around sensorimotor coupling.

4.1 From Metabolic Adaptation to Minimal Cognition

The earliest forms of ontogenetic adaptation in unicellular organisms were probably governed by metabolic reactions[v]. The evolution of molecular sense-mechanisms, such as configurable membrane proteins coupled to processes that rapidly adjust and regulate gene-expression and metabolism, allowed organisms to better adapt to rapidly changing environmental conditions (Bonner, 2000). These signal-regulation systems may have partly consisted of locally acting regulator genes that were responsive to very specific environmental features. Throughout the course of evolution, more complex forms of these hierarchical regulatory control systems appeared, permitting regulator genes to exert increasingly global control over metabolic functions, thereby becoming sensitive to more overall physiological and external features (Lengeler, 2000).

A modern example of such a basic form of metabolic adaptation can be found in the 'lac operon'

system, which regulates the metabolism of lactose in *E. coli*. This cluster of genes is normally dormant, because the bacterium predominantly metabolizes glucose. However, when the bacterium detects that glucose levels are very low and lactose is abundantly present in the environment, the lac operon system becomes dis-inhibited, subsequently allowing the transcription and expression of genes that enable lactose metabolism (Todar, 2004). This form of metabolic adaptation is induced by environmental conditions, but still a part of the organism's metabolic organization. The process consists of a change in the set of chemical reactions that together constitute the bacterium's metabolism.

Chemotaxis, on the other hand is a different kind of process. It is itself not constituted by chemical reactions, but by physical changes in the position of the bacterium with respect to its environment. In other words, the environment is manipulated at a larger, physical level so that metabolic processes, and thus the bacterium, benefit from the change, but this manipulation of the environment—moving towards a food source, for example—is itself not part of the metabolism. With respect to metabolism, chemotaxis is a second-order process, which is relevant for changing metabolic opportunities, and in this way expanding the adaptive opportunities of organisms to a considerable degree. In our view, chemotaxis is a good example of how sensorimotor coordinations expand metabolic forms of adaptation, how they are closely related to the latter and at the same time intrinsically different.

Chemotactic processes, or rather more generally, sensorimotor coordinations also provide a good starting point for cognition. What occurs here in bacteria is a kind of process that can be expanded in increasingly complex ways in larger organisms, such as ourselves, while all the time remaining a clear case of sensorimotor coordinations. While metabolic processes involve particular chemical reactions, sensorimotor coordinations play on a larger scale and require a particular physical embodiment of an organism, be it bacterium or monkey. For bacteria, this comes in the form of specific chemical receptors such as methyl-accepting proteins, and actuators such as flagella or pili that enable the bacterium to move about (Berg, 2000). In addition, we have seen that there is also, in *E. coli* and many other bacteria a TCST-system which acts as a memory and inner connection between sensors and effectors in a way that is functionally similar to the nervous system in multicellular animals. TCST-systems probably evolved by integration of pre-existing signaling pathways that were in the first place metabolism related, but later evolved to serve these other purposes (Alexandre & Zhulin, 2001; Bourret, Charon, Stock & West, 2002). The use of these pathways for sensorimotor functions was the beginning of a structural organization dedicated to reacting to the environmental dispersal of metabolic requirements, rather then these requirements themselves.

Casting biological forms of sensorimotor coordination as the minimal form of cognition provides a clear and transparent starting point for thinking about cognition. Of course, there is an enormous gap between the bacterial TCST-system and human reflection, but there is also a clear commonality. Both can be described in terms of perception, memory and action, and both have their organizational foundation in some form of sensorimotor coordination. In addition, in the bacterial case one already finds the basic ingredients that have been expanded on in evolutionary history, and for this reason it provides a plausible minimal case of cognition.

Dobzhansky said that nothing in biology makes sense except in the light of evolution; Maturana could have added that the same applies for metabolism or autopoiesis. Metabolism and cognition remain intrinsically connected even when they are clearly different kinds of processes: Metabolism is based in chemistry. Cognition is based in sensorimotor coordination, which modulates the conditions of metabolic processes. This way of casting minimal cognition is also highly congenial to the notion of cognition which is now being developed within the domain of situated cognition.

4.2 Situated Aspects of Minimal Cognition

The dominant paradigm in the cognitive sciences, i.e. cognitivism, assigns cognition to the internal workings of the brain, an assumption that is increasingly under attack nowadays (e.g. Brooks, 1999; Clark, 1997; Keijzer, 2001; O'Regan & Noë, 2001). At least at the level of minimal cognition, it is clear that a thorough understanding of bacterial behavior molded exclusively in computational terms would be incomplete. The characteristics of the embodiment of the *E.coli* bacterium can teach us about the biological preconditions for minimal cognition. For example, *E. coli's* rod-like shape diminishes the impact of Brownian motion so that less randomization in orientation occurs, thereby optimizing chemotaxis behavior (Dusenbury, 1998). Another such embodied feature can be found in the spatial

location of the bacterial receptors: *E. coli* possesses complex interacting arrays of receptors clustered at its poles. It has recently been suggested that this contributes to a more uniform response of the flagellar motors, which are located at different distances from the receptors (Sourjik, 2004, p. 572).

Besides the embodied characteristics, the complexities of minimal cognitive behavior are equally dependent on the dynamic interaction of the minimal cognizer with its environment. Chemotaxis is a good example of minimal cognitive behavior that can only be fully understood as an environmentally extended or 'situated' phenomenon. That is, *E. coli's* inherent behavioral patterns interact with gradients or structures in the environment. 'Situatedness' is more than just a precondition for minimal cognitive behavior. Whereas preconditions such as viscosity provide a stable background for the occurrence of the cognitive processes themselves, the sensorimotor interaction of the minimal cognizer is constitutive of the cognitive process itself. Such interaction spaces are species specific, since they depend on the embodiment of the organism in question. As von Uexküll (1937) phrased it almost three-quarters of a century ago: "Every animal is surrounded by different things, the dog is surround by dog things and the dragonfly is surround by dragonfly things. Every *Umwelt* has its own spatio- and temporal dimensions." (p117).

From this perspective, minimal cognition is not so much a centralized property of biological hardware of an organism, or a set of internally computed algorithms, but instead denotes an abstraction of organism-environment reciprocity. This reciprocity is dynamic in that it is meaningless if regarded at a single point in time. Not until one regards the unfolding of the behavior over time do the differences between the fast activity of the phospho-relay signaling pathway and the slower response of the methylation/demethylation pathway become apparent: the transient feedback that is induced by the methylation pathway operates on a much slower timescale, in the range of seconds to minutes, compared to the perception pathway, which operates on the level of milliseconds. At least at the level of minimal cognition, it therefore appears that embodiment, situatedness and dynamics are on an even footing in the establishment of cognitive behavior.

5 Implications

Our interpretation of minimal cognition (1) opposes the common anthropocentric interpretation of cognition as well as the general dichotomy it induces between intelligent cognizers, and mechanic-like organisms merely capable of reflexive/instinctive behaviors. In addition, (2) it stretches the scope of the concept of cognition to include basic sensorimotor behaviors, which also supports and grounds currently developing ideas in cognitive science that emphasize the dynamic, situated and embodied aspects of cognition (e.g. Clark, 1997, Brooks, 1999; O'Regan, & Noë, 2001). We elaborate on each of these implications:

(1) Anthropocentrism and the classical dichotomy between cognition and reflexes/instincts

We have discussed how the *E. coli* bacterium is capable of traversing gradients of attractant or repellant chemicals in its environment. This behavior involves many of the components it needs to qualify for traditional definitions of cognition i.e., perception, memory, and action. Indeed, from a third-person perspective, this behavior might even be described as decision-making: to run or to tumble (Jonker *et al*., 2001). However, the purpose of our case study was not to propose that bacteria be labeled genuine (minimal) cognizers in the traditional anthropocentric sense of the term; obviously, bacterial chemotaxis is a long way removed from human beings having to decide to go to a Mexican or to a Chinese restaurant. Instead, we wish to stress that minimal cognition and the evolutionary advantages it provided can only be misinterpreted from an anthropocentric perspective. From our point of view, the issue is not whether bacterial behavior involves genuine decision making, or whether this and other similarly antropomorphic capabilities are merely used instrumentally to interpret bacterial behavior from an intentional stance. Instead, we would rather ask questions about the evolution of cognition and its biological boundary conditions. The reason why minimal cognition evolved probably was in the first place metabolism related: these organisms were all faced with the general problem of optimizing the conditions for upholding their metabolism. We suspect that this fundamental problem lies at the origin of many, if not all, basic forms of cognition, and that it is crucial to understand nature's solutions to it in order to understand (complex) cognition. Reserving the term cognition for typically human problem-solving abilities like those involved in the restaurant dilemma, and

dismissing simpler behavior as mechanistic, reflexive, and hard-wired does not do justice to the behavioral complexities of even the simplest of organisms. This injustice might also work the other way round in that this posited dichotomy leaves room for, and even induces the over-privileging of human thinking. While anthropocentric explanations to cognition tend to focus on the divergences between "man and animal", we believe that there is much more overlap than is generally acknowledged. Our hope is that the further development of a biogenic (Lyon, *in preparation*) perspective on cognition may eventually lead to less biased, more natural descriptions of these complex behaviors, as well as their determinants.

(2) Minimal cognition as Sensorimotor Coordination
    If cognition is truly grounded in sensorimotor processes as we suspect, it implies that the study of cognition in other organisms should aim for a better understanding of the dynamics of relatively simple sensorimotor coordinations, rather than typically human capabilities such as reasoning, explicit problem-solving or symbolization (e.g. Heinrich, 2000; Gould & Gould, 1998; Smirnova *et al*., 2003).
    In this respect, the behavior of the *E. coli* bacterium teaches us some valuable lessons. Three aspects of the chemotaxis behavior stand out: the behavior is embodied, dynamic and situated. The behavior is embodied, in the sense that it is fully determined by the specific properties of the bacterium's body, which can teach us about the biological preconditions for minimal cognition: *E. coli*'s rod-like shape enhances its efficiency to perform chemotaxis behavior. The difference in time scale of both pathways is crucial in the generation of chemotaxis: the transient feedback induced by the methylation pathway of the *E. coli* bacterium operates on a much slower timescale compared to its fast-paced perception pathway.
    Minimal cognition in general, and our case study in particular, can provide simple models for ideas that currently circulate in cognitive science (Brooks, 1999; Clark, 1997; O'Regan, & Noë, 2001; Port & Van Gelder, 1995; Thelen & Smith, 1994). These ideas all subscribe to the general view that cognition is not centered on internal computations, but that situated action is key in cognition. Our review of chemotaxis in the *E. coli* bacterium explicates and grounds some of these ideas in solid empirical work, and shows that there is much more to cognition than human reasoning.
    Taking sensorimotor coordinations as a starting point for cognition supports a biogenic perspective (Lyon, *in preparation*) on the evolution of cognition. Moreover, based on our interpretation of minimal cognition, the evolution of cognition can be seen as a process of incremental differentiation and expansion of sensorimotor coordination abilities (Keijzer, 2001). On our view, the sensorimotor principles that underlie brains and nervous systems are rooted in the very same sensorimotor principles that can be found in bacteria. Our hope is that the further development of such a biogenic perspective will allow for a better differentiation of cognitive abilities, and with that a more fundamental understanding of cognition as sensorimotor coordination.

6 Conclusion
    In this article, we have attempted to get clearer on what defines minimal cognition. Against the contention that nervous systems are required for cognition, we argued that minimal cognitive processes can already be witnessed in prokaryotes that possess what in some ways is a functional sensorimotor equivalent of the nervous system, the TCST system. Our case study of the *E. coli* bacterium demonstrated the structural and dynamical complexities behind minimal cognitive behavior. With our account of minimal cognition we hope to contribute to the growing consensus that the core of cognition revolves around sensorimotor coupling, and underscore the importance of understanding dynamical, situated, and embodied aspects of minimal cognition, and cognition in general. Additionally, our study of minimal cognition suggests that cognition should not be seen as a prerogative of a handful of 'elite' organisms, but indicates that there exists a vast cognitive spectrum that fills the gap between the mindful and the mindless.

Notes

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[i] This empirically questionable anecdote has been analyzed in Keijzer (2001).

[ii] It is important to draw a contrast between our own project and other, possibly more dominant evolutionary approaches to cognition (e.g. Dennett, 1996; Godfrey-Smith, 1996, 2001; Sterelny, 2001). Godfrey-Smith (1996) makes a very broad distinction between externalist and internalist explanations of organic systems. He uses the term externalism "for all explanations of properties of organic systems in terms of properties of their environment" (p.30) and names empiricism and adaptationism as examples. In contrast, internalism explains "one set of organic properties in terms of other internal or intrinsic properties of the organic system" (ibid.). Godfrey-Smith stresses that both forms of explanation are not disjunctive but a matter of setting different explanatory priorities to either internal or external factors. Without subscribing to this general distinction, it is nevertheless a useful one for distinguishing our project from the externalism professed by authors like Godfrey-Smith, Dennett, and Sterelny, among others. Externalism, as a form of adaptationism, describes in our eyes how and why simple agents evolve and develop into more complex ones as a result of environmental pressures. However, casting cognition as adaptation does not target the phenomenon of cognition itself, the process or set of processes that makes such adaptation possible in the first place. John Staddon (2001) made the point very nicely when he argued that the optimization of adaptation provides a "tolerably good picture of what animals manage to achieve, but a poor picture of how they actually do it. Animals often behave optimally; they almost never optimize in any literal sense." (p.77) Externalism may explain why cognitive processes have evolved, but this does not give an account of what these processes consist of. This point is particularly important because an externalist perspective very easily obscures the cognitive process itself by defining it in terms of the function it performs. The physical cognitive process then simply becomes whatever produces the required function and it looses its own status as a separate phenomenon. We oppose this externalist tendency and try to articulate the notion of minimal cognition as a material process with its own specific characteristics.

[iii] In this article, we concentrate on the 'cognition = life' thesis, rather than on other aspects of autopoietic theory. For recent detailed reviews and overviews of autopoietic theory the interested reader is referred to: Beer, 2004; Luisi, 2003; Lyon, *in press*.

[iv] The TCST system is not the only one that is used by enteric (gut living) bacteria, there is abundant evidence that there exist other less well understood forms of taxis that rely on different underlying pathways, which may or may not share common components such as phospho-dependent or MCP dependent sensing (see also Alexandre & Zhulin, 2001; Lengeler & Postma, 1999).

[v] In this article, 'metabolism' is interpreted as the sum of processes that continuously maintains functional cell integrity.

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