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The biocognitive spectrum

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THE BIOCOGNITIVE SPECTRUM

Biological Cognition as Variations on Sensorimotor Coordination

The cover features a photoshopped version of a snapshot I took in 2003 on a boat in the Mediterranean Sea of the coast of Crete. The original picture captured the deep crystalline turquoise waters illuminated by the piercing sun. Inspired by David Marr's work on visual perception, I used a Laplacian of a Gaussian filter, which calculates the zero-crossings in the picture obtaining what Marr called a 'primal sketch' of the photograph, revealing the patterns of the perturbed water in a blend of colors. The superimposed picture of the *E.coli* bacteria is made by S. Kaulitzki.

Doctoral Dissertation for Philosophy
The Biocognitive Spectrum
Biological Cognition as Variations on Sensorimotor Coordination

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Biological Cognition as Variations on Sensorimotor Coordination

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Chapter 4 features a slightly revised version of a paper that was previously published by Taylor & Francis Group as: van Duijn, M., & Bem, S. (2005). On the Alleged Illusion of Conscious Will. *Philosophical Psychology, 18(6),* 699-714.

In the distant future I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history (p.488).

Charles Darwin (1859)

Contents

General Introduction

> *If we are to believe that neurons are the only things that control the sophisticated actions of animals, then the humble paramecium presents us with a profound problem. For she swims about her pond with her numerous hairlike legs - the cilia - darting in the direction of bacterial food which she senses using a variety of mechanisms, or retreating at the prospect of danger, ready to swim off in another direction. She can also negotiate obstructions by swimming around them. Moreover, she can apparently even learn from her past experiences - though this most remarkable of her apparent faculties has been disputed by some. How is this all achieved by an animal without a single neuron or synapse? Indeed, being but a single cell, and not being a neuron herself, she has no place to accommodate such accessories* (p.357).
>
> Roger Penrose (1994)

What is cognition? The term cognition has strong connotations with knowledge and reasoning. The etymological origin of cognition is found in the Latin verb *cognoscere*, which translates as “to get to know” or “to be acquainted with” (Gershenson, 2003). In most introductory cognitive science textbooks, cognition is used as a wastebasket term involving sophisticated human cognitive skills such as language, decision-making, and problem-solving. This anthropocentric interpretation of cognition, however, is by no means the only viable interpretation of cognition in modern-day cognitive science. Cognitive science is a fragmented science that consists of many scattered sub-disciplines, including cognitive neuroscience, linguistics, artificial intelligence, psychology, cognitive ethology, and philosophy of mind. Throughout these different research fields, cognition is interpreted in a wide variety of ways, such as: cognition as computation (e.g. Newell & Simon, 1976; Newell, 1980; Pylyshyn, 1984), cognition as information-processing (e.g. Broadbent, 1958; Atkinson & Shiffrin, 1968), cognition as the state-space evolution of dynamical systems (van Gelder, 1995; Port & van Gelder, 1995), or less mainstream, such as cognition as autopoiesis (Maturana & Varela, 1980; Heschl, 1990; Stewart, 1996), cognition as neural agency (Moreno, Umerez, & Ibañez, 1997; Moreno & Etxeberria, 2005), and the now popular view, cognition as a dynamically coupled brain-body-environment system (e.g. Clark, 1997, 2008; Beer, 2008; Montebelli, Herrera, & Ziemke, 2008; Robbins & Aydede, 2008). Given that there exists no single agreed upon interpretation of cognition that is shared throughout these research fields, modern-day cognitive science still lacks a shared understanding of what cognition *is* and what cognition *does,* as Lyon (2006a, p.13) put it. Cognitive science has still not succeeded in becoming a unified research field: the lack of consensus on what constitutes cognition is a major theoretical bottleneck that hampers unification in the cognitive sciences.

In the last two decades, however, two global theoretical developments have fundamentally changed the way in which cognition was traditionally interpreted, which was mainly centered on the symbolic properties of cognition, such as its linguistic, logical, and computational aspects. First, in this era by some called ‘post-cognitivism’, cognitive science seems to be converging towards a more embedded and embodied view of cognition by also incorporating morphological, situational, and dynamical factors in the study of cognition (e.g. Anderson, 2003; Beer, 2008; Bennett & Hacker, 2003; Calvo & Gomila, 2008; Clark, 1997; Keijzer, 2001; Pfeifer & Scheier, 1999; Pfeifer & Bongard, 2006; Polani, Sporns, & Lungarella, 2008; Wilson, 2002). Some authors argue that cognitive science is undergoing a Kuhnian paradigm shift toward such an embodied/embedded view (Chokr, 2008; Froese, 2007), and indeed, recent developments show that the foundations of such an embodied/embedded paradigm are well in place (see Calvo & Gomila, 2008; Robbins & Aydede, 2008).

Second, there is a strong shift towards a more biologically oriented explanation of cognition (e.g. Christensen, 2007; Garcia, 2007, 2010; Geary, 2006; Godfrey-Smith, 2002; Griffiths & Machery, 2008; Lyon, 2006a, 2006b; Tommasi, Peterson & Nadel, 2009). This biological approach to cognition is less centered on explaining human cognition, but tends more to investigate and explain the fundamental aspects of natural forms of cognition, such as by examining its evolutionary and biological basis, and by asking questions such as why cognition evolved in the first place. Like the embodied/embedded interpretation of cognition, adherents of the biologically oriented view often stress the importance of the morphological and ecological factors that govern cognition (e.g. Christensen, 2007; Prescott, 2007). When combined, these two theoretical perspectives shed a different light on some popular assumptions about the nature of cognition. In particular three of such premises have become questionable or are seen differently due to these developments: (1) the idea that cognition is brain-based, (2) the view that cognition is computation, and (3) anthropocentric interpretations of cognition:

(1) *Cognition is brain-based*

The view that cognition is 'something done by the brain' seems so self-evident that it is hardly ever questioned (Almeida e Costa & Izquierdo-Torres, 2006). According to the brain-based view, the brain is *the* organ for cognition, and cognition is what the brain does. Only brains are presumed to be complex enough to generate cognitive processes such as memory, thought, and reasoning. From this perspective, the behaviors of 'simple' organisms that lack a strongly cephalized nervous system such as jellyfish and unicellular organisms such as protists and bacteria do not raise any serious cognitive research interest. Indeed, research on the evolution of cognition is primarily centered on animals equipped with relatively complex brains, such as mammals and birds (see for example Heyes & Huber, 2000; Roth & Wullimann, 2001). Proponents of the brain-based view (often implicitly) assume that the evolution of cognition coincides with the evolution of the brain. The standard view is that cognitive abilities evolved by increased encephalization quotients, increased conduction velocity of nerve fibers, and the allometric growth of the prefrontal cortex (e.g. Gould & Gould, 1998; Roth & Dicke, 2005). On this view, cognition is a property that developed relatively late in evolution, at the earliest with the evolution of the first centralized nervous systems, which rough estimates suggest occurred not long before the Cambrian explosion that initiated roughly about 542 million years ago (Arendt, Denes, Jékely, & Tessmar-Raible, 2008; Balavoine & Adoutte 2003; Levinton, 2008). By default, brain-based approaches to cognition therefore ignore roughly the first 3 billion years of biological evolution.

The view that cognition requires a brain or a central nervous system is contested by empirical research from a variety of research fields, including micro-biology and comparative behavioral studies, which is interpreted as convincing evidence for cognitive-like abilities in single-celled organisms (e.g., Ben-Jacob, Shapira & Tauber, 2006; Bitboll & Luigi, 2004; di Primio, Müller & Lengeler 2000; Lengeler, Drew & Schlegel, 1999; Taylor, 2004). Jennings (1906) already noticed over a century ago that the complexity of the behaviors of some unicellular organisms rivals that of organisms equipped with nervous systems or simple brains. As Jennings showed, organisms with primitive nervous systems are not necessarily smarter in terms of the complexity or adaptiveness of their behavior than organisms without them (see Keijzer, van Duijn, Lyon, *submitted*). Recent microbiological evidence dovetails with Jennings views and shows that bacteria already exhibit complex cognitive-like capabilities that are often presumed to be precluded to organisms with centralized brains. For example, research shows that some of the capacities that are found in bacteria include: indirect and modifiable stimulus-response couplings, robust sensory adaptation, memory, and social co-operation (Müller, di Primio, & Lengeler, 2001). In his lauded book *Evolving Brains*, John Allman (1999) states:

> *Some of the most basic features of brains can be found in bacteria because even the simplest motile organisms must solve the problem of locating resources and avoiding toxins in a variable environment. Strictly speaking, these unicellular organisms do not have a nervous system, but nevertheless they exhibit remarkably complex behavior. They sense their environment through a large number of receptors and store this elaborate sensory input in the form of brief memory traces. Moreover, they integrate the inputs from multiple sensory channels to produce adaptive movements* (p.3).

The idea that prokaryotes are already capable of cognitive-like behaviors suggests that cognition represents a phylogenetically ancient adaptive process that evolved long before the establishment of cephalized nervous systems. All this seems to undermine the brain-based view of cognition; brains and, more generally, nervous systems therefore appear sufficient but not necessary for cognition.

(2) *Cognition is computation*

Cognitivism has been the predominant research paradigm in the cognitive sciences since roughly the late 1950's. Cognitivism holds that the brain is a formal symbol manipulation device of which the operations are formally equivalent to those of a computer (e.g. Newell, 1980). On this popular view, cognition is the software that runs on the hardware of the brain; or, *cognition is what the brain does*. Nervous systems pick up environmental information from sensors and use this information to select, initiate and guide behavior fitted to the perceived information. Neurons integrate information by making a summation on the inputs they receive from their dendritic connections and based on the calculation of these weighted values they generate an all-or-none action potential; a process that can also be viewed as a way of binary coding. Cognitivists assume that cognition is an 'embrained' process that takes place somewhere between the reception of peripheral sensory input and the generation of motor output. According to Hurely (1998), cognitivists presume that cognition is a process that is separate and functionally detached from perception and action; cognition is 'sandwiched' in between perception and action buffer zones: perception encodes incoming (e.g. visual, auditory, chemical) signals into neural codes, which are processed by cognition in a (sub)symbolic format, after which an appropriate behavioral output is generated (Hurley, 1998, 2001; Freeman, 1999b).

In the last two decades, after some earlier criticisms (e.g. Dreyfus, 1979; Searle, 1990), the computational view of cognition is increasingly criticized. The now popular embodied/embedded approach to cognition (henceforth EEC) has in particular taken a stance against the cognitivist' interpretation of cognition (e.g. Brooks, 1999; Freeman & Núñez, 1999; Hurley, 1998). Advocates of EEC claim that cognition is not restricted to the brain but that it also involves morphological, dynamical, and situational factors (e.g. Clark, 2008; Keijzer, 2001; Pfeifer & Scheier, 1999; Pfeifer, Lungarella, Sporns & Kuniyoshi, 2007; Beer, 2008). On this view, cognition is constituted by the tightly coupled dynamics between an agent and its environment (e.g. Clark, & Chalmers, 1998; Port & van Gelder, 1995; Wilson & Clark, 2008). Most proponents of EEC dispute the idea that computations alone can provide an exhaustive explanation for cognition. Corporeal features and organism-environment interactions can help resolve problems that from a cognitivistic perspective appear to be strict computational issues. That is, the body's biomechanical features such as the inherent rigidity of bone or elasticity of muscles, and the morphology of sense organs generate their own intrinsic dynamics that are passively and actively exploited to relieve the burden for neuronal control processes. On this view, there is more to cognition than mere computation: morphological factors and organism-environment interactions are part and parcel of the cognitive process they help to instantiate; processes that cannot be understood in computational terms alone (Pfeifer, Iida & Gómez, 2006).

EEC also challenges the cognitivist' view that cognition can be understood separately from perception and action. Instead, the idea that perception and action are in fact part and parcel and constitutive of cognition has gained in popularity in a wide variety of research fields. In cognitive and developmental psychology, action-based robotics, and philosophy of mind, the study of perception-action has even become a central theme (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Jeannerod, 1997; Prinz & Hommel, 2002; Pfeifer, Ilda, & Bongard, 2005). Modern research shows that perception-action contributes to the development of cognitive processes such as depth perception, object classification, category learning (e.g. Pfeiffer *et al.*, 2006), imagination (Oullier, Jantzen, Steinberg & Kelso, 2005), learning by imitation (Rizzolatti & Craighero, 2004), and Theory of Mind (Blackmore & Decety, 2001). This research suggest that cognitive skills are often, if not always, ultimately dependent on perception-action coupling. Many of authors therefore argue that cognitivism has provided a one-sided view of cognition that fails to consider the role of perception and action, and also the embodied and situated factors that play a role in cognition.

(3) *Anthropocentrism*

Psychology is since long criticized because of its anthropocentric approach to cognition (e.g. Yerkes, 1933; Staddon, 1988). That is, psychology as a scientific discipline is centered on human behavior, and its central concepts such as 'intelligence', 'learning', and also 'cognition' therefore have strong connotations with human abilities. Even biologically oriented approaches to the study of cognition often retain this anthropocentric interpretation of cognition. Although it has since long been advocated that cognition and behavior are best understood in the context of biology and evolution (e.g. Darwin, 1859; James, 1890; Tinbergen, 1963), modern approaches such as evolutionary psychology have remained stuck in the anthropocentric modus and are still centered on explaining human-behavior in an evolutionary context. Cognition is usually defined in terms of these typically human-like cognitive abilities. That is, in the eyes of many cognitive scientists, human cognition provides us with the only unquestioned and uncontroversial examples of cognition, such as language, reasoning, and self-awareness. It then becomes a research question in which ways and to what extent other animals exhibit these human-like abilities (see for example, Heinrich, 2000; Smirnova, Lazareva & Zorina, 2003). Lyon (2006a) calls this the anthropogenic (*genic* = starting point) interpretation of cognition. Anthropogenic approaches to cognition presuppose (often implicitly) that human cognition is the best place to start thinking about cognition. Lyon (*Ibid.* p.52) argues that anthropogenic interpretations take human cognition as a measure with which the cognitive abilities of other animals are to be compared. Other organisms then have to satisfy these benchmark criteria in order to be qualified as genuine cognitive agents. Only complex animals such as primates, birds, and aquatic mammals then either qualify as genuine cases of cognition or represent the borderline cases of cognition depending on to what extent they exhibit these human-like qualities. Organisms incapable of such complex feats, such as invertebrates and single-celled organisms are subsequently left out of the picture. The behavior of these primitive organisms is usually regarded to be the product of species-specific instincts or hard-wired reflexes; inflexible, reactive behaviors that have little to do with cognition (Godfrey-Smith, 2002; Keijzer, 2001).

An alternative to the anthropocentric approach is the so-called *biogenic* approach to cognition (Lyon (2006a). This approach tries to anchor the concept of cognition itself in biology. On this approach, cognition is in the first place a form of biological adaptation that confers certain specific selective advantages for organisms by allowing them to cope with environmental complexity (Godfrey-Smith, 2002). From this bottom-up view, it becomes important to specify these adaptive advantages, to be more specific about the structural demands and functional mechanisms of cognition, to distinguish cognition from life itself, and to distinguish it from other forms of biological adaptation, such as genetic adaptation. Human cognition and computer cognition then become special instances of cognition rather than the theoretical starting-points for understanding what cognition is. That way, a more neutral biological conception of cognition can be obtained that is not riddled with anthropocentric connotations. This biogenic approach to cognition also aims to integrate psychology with biology by providing a common conceptual understanding of cognition.

Goals and Overview

The aim of this thesis is to provide a bottom-up conceptual interpretation of biological cognition - or *biocognition* - that focuses on the shared mechanisms and organizational principles that mark all natural cognitive systems. Such an interpretation of biocognition may ultimately help to facilitate theoretical unification in the cognitive sciences by providing a common conceptual understanding of natural cognition. The three issues outlined above form the theoretical backdrop for each of the chapters in this thesis: (1) The evidence that supports cognition in single-celled organisms warrants a closer look into the underlying mechanisms that govern these minimal cognitive abilities. The first goal of this thesis is to specify the minimal requirements for the generation of cognitive behavior and to distinguish minimal cognition from other forms of biological adaptation; (2) The second goal is to merge EEC with a biogenic approach to cognition and to focus on all the ways in which organisms adaptively use sensorimotor coordination; (3) The third goal is to examine the major biological organizational principles that underlie different forms of natural cognition, and to specify the concept *biocognition*. This thesis contains five chapters which serve to tackle these three issues, while chapter 6 summarizes the main findings of this dissertation.

Chapter 1 – Historical Introduction: Schools of Thought on Cognition

This first chapter provides a brief historical overview of the most relevant theoretical approaches to cognition in modern-day psychology, including cognitivism, Gibson's ecological approach to cognition, the dynamic systems approach to cognition, and embodied/embedded cognition. The final section of this chapter motivates the biogenic approach to cognition taken in this thesis. In that section, I argue that a fundamental theory of natural cognition is best grounded in a biological explanation that is rid of the common brain-based, computer-based, and anthropocentric biases. On this biogenic approach, cognition is first and foremost a form of biological adaptation that confers selective advantages for organisms by coordinating their sensorimotor behavior. Sensorimotor coordination is an adaptive strategy that is ubiquitous in the animal kingdom and is also exhibited by organisms that lack a central nervous system, such as bacteria.

Chapter 2 – The Lower Bound: Principles of Minimal Cognition
This chapter specifies the minimal requirements for cognition. It features a case-study of the *Escherichia coli* bacterium and its sensorimotor system, the two-component signal transduction system (TCST); a functional sensorimotor analogue of the nervous system. This bacterium also exhibits a molecular form of memory, which it uses to perform chemotaxis; a form of sensorimotor coordination that enables the bacterium to travel to an optimal physico-chemical environment. Sensorimotor coordination enables organisms such as bacteria to modulate and optimize the external conditions for their metabolism. This interpretation of minimal cognition forms the basis of the growing consensus that the phylogenetic basis of cognition revolves on sensorimotor coordination.

Chapter 3 – The Middle Ground: Biological Principles of Cognitive Organization
This chapter explores the transition from bacterial cognition to human cognition by investigating how biological organizational principles shape and constrain natural cognition. The key concept that makes the transition from bacterial cognition to human cognition thinkable is *modularity*. Modularity is a fundamental biological principle that is also relevant to understanding the organization of natural cognitive systems. For example, some evolutionary psychologists claim that our cognitive architecture is massively modular, consisting of an array of specific-purpose computational units in the brain that are responsible for certain cognitive operations. On this view, the brain is organized much like a Swiss-Army knife; a neonates brain comes pre-equipped with a large set of specific-purpose tools that evolved as solutions to specific adaptive problems, such as face recognition, language, and numbers. However, evolutionary psychology's notion of cognitive modularity is regarded problematic because of its gene-centered view of cognitive modularity, which provides a highly restricted view of cognitive modularity. This chapter aims to provide a more biologically plausible account of biocognitive organization. Based on four fundamental biological organizational principles, (1) modularity, (2) hierarchical organization and reuse of components, (3) epigenetic organization, and (4) bow-tie organization, this chapter develops four biocognitive organizational principles. In each case, I will first describe how the principle operates in a general biological context. Subsequently, I will discuss how the principle can be applied to the biocognitive domain.

Chapter 4 – The Upper Reaches: On the Alleged Illusion of Conscious Will
This chapter focuses on the upper reaches of the biocognitive spectrum by discussing the causal efficacy of human consciousness. A biological perspective on consciousness suggests that consciousness evolved because it provides higher order regulatory cognitive functions. In modern-day cognitive science, however, the view that consciousness is action-based is not widely accepted: many scientists and philosophers instead argue that

our subjective experience of having a conscious will that causally contributes to behavior is an illusion created by the brain. In this chapter, I discuss the empirical and theoretical validity of this illusion-claim. I argue that the illusion-claim is rooted in a category mistake, which holds that neuronal activity causes conscious will. In the final sections, I discuss a tentative theoretical view of conscious will as a causal mechanism that affects coordination dynamics by modulating behavioral patterns to match goal-states using sensorimotor coordination.

Chapter 5 – The Biocognitive Domain: Explicating Biocognition

This final chapter integrates the views developed in the previous chapters by providing an explication of the notion *biocognition*. According to this explication, biocognition is a form of biological adaptation exhibited by motile organisms capable of sensorimotor coordination. Biocognition enables organisms to optimize the external conditions for their metabolism so that they can seek out and select more favorable habitats, and are able to hunt down and capture prey. Sensorimotor coordination governs the broad spectrum of biocognitive abilities that are spread all throughout the phylogenetic tree: from bacterial chemotaxis to human reasoning. In this chapter, I also evaluate the plausibility of plant cognition. I argue that although large multicellular plants are capable of complex adaptive responses such as solar-tracking, tropisms, and nastic movements, these behaviors are better explained in terms of phenotypic plasticity, which is the ability of an organism to alter its physiological and morphological characteristics in response to or anticipating changes in environmental conditions. This explication stresses the central importance of sensorimotor coordination in biocognition, the cost-benefit trade-offs that come with sustaining a motile lifestyle, and the importance of size in determining trade-offs between metabolic costs and adaptive benefits of biocognition.

1. Historical Introduction:
Theoretical Approaches to Cognition

> *The cognitive system is not a computer, it is a dynamical system. It is not the brain, inner and encapsulated; rather, it is the whole system comprised of nervous system, body, and environment. The cognitive system is not a discrete manipulator of static representational structures; rather, it is a structure of mutually and simultaneously influencing change. Its processes do not take place in the arbitrary, discrete time of computer steps; rather, they unfold in the real time of ongoing change in the environment, the body, and the nervous system. The cognitive system does not interact with other aspects of the world by passing messages or commands; rather, it continuously coevolves with them (p.3).*
>
> Port (2002)

1.1 Introduction

This chapter provides a short overview and discussion of the different modern theoretical approaches to cognition so as to provide historical context for the views developed in this thesis. The historical overview describes how cognitive science progressed from a computational interpretation of cognition, i.e. cognitivism, to a more dynamic, environmentally situated, and embodied view. The last section of this chapter (section 1.6) discusses and motivates the more specific biogenic approach to cognition taken in this thesis, which merges a biological interpretation of cognition with an embodied/embedded view of cognition. In contrast to the mainstream theoretical approaches to cognition, this biogenic approach focuses exclusively on explaining natural cognition or biocognition, leaving aside cognition in artifacts such as computers. The aim of this approach is to integrate psychology with biology by providing a common conceptual understanding of biocognition as a form of biological adaptation that revolves on the sensorimotor coordination capabilities of motile organisms. Sensorimotor coordination is ubiquitous in the animal kingdom and is also exhibited by single-celled organisms such as protists and bacteria. The biogenic approach taken in this thesis homes in on the sensorimotor mechanisms that govern the most elementary cases of biocognition, and uses these simple cases as a theoretical starting-point to ultimately also explain more advanced cases, such as human cognition.

1.2 Cognitivism: The Computational Approach to Cognition

Cognitivism has been the dominant paradigm in cognitive science since roughly the late nineteen fifties and the cognitivist interpretation of cognition is still highly influential

(Viney, 1993; see for example, Gallistel & King, 2009). Cognitivists infer mental structure by examining how knowledge is stored, transferred, retrieved, and used. Cognitivists focus their study of cognition on the contents of the behaviorist's black box; the internal mechanisms of cognition that mediate in between stimulus and response (Shannon & Weaver, 1949). Cognitive behaviorists such as Tolman (1948) already postulated ”cognitive maps” in the brain order to explain maze-learning in rats, which was soon after followed by research on the internal mechanisms of memory (Miller, 1956), attention (Broadbent, 1958), and linguistics (Chomsky, 1959). On the cognitivist view, cognition is associated with: (1) computation, (2) symbolic representation, and, (3) information-processing:

1. *Cognition as Computation.* The invention of computers and A.I. gave an important initial impetus to cognitivism which drew heavily from computer science and information theory (Von Neumann, 1946; Shannon, 1948;). The Turing machine and the computer provided a powerful metaphor for cognition: cognition as computation (Newell & Simon, 1976; Newell, 1980; Von Neumann, 1958). Cognitivists hold that the brain is an analog symbol manipulation device whose workings are formally equivalent to the operations of digital computers. According to Von Neumann (1958), who laid the mathematical foundation for cognitivism, neurons operate as digital Boolean operators, such as AND, OR, and NOT gates, which obey the rules of a formal logic: neurons integrate information and make a summation on the input they receive from their dendritic connections, and based on the calculation of these weighted values neurons generate an all-or-none action potential that propagates along the axon; a process that can also be viewed as a way of binary coding (McCulloch & Pitts, 1943). On this interpretation, cognition is the operating software that runs on the neurological hardware or ‘wetware’ of the brain. Cognitivism also sustains arguments about the multiple realizability of cognition: what matters in cognition is the computed input-output function between stimulus and response; whether this computational process is implemented in silicon based computer chips or neurons is deemed irrelevant (Pfeifer & Scheier, 1999).

2. *Cognition as Symbolic Representation.* Cognitivists endorse the so-called 'physical symbol systems hypothesis'[1], which holds that all systems capable of generating symbolic representations are cognitive systems. Symbolic representations are internal models of

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[1] Newell and Simon (1976) explain the physical symbol systems hypothesis as follows: “The Physical Symbol System Hypothesis clearly is a law of qualitative structure. It specifies a general class of systems within which one will find those capable of intelligent action. This is an empirical hypothesis. We have defined a class of systems; we wish to ask whether that class accounts for a set of phenomena we find in the real world. Intelligent action is everywhere around us in the biological world, mostly in human behavior. It is a form of behavior we can recognize by its effects whether it is performed by humans or not. The hypothesis could indeed be false. Intelligent behavior is not so easy to produce that any system will exhibit it willy-nilly. Indeed, there are people whose analyses lead them to conclude either on philosophical or on scientific grounds that the hypothesis is false. Scientifically, one can attack or defend it only by bringing forth empirical evidence about the natural world” (p.116).

external features or events; the internal bearers of meaning and intentionality (Newell & Simon, 1976). Symbolic representations are often held to be linguistic propositions mediated by the laws of some kind of inner mental logic, such as Fodor's (1975) "language of thought". The mapping between aspects of the external world and internal representations is achieved by an encoding and decoding function. Cognitivists describe the flow of information from sensors to effectors as a sequential, iterative process: perception encodes incoming (e.g. visual, auditory, chemical) signals into symbolic representations, after which a motor response is created. The brain generates symbolic representations of the environment by translating sensory input into symbolic representations, next, cognitive mechanisms manipulate these representations according to a set of generative syntactical rules, and finally, motor output decodes the symbolic representation into overt behavior (Pfeifer & Scheier, 1999). On this view, cognition exerts a causal role in behavior by performing transformations on internal symbol strings (e.g. Fodor, 1975; Keijzer, 2001).

3. *Cognition as Information processing*[2]. Cognitivism also drew heavily on information theory. Information theory (Shannon, 1948; Shannon & Weaver, 1949) is a classic linear transmission model of communication. Information theory is a quantitative mathematical method that specifies the statistical entropy[3] (disorder) of an information channel in order to separate noise from information. The theory laid the foundation for encoding information into binary code or "bits". Information theory fitted well with computational views that had been developing in neurophysiology. The information-processing picture of cognition describes the flow of information from sensors to effectors, mediated by the nervous system: sensors pick up environmental information and the nervous system uses this information to select, initiate and guide motor systems in a way that fits the perceived information. The highly influential information processing view developed in pre-cognitive science mathematics thus fed back into neurophysiology and became the standard view concerning the operation of brain and nervous systems. Even when the phrase 'information processing' is not always explicitly used, the information processing interpretation is still omnipresent in the basic textbooks of cognitive science and psychology (e.g. Kahle & Frotscher, 2003; Leal, 1994; Pfenninger, 2001; Wulliman & Roth, 2001).

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[2] The notions of 'information-processing' and 'computation' are closely related and often used interchangeably. However, according to Piccinini & Scarantino (2010) there are also important differences; as they put it: "the vehicles over which computations are performed may or may not bear information. Yet, as a matter of contingent fact, the vehicles over which cognitive computations are performed generally bear information, in several senses of the term. […] information processing must be carried out by means of computation in the generic sense, although it need not be carried out by computation in either the digital or the analog sense" (p.28, my brackets).

[3] In information theory, entropy is a measure of randomness in a signal. Erwin Schrödinger's notion of "negentropy" (negative entropy) corresponds to information (Buzsaki, 2006).

David Marr's (1982) computational theory of vision is a prototype example of a cognitivist theory. Marr’s work was an important source of inspiration for cognitivists such as Jerry Fodor and Zenon Pylyshyn. Marr argued that vision is in the first place an information-processing task: vision is a process of extracting images from the world and representing them internally in order to make it available for cognitive processes such as decision-making and reasoning. Marr's computational theory[4] of vision starts with the two dimensional array of raw intensity changes in electromagnetic radiation that reflect on the retina and culminates with a full-blown, highly detailed 3-D symbolic representation of the world.

The first scene analysis is called the primal sketch, which encompasses three phases: (a) Detection of zero-crossings - The so-called “DoG-filters” in the retina serve as zero-crossings detectors. DoG-filters (Difference of Gaussians) are implemented in the retina as the on-center/off-surround and off-center/on-surround ganglion cells[5], whose receptive fields are sensitive to zero-crossings, sudden intensity changes in electromagnetic energy across the retinal surface; their receptive fields pick up contours and boundaries, called “tokens”, from the retinal surface, (b) The raw primal sketch combines information about zero-crossings on different spatial resolutions to detect edges, bars, blobs, and termination points, finally, (c) The full primal sketch joins these elementary features into larger groupings in a ways which resemble Gestalt laws. The second scene analysis constructs the 2-D sketch, which is a dynamic buffer that represents the vantage point of the perceiver with respect to its orientation and distance from objects. In the 2-D sketch, information about binocular disparity, shape, contours, color, optical flow, surface texture and orientation is computed. In the final 3-D sketch, a volumetric, object-centered representation (rather than a viewer-centered representation) is constructed which is suitable for recognition. According to Marr (1982), cognition has no influence on the early stages of the scene analysis but only on the final stage of symbolic 3-D representation, where perception and cognition interface. Marr’s approach to vision thus separates perception, cognition, and action, and postulates a unidirectional flow of information from perception to behavior.

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[4] Marr (*ibid*. p.24-25) claimed that any information-processing task can be subdivided into three levels of analysis: first, the abstract computational level, which specifies the goal of the computational process in terms of transforming a certain input into an output, and the computational strategy (e.g. the mapping of one representation onto another), second, the algorithmical level, which provides a more detailed description of the specific method that specifies *how* the representations map onto another, third, the implementational level, which deals with how representations and algorithms are realized in physical systems. According to Marr, a complete theory of vision specifies all three levels, but starts at the computational level.

[5] These ganglion cells approximate the computation of the second derivative of a Gaussian function, also known as the “Mexican-hat-shaped function”, which allows them to pick up contours and boundaries, called “tokens”. Analysis of zero-crossings occurs at different spatial resolution scales: large filters are sensitive to blurry edges, while small filters are more attuned to detail (Winston, 1992).

1.2.1 Problems with Cognitivism

Many philosophers and scientists have objected to cognitivism and the computer metaphor of brain and cognition (e.g. Van Gelder, 1995; Searle, 1980; Clark, 1997). It falls beyond the scope of this chapter to review and discuss these very many detailed criticisms in depth. Instead, I here summarize some main problems with the view of cognition as (1) computation, (2) symbolic representation, (3) information-processing:

(1) Problems with Cognition as Computation

The view that cognition is best understood as computation is disputed by philosophers such as Dreyfus (1992) and Searle (1980; 1990) who both argue that computation is far too abstract a notion to capture the biological reality of cognition and that it therefore constitutes a poor starting-point for understanding cognition. In a similar vein, modern approaches to cognition such as the now popular embodied/embedded approach to cognition (EEC) challenge the view that cognition boils down to mere computation. These approaches stress that by focusing on computation cognitivism ignores three factors: (i) time, (ii) embodiment, (iii) situatedness:

(i) According to proponents of the dynamical system approach of cognition (see also section, 1.4), computational systems such as the Turing machine are poor approximations of dynamical cognitive systems (Van Gelder, 1995). They claim that cognitivism ignores the role of real-time dynamic factors by depicting cognitive processes as a sequence of computational transformations on static symbolic states (e.g. Port & van Gelder, 1995). That is, cognitivism reduces the continuous dynamics of cognitive tasks to a mere succession of discrete symbolic states in *ersatz* time, which is disconnected from how cognitive processes unfold in real-time and how they are intrinsically connected to morphological and situational dynamics (Port, 2002).

(ii) Proponents of EEC stress that cognitivism ignores bodily factors that contribute to cognition by using the nervous system as the focal point for the study of cognition (Chiel & Beer, 1997). The biophysical and biomechanical properties of the body actively and passively pre- and post-process sensory inputs and outputs: bodily features amplify and filter information and generate their own intrinsic dynamics. Pfeifer, Iida and Gómez (2006) refer to these kinds of cognitively relevant embodied processes as 'morphological computation'. Pfeifer *et al.* (2006, p.24) point out that the kinds of morphological processes that play a role in cognition are physical processes that are computationally relevant, but that these morphological processes are not computational processes *an sich*. These biophysical and biomechanical properties of the body are actively exploited during motor actions to simplify neuronal control and to facilitate and optimize cognitive processes (Chiel & Beer, 1997; Pfeifer, *et al.*, 2006).

(iii) Situational factors can also create opportunities for organisms to resolve problems that from a cognitivistic perspective appear to be strict computational issues.

Proponents of EEC stress that cognitive activities such as counting on ones fingers, to use pen and pencil to do arithmetics, or to solve a jigsaw puzzle are all examples of how cognitive activity involves the tight interplay between perception and action (Clark, 2001). On this view, cognition is not so much about inner computation, but rather about our embodied interactions with the world (see also, section 1.5). Critics to cognitivism argue that by focusing on internal computation, cognitivism ignores these embodied and situated factors that contribute to cognition (e.g. Chiel & Beer, 1997; Pfeifer & Scheier, 1999).

(2) Problems with Cognition as Symbolic Representation

The symbol grounding problem has led many philosophers to argue against the idea that cognition is equivalent to symbol crunching (e.g. Searle, 1980; Harnad, 1990). GOFAI (Good Old Fashioned Artificial Intelligence, see Haugeland, 1986) has in particular revealed the limitations of the representational approach to artificial intelligence. It turns out that symbolic representations provide a rather crude method for learning (Pfeifer & Scheier, 1999). That is, autonomous robots which make use of symbolic representations need ways to ground the meaning of the symbols they use in their interaction with objects in 'the world out there'. This mapping has proven to be an exceedingly difficult task for robots that rely on symbolic representations, even for robots in very simple and highly constrained artificial environments such as simple 'block worlds' where formal rule-based strategies are practical. GOFAI systems employ the “sense-model-plan-act” methodology, which is based on a functional decomposition between perceptual input, high level cognitive/representational processes, and motor output. This approach presupposes that cognition is the result of sequential information-processing cycles consisting of sensing, thinking, and acting (Clark, 2001). Hurley calls this “input-output picture” of cognition: cognition is sandwiched between peripheral buffer zones of perceptual input and behavioral output (Hurley, 1998). GOFAI systems rely on a constant supply of “snapshots” of the environment to update the internal world model, which guides the behavior of the robot; this forms a major information-processing bottleneck, which makes it difficult to achieve fast actions (Pfeifer and Scheier, 1999, pp.63-64). Whereas GOFAI systems perform well in predictable, rule-based, artificial environments they perform rather poorly in dynamic, unpredictable, real-world environments. GOFAI systems are typically slow and suffer from poor noise and fault tolerance because of this strong reliance on symbolic representation. The lesson that can be drawn from GOFAI is that the cognitivist interpretation of symbolic representation is not biologically plausible. What is characteristic of human cognition and other forms of natural cognition is not their reliance on explicit rules and symbol manipulation, or declarative knowledge, but rather domain-general procedural knowledge (Pfeifer & Scheier, 1999).

The matter whether and if so to what extent internal (non-symbolic) representations are required for cognition remains a controversial issue in cognitive science (Clark, 1997; Keijzer, 2001; Haselager, Bongers, van Rooij, 2003). Whereas roboticists such as Brooks

(1999) advocate an interpretation of cognition without detailed internal world models, authors like Clark (1997, p.166-170) point out that in the case of representation-hungry problems, internal representations need to be invoked in order to account for complex cognitive behaviors, such as goal-directed behaviors and reasoning about absent or counterfactual states of affairs. Clark proposes an alternative, more graded and dynamical view of representation that has little to do with the symbolic representations and the highly detailed inner world-models which were postulated by cognitivism. These representations are not static symbols but take on different forms, such as attractors in a coupled brain-body-environment system; these representations are inherently action-based and embodied (e.g. Clark, 1997).

(3) Problems with Cognition as Information-Processing

The issue whether nervous systems are information-processing systems is rarely discussed, as the issue seems rather to be *how* nervous systems process information (Koch & Segev, 2000). However, evidence from biology and neurophysiology can be used to question the standard view of neurons and nervous systems as information-processing devices. The information-processing view of the nervous system is based on a highly idealized and impoverished picture of the various processes and systems actually occurring within nervous systems (Smythies, 2002). It has long been known that the standard picture of nervous systems consisting of neurons comprised of a cell body, dendrites and axon is highly idealized and glosses over a wide variety of anatomical and physiological details. For one, the dramatis personae of the nervous system have expanded to include multiple types of glial cells, which outnumber neurons by a ratio of approximately 10:1, proliferating numbers and types of messenger molecules (large and small), some of them volume dispersing, structures such as dendritic trees, rampant endogenous neural oscillations, and also neural cilia (Whitfield, 2004).

Some neuroscientists now even argue that the “classic picture” of the neuron as a linear computational unit is not merely highly idealized but “wildly inaccurate” (Smythies, 2002, p.2). Smythies argues that the standard view misses the astonishing dynamism of the neuron, and thus of the nervous system more generally. This dynamism begins with the plasticity of the synapses, which “are not fixed structures, but are subject to a process of continual pruning, and replacement by new synapses — the real driver of neural learning, rather than mere changes in synaptic weights” (Smythies, 2002, p.2). In fact, differences in cell type, history of activity, developmental status and environmental factors may mean that each synapse is biochemically unique. Receptors for neurotransmitters, neuropeptides and other signaling molecules in the neural membrane have proved not to be roving iceberg-like structures awaiting ligands, as long supposed, but are subject to but “a continual dynamic process of rapid internalization into the postsynaptic neuron”, where they may be broken down or recycled to the surface and reused (Smythies, 2002, p.2). Likewise, the interior of the neuron is not a biochemical soup that acts principally as a conductor, as presumed, but is highly structured and bustling with processes controlled by enormously complex signaling systems. So Byzantine has the picture grown that it is increasingly difficult, if not impossible, to ascertain how multiple, sometimes opposing inputs from a single stimulus are integrated to yield a final cellular response—not least because "a molecule may have one effect on a system under one set of circumstances, but the opposite effect under a different set of circumstances" (Smythies, 2002, p.91).

One might insist that none of this forces the conclusion that something is seriously wrong with interpreting nervous systems as information processing devices. What ought to be clear, however, is that the information-processing view is based on a highly idealized and impoverished picture of how nervous systems work and what they do. By neglecting the physiological complications, the standard view implicitly assumes — arguably *a priori* — what the relevant characteristics of nervous systems are for explaining behavior and cognition, and thus may be blind to other factors that are relevant for understanding cognitive processes. Other theoretical approaches to cognition that emerged as a reaction to the restricted cognitivistic interpretation of cognition attempt to stress these other factors in order to provide a more thorough account of cognition. In the next sections, I review some of the other main options for understanding cognition.

1.3 Gibson's Ecological View

The scientific study of vision is one of the main precursors to modern-day cognitive science and many classical views on cognition are derived from vision research (Gordon, 2004; Lindberg, 1976; Meyering, 1989). According to 19th century psychophysicists such as Von Helmholtz, vision is a process of inference that relies heavily on top-down cognitive processes. In his early works, James Jerome Gibson, a former student of Gestalt psychologist Koffka, attempted to revise and improve upon the classical Helmholtzian approach to visual perception, but later on he came to realize that its foundations were simply erroneous (Hagen, 1992). According to Gibson (1966), classical approaches such as psychophysics and cognitivism mainly focused on *snapshot vision* and *aperture vision* by studying passive, stationary subjects exposed to unnatural, often briefly flashed stimuli. Gibson (*ibid.*) argued that real life vision instead involves *ambient vision,* which involves looking around using eye and head movements, and *ambulatory vision,* which involves actively moving about through the environment. Gibson (1966) claimed that the many theoretical problems that bug the classical theories on visual perception were due to false analogies: vision is not a step-wise process that starts at the retinal image eventually yielding an internal replica of the world "out there"; this approaches implicitly presupposes a homunculus that observes the retinal image. Gibson therefore abandoned what he called "eye-ball optics" as his theoretical starting point and moved on to what he termed "ecological optics", which is concerned with the objective, unambiguous information present in the light itself (Hagen, 1992).

According to Gibson's (1966; 1979) theory of 'direct perception' all the information that organisms need to survive is simply present in the light itself and can be picked-up through motion, without the help of computational or representational resources. Gibson (1979) argues that the light itself contains stable *a-priori* information, which he called “ambient optic array” information (*Ibid.* pp.65-92). Ambient optic array information is provided by the reverberating light which is reflected off the surfaces of objects all around us, and converges to the observer's unique vantage point. When the observer moves through the ambient optic array this gives rise to “optic flow patterns” in which all kinds of invariances become available to the observer providing unambiguous information about contours, depth, texture gradients, forms and shapes. Optical flow patterns are patterns of visual streaming of inflow and outflow of environmental features that arise from the relative motion of an observer and objects in the environment (Heft, 2001). Gibson (1966) uses the well-known example of an airline pilot that approaches a runway from the sky: a small patch of the visual array toward which the plane is moving remains motionless - the pole - while the features surrounding it seem to radially expand from it; objects that are near the pole generally move slower than those in the periphery. These optical flow patterns provide the pilot with depth cues, cues about the spatial arrangement of objects, information about the direction towards which the plane is moving, and the speed at which the plane travels.

Based on his theory of visual perception, Gibson (1979) devised a new and still influential ecological interpretation of cognition that is rooted in bottom-up ecological processes. On this view, cognition does not revolve on internal representations but is rooted in perception-action loops that facilitate the interaction between an observer and his environment. According to Gibson, perception and action make up a continuous cycle of causes and effects: perception facilitates action control, while action facilitates perception; a perception-action coupling. The notion of perception-action coupling designates that perception and action are not independent but inextricably connected: perception is not passive but is in itself a way of acting that induces law-like changes in sensory patterns, while motor actions partially determine the sensory patterns that organisms receive from the environment (Lombardo, 1987). For example, according to Gibson, vision is not just an exteroceptive sense that provides information about environmental features; it also facilitates action by delivering kinesthetic and proprioceptive information that deals with the coordination between body parts and the relative coordination between body and environment (Gibson, 1966).

The reciprocal relation between perception and action is also stressed in Gibson's notion of “affordances”. Affordances highlight the congruence between structural features in the environment and their perceived functional significance for the observer (Heft, 2001; p.287). According to Gibson (1979), our perceptions contain pragmatic information about the possibilities for certain actions, such as whether objects or terrain features are 'walk-on-able', 'get-underneath-able' or 'sit-able'. Gibson claims that affordances can be directly extracted from the ambient optic array by the observer. On Gibson’s view, affordances are part of the ecological niches of organisms, which are determined by the interaction between the organism and its environment (Gibson, 1966, p.285). Since the functional significance of environmental features differs from ones species to the next, the term affordance is a species relative concept (Jenkins, 2008).

Gibson's ecological view is as controversial as it is original. Many workers in cognitive science have criticized Gibson's outright dismissal of representations and inferences (Gordon, 2004). Some critics have stated that the notions of direct perception and invariants as Gibson employs them are simply "cheating" (see Fodor & Pylyshyn, 1981). For example, Marr (1982, p.29) argued that Gibson seriously underestimates the computational processes required to obtain information from the environment and that the ecological view paints a grossly oversimplified picture of information pick-up. Fodor and Pylyshyn (1981) provided an in-depth critique on Gibson's views. According to Fodor and Pylyshyn (1981), Gibson's theory of direct perception ignores the importance of top-down processes in perception. They argue that the notions of 'invariance' and 'pick-up' as Gibson employs them are so unconstrained and ill-defined that they are simply rendered meaningless (p.142). The more these notions are constrained, so Fodor and Pylyshyn claim, the more one needs to invoke top-down processes such as inferences and representations.

Gibson provided a radical alternative way of thinking about cognition, and Ulrich Neisser, one of the leading cognitivists and author of a popular textbook on cognitive psychology, revised many of his ideas about perception and cognition after his encounters with Gibson (Viney, 1993). While influential, his views did not seriously affect the status of cognitivism as the dominant research paradigm in psychology. Nevertheless, Gibson's emphasis on the dynamic interaction between observers and their environments is a major source of influence to the dynamical systems approach to cognition (Port & van Gelder, 1995), while the central role of perception-action loops and the ecological aspects of cognition are now highlighted by the embodied/embedded approach to cognition.

1.4 The Dynamical Systems Approach to Cognition

Dynamical systems theory forms the theoretical basis for the dynamical systems approach to cognition. Dynamical Systems Theory (DST) is a branch of mathematics that studies how complex systems change over time (Port & van Gelder, 1995). The goal of DST is to uncover mathematical regularities in the behavior of dynamical systems and to model these phenomena by isolating control parameters and collective variables that govern the patterns of their change. DST is rooted in the works of physicists such as Newton and Galileo, which mathematically describes the temporal behavior of the celestial bodies in our solar system. In principle, however, DST is applicable to events at all levels of analysis and time scales (Ward, 2002). The first application of DST in the study of cognition started in the 1950s with the modeling of the behavior of single neurons

(Hodgkin & Huxley, 1952); these models remained rather simple because of computational restrictions (Port, 2002). In the late 1950s and 1960s, with the introduction of connectionist models, such as perceptrons, cognitive functions such as memory, pattern recognition/completion, and category learning were successfully mimicked. The many features of connectionist model[6], i.e. parallel and distributed processing, pattern completion abilities, content addressable memory, and their inherent robustness (such as fault tolerance and graceful degradation), left a lasting impression on many psychologists and philosophers and have shaped many discussions on the nature of cognition (see Churchland, 1995). Some researchers argue that connectionism fundamentally challenged cognitivist' assumptions about cognition, in particular about the role of symbols and (distributed) representations in cognition. However, other researchers argue that the connectionist' models target a lower, *sub*-symbolic level of description, and that connectionism is quite compatible with the cognitivist frame of thought. Connectionism is therefore often taken to be a halfway house between cognitivism and the dynamical systems approach to cognition; the latter aims for a more thorough break with cognitivism (Van Gelder, 1999; Bem & Looren de Jong, 2006).

The dynamical systems approach to cognition (DSC) is an interdisciplinary framework that combines research efforts from developmental psychology, linguistics, cybernetics, and action-based robotics (see Beer, 2008; Kelso, 1995; Port & van Gelder, 1995; Thelen & Smith, 1994; van Gelder & Port, 1995). In many ways DSC forms the theoretical counterpart to cognitivism. According to proponents of DSC: (1) cognitive systems are not static symbol systems that perform sequential, logical operations, rather, cognition is an intrinsically temporally structured phenomenon, which is best understood in and captured by the tools and vocabulary of DST, such as attractors, chaos and self-organization, state-spaces, bifurcations, and coupling[7] (van Gelder, 1999), (2) Cognition is

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[6] Classical connectionist models typically consist of a large number of nodes divided in an input layer, a hidden layer, and an output layer. The nodes that make up the network are analogous to neurons and are linked together by local axon- and dendrite-like connections with adjustable weights, which, much like synapses, reflect the strength of connections between the nodes. Each node in the network is connected to a small group of neighboring nodes, and passes on its output to a small number of units (Clark, 2001). Connectionist models learn to generate a certain desired output pattern given an input pattern by gradually adjusting the weights (often starting with randomly assigned values) between the nodes with the help of learning algorithms, such as back-propagation (synaptic adjustment of the weights by the successive back-propagation of errors), which provide feedback on the discrepancy between the current output and the desired output (Rumelhart, 1989). From the 1980s onwards, the connectionist incorporated more biologically plausible learning algorithms, such as Hebbian learning, and put more emphasis on dynamics, such as by using recurrent networks, which also use feedback (rather than just feedforeward) connections so as to exploit temporal structure in the activity patterns (See Bechtel & Abrahamsen (2002) for an in depth discussion on connectionism).

[7] The dynamical relationship between external parameters and the variables that make up the system can exhibit reciprocal causality i.e. two or more systems simultaneously influencing each other and so forming a larger system; this is reflected by the notion of *coupling.* As Van Gelder (1999) explains the notion of coupling: "Sometimes, changes in a parameter depend in turn on the

not a brain-bound, representational processes but is grounded in the bodily interactions with the world: brain, body, and environment form a tightly coupled dynamical cognitive system (e.g. Van Gelder & Port, 1995; Beer, 2000; 2008), (3) Cognition is not separate and distinct from perception and action, but rather instigated by the coordination dynamics between sensory and motor processes that continuously self-organize to give rise to stable, coherent spatiotemporal patterns (Kelso, 1995; 2003), (4) There is a continuity between lower level on-line cognition and higher level, off-line cognitive abilities such as imagination, judgment and reasoning. Higher cognitive processes are derivatives of on-line sensorimotor processes (e.g. Thelen & Smith, 1994).

An application of DSC can be found in developmental psychology, which challenges long held views on the nature of cognitive development in human infants. According to Piaget, young infants roughly between 8 and 12 months of age in stage IV of the sensorimotor period, learn that objects that have disappeared from sight do not vanish into thin air, but continue to exist despite being out of sight (Siegler, 1998). In this cognitive developmental stage, infants learn to develop a notion of object permanence and first search for objects that are hidden from sight. At this stage in development, under certain circumstances a curious phenomenon occurs, the A-not-B error or stage IV error, which is a canonical problem often investigated by developmental psychologists. The experimental set-up typically involves an investigator who hides an interesting toy under a cover at location A; this act is witnessed by an infant seated on a parent's lap. After a delay of a couple of seconds, the infant is allowed to reach for and uncover the hidden toy, which is usually no problem at this age. This procedure is repeated several times. Next, the investigator hides the toy under a cover in a nearby location B; again witnessed by the infant. After a short delay the infant is allowed to reach for the toy. But lo and behold, 8-to-12 month old infants usually show pervasive reaching towards location A instead of B despite just having witnessed the toy put under cover B. According to Piaget, who invented the procedure, infants in stage IV show perseverance reaching toward location A where they found the object earlier on because they have uncovered it there before and their notion of object permanence is still incomplete. In the eyes of young infants, it is as if location A has assumed the status of a hiding place where lost objects magically pop-up (Siegler, 1998).

By contrast, Thelen, Schöner, Scheier and Smith (2000) claim the behavior of these infants has little to do with representational capabilities or the lack thereof. According to Thelen *et al.*, (2000) the crux of the problem lies in the dynamics of the task itself rather than in a notion of object permanence of infants: the experimental procedure generates a

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system itself. For example, the position of the moon both depends upon, and affects, the position of the planets. This kind of reciprocal, direct dependence is known as coupling. System variables and coupled parameters can be regarded as forming a larger system. This illustrates the semi-arbitrariness of systems. It is always up to us to nominate a set of concrete variables as the system we will study. Reality determines whether that set is in fact a system, and how it behaves" (p.5).

strong motor bias in infants toward reaching to location A, because of repeated exposures and actions toward it. This bias is not compensated for by watching the experimenter hide the object in location B. Thelen *et al*.,'s (2000) dynamical field model provides a dynamic systems perspective on the A-not-B error. The model represents the decision to reach for A or B as activations in a dynamic field. It shows that variations in three directional movement parameters in the A-not-B task, such as (1) changing the specifications of the task environment to relieve the ambiguity of the task, (2) manipulating the strength of the specific input to reach for A or B, such by for example presenting a cookie at location B, or (3) varying the delay times in the task, all have a significant impact on the perseverance response toward location A. For example, when infants were allowed to stand up rather than to sit on their parent's lap, the motor bias toward location A was considerably reduced. According to Thelen *et al*., (2000) this shows that the real-time processes involved in the A-not-B error are intimately coupled to the sensory-motor system of infants.

These findings are hard to reconcile with Piaget's interpretation which is centered on representational capabilities such as having a notion of object permanence. Instead, Thelen *et al*., (2000) argue that their dynamic systems interpretation of the A-not-B error task shows that the division between off-line cognition and on-line sensorimotor processes is hard to draw because they are meshed and continuous, and ultimately rely on the same real-time dependent processes. DSC collapses the traditional distinction between high-level, centralized cognition and low-level, peripheral cognition. On this view, high-level properties of cognition such as our ability to do math or to play chess may turn out to be entirely borne out of time-sensitive sensorimotor abilities (Port, 2002). Given the emphasis on the coupling between body, nervous system, and environment, DSC also theoretically overlaps with the embodied and embedded approach to cognition.

A common criticism to DSC concerns the notion of coupling as an explanatory concept for cognition. Based on his well-known example of the Watt governor[8], Van Gelder (1995, p.373) and other adherents of DSC argue that cognition can be understood

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[8] Van Gelder (1995) introduced the Watt Governor as an example to replace the Turing machine as the paradigmatic model for understanding cognition. The Watt governor is a centrifugal governor designed by James Watt that allows a steam engine to maintain a constant speed of its flywheel despite fluctuations in pressure and load. The Watt governor does so by regulating the engine's steam pressure input: the governor regulates the aperture of a throttle valve in order to dampen fluctuations in engine speed. If engine speed increases, the governor starts rotating at a faster rate, which closes the throttle valve, which in turn reduces steam input to the engine, slowing it down until its speed stabilizes. If engine speed decreases, the governor starts to rotate at a slower rate, which causes the throttle valve to open up, allowing increasing steam input into the engine; this causes the engine to run faster until its speed again stabilizes (See also Clark, 2001). Although Van Gelder (1995, p.348) notes that although the workings of the Watt governor can also be described in computational terms as an iterative algorithm, the Watt governor does not literally compute, nor does it require a symbolic representation of the current state of the engine. Rather, it is the real-time coupling between the engine and the governor that determines the behavior of both; the engine and the governor can be seen as a tightly coupled system with a single state-space.

as a tightly coupled, unified system that comprises the nervous system, the body, and the environment. According to authors such as Clark (2001) and Keijzer (2001, pp.186-187) this view is problematic in the sense that it reduces the brain to just another variable in a dynamic system; DSC does not specify how dynamical coupling gives rise to distal, goal-directed behavior. Kelso (1995) and Keijzer (2001) each in their own way provide more advanced interpretations of DSC which allow for a distinction between goal-directed dynamical systems and physical-causal dynamical systems so as to leave room for intentional dynamics and anticipatory behavior. These dynamical accounts of cognition invoke *specific parameteric influences* (Kelso, 1995, p.138) and *internal control parameters* (Keijzer, 2001, pp. 216-220) generated by the nervous system that modulate and coordinate the dynamics of behavioral trajectories towards reaching certain behavioral goals. Instead, Clark (2001, p.133) proposes a theoretical middle ground between DSC and cognitivism by combining a representational account of cognition with a dynamical, embodied/embedded interpretation; he talks about "partial programs" that operate within the dynamical constraints of body-environment interactions. These partial programs are not blueprints for behavior, such postulated by cognitivism, but rather minimal instructions/representations that help to guide and to constrain behavior, giving rise to future-oriented actions. It remains an open question whether DSC is suited to provide a full-fledged account of cognition or whether it needs to be augmented by more classical views that invoke representations and information-processing strategies.

A related problem with DSC involves the postulated continuity between low level, on-line sensorimotor cognition and off-line cognitive processes. Clark (2001, p. 135) calls this view "cognitive incrementalism"; the idea that there is no essential difference between the processes that govern, say, walking and playing a game of chess (e.g. Thelen & Smith, 1994). However, it might turn out that our ability to do math, to learn languages, to simulate or emulate events off-line, to have subjective experience, to reason abstractly, and so on, seem to rely for a large part on the brain's inherent capacity to process, to remember, and to manipulate different kinds of information, such as conscious and unconscious processing, rather than on low-level sensorimotor skills. For example, Clark (2001) argues that it is more likely that the brain employs a mixture of different strategies rather than merely those dealing with sensorimotor control, and that cognition is therefore discontinuous; or as Clark (ibid.) puts it: ”... some cognitive functions may depend not on the tweaking of basic sensorimotor processing, but rather on the development of relatively (functionally) independent and (functionally) novel kinds of neural processes" (p.136). Even though these internal mechanisms of cognition might be relevant for modulating sensorimotor cognition, it is questionable whether off-line cognitive skills can be fully derived from basic sensorimotor actions.

Another criticism pertains to whether the tools of dynamic systems theory are adequate to model and account for higher level cognitive phenomena such as mathematics, abstract thought, and decision-making (Eliasmith, 2001). That is, dynamical modeling techniques have proven their worth in describing relatively simple systems (Beer, 1995). However, it is unlikely that complex, higher cognitive processes can be understood in terms of relatively few low level collective variables and control parameters. Although the mathematics of relatively simple (non)linear models is well developed and understandable, complex dynamical models have to be highly constrained in order not to get too complex even for highly advanced parallel computers to calculate. Perhaps it is the case that dynamical models are best suited to account for low-level, sensorimotor cognition and that classical models simply do a better job in explaining higher level cognition (Port, 2002).

1.5 Embodied/Embedded Cognition

Champions of the embodied/embedded approach to cognition (henceforth EEC9) hold that cognition is an inherently embodied and environmentally situated phenomenon (Anderson, 2003; Beer, 2000; Bennett & Hacker, 2003; Calvo & Gomila, 2008; Keijzer, 2001; Pfeifer & Scheier, 1999; Robbins & Aydede, 2008; Varela, Thompson & Rosch, 1991). EEC and DSC show a substantial theoretical overlap as both are rooted in systems thinking; although EEC has its own independent historical background. EEC has its historical antecedents in a number of different research fields including psychology, in particular in the views of Dewey, Vygotsky, and Gibson, who all emphasized the reciprocity between perception and action and environmental feedback in cognitive processes; and philosophy, in particular in the views of Merleau-Ponty, Heidegger and Dreyfus who stressed the role of the body and body-environment interaction in perception and knowledge (Anderson, 2003; Clancey, 2008; Galagher, 2008). EEC is a research paradigm in the making of which the foundations are already well in place (see Calvo & Gomila, 2008; Robbins & Aydede, 2008).

A major initial development in EEC can be found in Rodney Brooks's (1986; 1990; 1998) behavior-based approach to artificial intelligence. This bottom-up approach to A.I. challenges some of the central tenets of GOFAI, such as the view that cognition revolves on symbolic representation and internal reasoning. Brooks (1990) argues that the traditional *physical symbol system hypothesis* is fundamentally flawed. He notes that when looking at evolution, it is clear that typically human capabilities often associated with representational capabilities and problem-solving skills are relatively recent developments, but that basic behaviors such as motility, navigation, and other simple goal-directed behaviors have been around for much longer; these simple behaviors are much more important when it comes to understanding cognition. Brooks' approach to A.I. is founded in the *physical grounding hypothesis,* which holds that the root of intelligent behavior lies in situated action, which requires agents that are firmly grounded in the physical world by means of their sensing and acting capabilities.

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[9] EEC includes 'situated cognition', 'enactive cognitive science' (Thompson & Varela, 2001) and 'embodied cognitive science' (Pfeifer & Scheier, 1999). The enactive approach in particular stresses the role of subjective experience in relation to situated and embodied actions.

Brooks' (1999) methodology for building intelligent systems, the subsumption architecture, is a bottom-up design methodology for constructing intelligent agents capable of simple but robust behaviors in real-time environments. The subsumption architecture relies on behavioral decomposition: the components in the subsumption architecture are task-achieving subsystems or 'layers'; each layer[10] is a behavior generating module. The layers in a subsumption architecture are organized in increasing levels of competence: the bottom layers provide the robot with elementary sensory-motor skills, such as obstacle avoidance and exploration, while the higher layers deal with more global behavioral goals, such as collecting cans, and building cognitive maps. The subsumption architecture is incrementally extendable: once a basic layer is built, debugged, and works properly, other layers can be placed on top, and subsequently be tested and debugged (See Brooks, 1998, p.153). Higher layers subsume lower layers in the sense that they can inhibit or suppress the input and inhibit the output of lower layers by adjusting gain, however, there is no control hierarchy in the sense that bottom-layers need to await orders from top-layers (see also Pfeifer & Scheier, 1999, pp.199-225, for a detailed discussion on subsumption architectures).

The subsumption methodology collapses the classical central/peripheral distinction and instead exploits the principle of parallel, loosely coupled systems (see Pfeifer, & Scheier, 1999, pp.327-376). That is, instead of having to rely on sequential sensing-plan-model-act cycles, which requires a great deal of internal processing, the layers in a subsumption architecture are active in parallel and function relatively independently, which allows for little internal processing. Brooks' robots are physically grounded in the sense that each layer in the subsumption architecture interfaces directly with the environment: each layer has its own sensory input directly coupled to motor output without the intervention of centralized modules. The robot's behaviors are determined by the ongoing interaction with the world rather than by some internal program. Since there is no internal central executive that tells the agent what to do next, Brooks's artificial agents show opportunistic behaviors given the proper circumstances, and they can respond flexibly to changed circumstances (Brooks, 1990).

Brooks' approach to action-based robotics comes with its own interpretation of cognition. According to Brooks (1999), cognition is not an internal property but an emergent phenomenon that arises through the interaction of a physically grounded agent with its environment. The core of cognition therefore lies in situated action rather than in reasoning skills and representational capabilities, which is reflected by his much quoted creed: "the world is its own best model" (1990, p.5). On this view, the world itself serves as a kind of external memory that can be sampled at will. Brooks's action-based approach

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[10] The layers in a subsumption architecture are composed of connected modules, i.e. augmented finite state machines that provide a repository for state, and which send messages to each other asynchronously (Brooks, 1998). The state of these finite state machine changes according to certain preprogrammed rules.

to cognition has become the theoretical stronghold for EEC. Two other central tenets of EEC are that cognition is a brain-body-environment system and the view that cognition is scaffolded by environmental features; in the next subsections, I discuss these two claims separately.

1.5.1 Cognition as a Brain-Body-Environment System

The cognitivist' view that cognition is a property of brain functioning tends to abstract away from the bodily and environmental determinants of cognition. According to proponents of EEC, cognition is not an internal property of the brain, but rather a much broader phenomenon that involves the ongoing interaction between a nervous system, a body, and the environment. More specifically, proponents of EEC hold that cognitive systems are non-linearly coupled nervous system-body-environment systems (see Figure 1; Anderson, 2005; Beer, 2008; Clark, 2008; Gallagher, 2005; Keijzer, 2008; Ziemke, 2008). According to Beer (2009), each of the components in the nervous system-body-environment system possesses its own intrinsic dynamics, but these features are tightly coupled and in continuous interaction, so that it becomes meaningless to consider just one of these components in isolation when it comes to studying cognition. As Beer (2009) explains:

> *A bird, for example, flies not only because of the patterns of muscle activation produced by its nervous system, but also because of the shape and composition of its feathers and the hydrodynamical properties of the air through which it moves. Furthermore, evolution selects only for the behavioral efficacy of this entire package, and it seems likely that it would take full advantage of any available freedom in distributing behavioral mechanisms. This suggests that behavior is best viewed as a property of a complete brain-body-environment system, and cannot properly be assigned to any individual component of this coupled system (p.7).*

The nervous system and the body are intimately coupled because of their long co-evolution. Nervous systems evolved to enable the control of movement and coordinations of multicellular bodies. In turn, bodily states such as emotive states provide brain and nervous system with somatovisceral information; a form of normative information that helps organisms to optimize fast context-sensitive action-selection, such as selecting between 'fight or flight' behavior. Body and environment also exhibit a strong reciprocal coupling. The body with its sensors and effectors has been shaped and optimized by natural selection to fit a certain ecological niche. Body and environment are coupled through perception-action loops; evolution selects organisms based on whether they exhibit appropriate adaptive actions based on the sensory input they receive. On this view, the brain is not so much the locus of cognitive control, rather, brain, body, and environment are more or less equally important determinants of cognition.

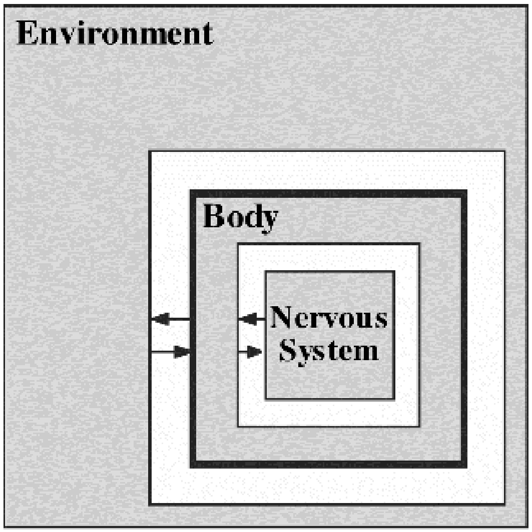

Figure 1. Cognition as a coupled nervous system-body-environment system. The tightly coupled nervous system-body subsystem is called “the agent”. The agent in turn is coupled to its environment through sensory input and motor output. The coupled agent-environment system is the cognitive system (from Beer, 2009).

The body contributes to cognition in many different ways. Chiel and Beer (1997) argue that the body contributes actively and passively to cognitive dynamics: morphological characteristics are often highly optimized by evolution to facilitate cognitive processes. A well-known example of how morphology augments cognition is that many predators have their eyes situated in the front of their heads which facilitates depth perception because of the slight disparity between the two retinal images. The exploitation of this type of sensory morphology to facilitate cognitive processes is ubiquitous in nature. The distribution of the light sensitive cells of the fly compound eye - the *ommatidia* - is dense in the frontal region and becomes increasingly less dense at the periphery. The uneven physical distribution of the facets of the fly compound eye performs 'morphological computation' by contributing to motion detection in straight flight (see Pfeifer & Iida, 2005; Pfeifer *et al.*, 2006, p.24). The body also comes with particular biomechanical and biophysical properties: rigidity of bone, elasticity of muscles, different degrees of stiffness or compliance of the tendons, and the physical make-up of sense organs, are all actively exploited during motor actions to simplify neuronal control and to facilitate and optimize cognitive processes (Chiel & Beer, 1997; Pfeifer, Iida & Gómez, 2006).

Recent research in EEC also focuses the relation between cognition, emotions, and embodiment (e.g. Lowe, Herrera, Morse & Ziemke, 2007; Morse & Lowe, 2007; Niedenthal, 2007; Winkielman, Niedenthal, & Oberman, 2008; Ziemke, 2008). According to Damasio (1999), emotions[11] form the very basis of cognition and (self-)consciousness (see also, Ziemke, 2008). Damasio (1999) argues that emotions provide a 'quick-and-dirty' appraisal of bodily states. Emotions enable normativity: emotions help organisms to attach values to objects and events which facilitates quick judgment about objects and events and so helps to ensure the survival and well-being of these organisms (Lowe *et al.*, 2007). The role of the body in emotions is very salient in social cognition: non-verbal behaviors such as body language form the basic means of communication among mammals and primates, which shows that emotions are phylogenetically ancient and deeply intertwined with body and cognition. For present purposes it would carry too far to discuss the role of emotions, cognition and embodiment in more depth (see Griffiths and Scarantino (2008) and Winkielman *et al.* (2008) for embodied/embedded perspectives on emotions).

Much like Gibson's ecological approach to cognition, proponents of EEC focus on how agent-environment interactions furnish cognition through perception-action coupling. By performing actions such as moving through the environment, organisms self-generate sensory stimulation by inducing proprioceptive and environmental feedback, which provides these organisms with information about correlations between their sensors and effectors. O'Regan and Noë (2001) refer to the detection of the law-like structure of changes in perception-action patterns as 'sensorimotor contingencies'. Sensorimotor contingencies are the systematic relations and the sensory consequences of action, i.e. correlations and causal relations, between self-initiated movements and the sensory changes that these movements elicit (Keijzer, 2009). The systematic relations between sensorimotor behaviors are different for vision compared to for example hearing or touch. According to O'Regan & Noë (2001), sensory modalities involve different modes of active exploration which are mediated by knowledge of the relevant sensorimotor contingencies (p.943). Sensorimotor contingencies can also involve learning of cross-modal patterns, such as relations between vision, proprioception, and hearing, which is for example important in learning to how to ride a bike or to play a musical instrument. By optimizing their sensorimotor patterns organisms engage in sensorimotor coordination (henceforth SMC). SMC is about detecting and making use of systematic invariances between sensory events and motor actions in order to achieve adaptive goals (Nolfi & Parisi, 1999). SMC induces correlations in sensory-information which simplifies learning and facilitates cognitive processes. The notion of SMC is rooted in the work of John Dewey (1896), who discussed it to make clear that perception is not passive and stimulus-driven, but that it is fundamentally action-based; or as Dewey put it:

> *Upon analysis, we find that we begin not with a sensory stimulus but with a sensori-motor coördination, the optical-ocular, and that in a certain sense it is*

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[11] Damasio (1999) uses the term 'emotion' in a very broad sense involving different levels of homeostatic regulation, ranging from basic bioregulatory functions, endocrine functions, somatovisceral functions, to feelings.

> *the movement which is primary, and the sensation which is secondary, the movement of body, head and eye muscles determining the quality of what is experienced. In other words, the real beginning is with the act of seeing; it is looking, and not a sensation of light. The sensory quale gives the value of the act, just as the movement furnishes its mechanism and control, but both sensation and movement lie inside, not outside the act (p. 358).*

This message conveyed by Dewey has become one of the central tenets in the EEC movement. According to Pfeifer and Scheier (1999) anything an agent learns is grounded in sensorimotor coordination. EEC stresses that higher forms of cognition, such as concept acquisition and our acquisition of numbers are derivatives of our bodily interactions with the world (Clark, 2008; Shapiro, 2007). Indeed, research in developmental psychology shows that human infants gradually learn to distinguish categories by actively manipulating objects in their environment, such as by lifting and rotating them. On-line infant-environment interactions therefore play a constitutive role in the development of off-line cognitive skills, such as conceptual thought (Chiel & Beer, 1997; Thelen & Smith, 1994). Off-line cognitive skills, such as imagination, reasoning, day-dreaming, are abilities that remain (temporarily) decoupled from overt behavior (Grush, 2004). The key role of sensorimotor behavior in the development of off-line cognition was already emphasized by Piaget and Vygotsky, who both claimed that the first two years of human development are entirely devoted to SMC, and that the development of reasoning skills crucially depends on the successful completion of early sensorimotor stages. Recent research dovetails with the view that many 'off-line' cognitive abilities are intimately tied to and ultimately dependent on sensorimotor functions, such as imagination (Carson & Kelso, 2004; Oullier, Jantzen, Steinberg & Kelso, 2005), object recognition, (Nolfi & Parisi, 1999), imitation and Theory of Mind (Gallese & Goldman, 1998; Rizzolatti & Craighero, 2004; Keysers & Gazzola, 2007), categorization (Thelen & Smith, 1994; Pfeifer & Scheier, 1999), working memory, episodic memory (Wilson, 2002), and conscious will (Kelso, 1995; see also chapter 4).

1.5.2 Environmental Scaffolding and Cognitive Extension

Clark's (1997; 2005; 2006; 2008) scaffolding approach stresses that situated factors such as our socio-cultural environment and technological artifacts form an intrinsic part of our cognitive make-up. The role of social situatedness in cognitive development, or social scaffolding, was already stressed by Vygotsky. Vygotsky's concept of the zone of proximal development provides a classic example of how a complex social environment can scaffold the cognitive problem solving skills of infants, allowing them to solve certain tasks in more advanced ways than they could have on their own (Siegler, 1998, p.17). Such scaffolds provide temporary frameworks which support children's thinking so that they can perform at a level that exceeds their current cognitive developmental stage.

According to Clark (2008), this type of cognitive extension not only occurs on a temporary occasional basis, but also on a more permanent basis with the use of cultural tools: agriculture, (sign)language, and the use of symbols are all examples of how humans actively use and permanently modify the organization in their environment to facilitate cognition. Through niche construction, certain aspects of the environment itself are modified to augment cognitive process (Keijzer, 2009). Processes such as niche construction and social cognition are also exploited by animals and plants to modify aspects of their environment so as to facilitate their needs (e.g. Dornhaus & Franks, 2008; Ben-Jacob, Becker, Shapira & Levine, 2004; Shapiro, 1998). Human beings exploit cultural, social, and technological artifacts, such as language and computers, as tools to construct cognitive niches that facilitate cognitive processes such as abstract thought. Clark (1997, pp.193-218) uses language as an example of a cognitive tool that operates as a double edged sword: not only does language facilitate communication but it also allows us to reshape complex problems in a format that drastically simplifies learning. As Clark (ibid.) puts it: “Language stands revealed as a key resource by which we effectively redescribe our own thoughts in a format that makes them available for a variety of new operations and manipulations” (p.210). Words and symbols can be used as constituents for complex thoughts, but also to simplify aspects of our environment such as informational transfer (Clark, 2006).

According to Clark, (e.g. Clark, & Chalmers, 1998; Wilson & Clark, 2008; Clark, 2008), cognition is literally an environmentally extended process. On his view, cognition is not bounded by the skull but is distributed across body and world; environmental features that facilitate cognitive processes temporarily become part of an agent’s cognitive organization. For example, consider a blind person using a cane. The blind person controls the cane by swinging it in front of her to detect objects and edges and so on, which helps her to navigate the environment. On Clark’s view, the cane becomes an integral part of the cognitive circuitry of the blind person, since it helps her to navigate her environment by extending her sense of touch so as to compensate for her visual handicap. Clark stresses that cognitive activities such as counting on ones fingers, to use pen and pencil to do arithmetics, or to solve a jigsaw puzzle are all examples of how cognitive activity is instigated by perception-action loops that flow across body and world (Clark, 2001). By physically manipulating objects in our environment we also off-load cognitive work into the environment, which relieves the burden for inner thought processes (Wilson, 2002; Pfeifer & Scheier, 1999). According to Clark (2008), this type of extended cognitive circuitry forms an important basis for higher cognitive processes such as thought and reasoning.

Many of the criticisms that pertain to DSC also pertain to EEC (see section 1.4). For example, it is a matter of ongoing discussion to what extent and in which ways typically human off-line cognitive abilities are ultimately rooted in on-line situated activity (e.g. Clark, 2008; Grush, 2004; Keijzer, 2009; Wilson, 2002). Some authors argue that although organism-environment interactions might be important in explaining low-level cognitive processes, a sound explanation of higher, typically human off-line cognitive processes still needs to invoke other cognitivistic explanations such as the computational strategies of the brain. A fundamental criticism specifically to EEC comes from Adams and Aizawa (2001) who argue that Clark's interpretation of extended cognition succumbs to what they call the “coupling-constitution fallacy”: the idea that objects or processes that are coupled to a cognitive agent are actually part of the agent’s cognitive organization. Clark’s scaffolding approach suggests that external objects that facilitate cognitive processes, such as pencils, notebooks, and computers, actually become part of an agent’s cognitive organization. Instead, Adams and Aizawa (2001) argue that the fact that cognition is causally coupled to environmental features does not imply that cognition itself is environmentally extended. They instead argue that features that are coupled to a cognitive agent do not automatically make them part of the agent; notebooks, pencils, or canes, are not constituents of cognition, such as neurons. According to Adams and Aizawa (2001), the weakness of environmentally extended interpretations of cognition is that they lack a proper “mark of the cognitive”, leaving it unclear what makes something a cognitive agent. They propose that such a mark of the cognitive can be found in the intrinsic causal processes that involve non-derived intrinsic content, such as thoughts and subjective experience (Aizawa & Adams, 2005). On this view, cognition is again reduced to a brain-bound process, which is essentially a return to cognitivism (see Clark, 2005; 2008; for critical response to Adam & Aizawa, 2001).

The coupling-constitution fallacy is part of a deeper problem that ultimately boils down to the question posed in the introduction of this thesis: what is cognition? Since there is no generally agreed upon definite answer to this question and as to what constitutes a proper “mark of the cognitive”, it seems that the outcome to these matters is arbitrary and depends on the paradigm at hand. A major drawback to most approaches to cognition (including EEC) that makes it even harder to frame a more objective answer to these questions is that all provide very broad and highly abstract characterizations of cognition that attempt to incorporate both artificial and biological cases. However, artificial cognition and natural cognition may likely turn out to be entirely different phenomena that each rely on their own unique set of mechanisms. If so, such a very general, abstract interpretation of cognition that includes both natural and artificial cases is not the best approach to answering such fundamental questions as what is cognition and what constitutes a proper “mark of the cognitive”. One possible solution to this problem is to develop a more restricted, less abstract, and more empirical approach that is specifically aimed at explaining natural cognition. The biogenic approach to cognition which I discuss in the next section aims to do just that.

1.6 The Biogenic Approach to Natural Cognition

Over the past few decades, cognitive science has progressed from a purely computation-based interpretation of cognition to a more embodied/embedded and biologically oriented perspective. Despite these developments, however, as discussed in the introduction, the common interpretation of cognition is still predominantly: (1) brain-based, i.e. the usual view is that the brain is a necessary condition for cognition, and that cognition represents a relatively late evolutionary development that presumably co-evolved with cephalized nervous systems, (2) computation-based, i.e. the notion of cognition has strong connotations with computation and information-processing, even for many workers in embodied/embedded cognitive science, (3) anthropocentric, i.e. human cognition is the yardstick, and organisms incapable of high-level cognitive skills, such as single-celled organisms are left out of the picture. Although the dynamical systems approach to cognition and EEC have already contributed in revising in particular the second assumption, these three biases still color the way in which the notion of cognition is commonly perceived. Even bottom-up, action-based approaches to cognition such as advanced by Brooks (1999) and Beer (2008; 2009) still cling to the brain-based view of cognition by taking insect-like creatures as the starting-point for thinking about cognition. However, insects are already well-developed, highly complicated organisms. This approach still ignores cognition in organisms that lack a brain or nervous system.

In order to tackle these persistent problems the approach to cognition taken in this thesis shifts its explanation of cognition even further towards biology by providing a more fundamental biological account of natural cognition. What separates the theoretical approach taken in this thesis from other theoretical approaches is that it abandons the brain-based approach to cognition, computer cognition, and human cognition as its theoretical starting-points, and instead starts with biology. Lyon (2006a; 2006b) calls this the biogenic approach to cognition. The biogenic approach focuses on explaining natural cognition or biocognition rather than cognition in artifacts such as computers and robots. From a biogenic perspective, artifacts such as the Turing machine or the Watt governor make rather poor starting-points for understanding what makes natural cognitive system tick. On this biogenic approach, computer cognition and A.I. fall in a separate category: artificial forms of cognition lack a biological basis and are designed rather than evolved.

We have seen in the former section that answering fundamental questions such as *what is cognition* by providing a single, highly abstract, generalized characterization of cognition that incorporates both artificial and natural forms of cognition has had limited success. By focusing exclusively on the biological basis of cognition the biogenic approach aims to gain more headway on answering such questions as to what cognition is, what biological function(s) it serves, and what constitutes a “mark of the cognitive” in natural cognitive systems. The biogenic approach firstly focuses on the most elementary cases of biocognition, and uses these simple cases as a theoretical starting-point to ultimately explain more advanced cases, such as human cognition. Natural cognition or biocognition is first of all a form of biological adaptation that confers selective advantages for organisms by sustaining the adaptive coupling of organisms with their ecological niches. As Lyon & Keijzer (2007) explain the biogenic approach to cognition:

> *[…] a biogenic approach assumes that because natural cognition is first and foremost a biological function, which contributes to the persistence and wellbeing of an organism embedded in an ecological niche with which it must continually contend, then biological principles are the best guide to what cognition is and what it does. Like other biological functions (e.g., respiration, nutrient acquisition, digestion, waste elimination) the general outline maybe broadly similar relative to the economy of an organism; some basic mechanisms may even be shared. On the other hand, the mechanistic details of how the function works are likely to differ from organism to organism, the result of making a living in a particular niche (p.137).*

The biogenic approach also uses biological principles as the basis for conceptualizing natural cognition (Keijzer, 2009). That is, natural forms of cognition share certain common characteristics, such as modularity and hierarchical organization, which evolved because they provide adaptive advantages. The aim of this bottom-up biogenic approach is to specify these adaptive advantages, to be more specific about the structural demands and functional mechanisms necessary for biocognition, to distinguish cognition from other forms of biological adaptation, such as ontogenetic adaptation and phenotypic plasticity, in order to address and answer fundamental questions such as why cognition evolved in the first place, and what separates cognition from life itself. What constitutes natural cognition then becomes an empirical issue; our notion of what (natural) cognition is then has to be adapted to the outcome of the investigations on the biological principles that underlie cognition (Keijzer, 2009). These biological principles can be used as a set of constraints that delineate the biocognitive domain (Lyon, 2006a). That is, biology shapes and constrains natural forms of what we can think of as cognition by providing boundary conditions and organizational principles. To illustrate, I consider three such biological constraints on natural cognition: (1) *Evolution*, (2) *Life*, (3) *Sensorimotor behavior:*

(1) *Evolution*. Evolution is the unifying principle in biology (Dobzhansky, 1973). Evolutionary theory holds that all complex biological functions have gradually evolved from simpler pre-existing processes by hereditary variation sorted by natural selection. According to evolutionary theory, there is a deep phylogenetic continuity between species, which is reflected not only in their genetic make-up but also in their behavior. Behavior and cognition are phenotypic traits; they are shaped by evolution just as any other trait (Futuyma, 1998). There is therefore also phylogenetic continuity in cognition: complex cognitive capacities have evolved from more basic cognitive capacities and one should therefore think in terms of grades of cognition (Keijzer, 2009). On this view, protists such as amoeba might exhibit some very basic cognitive skills, whereas invertebrates such as squids display more advanced cognitive abilities. From this perspective, it becomes meaningful to ask questions about the phylogenetic origins of cognition and its selective

advantages, how the most elementary forms of cognition evolved into more complex forms, and how different forms and mechanisms of natural cognition are related.

(2) *Life*. Living systems are geared to continuously uphold and maintain their own organization in the face of internal and external perturbations (Jantsch, 1980). In order to stay alive, organisms need to take in food, water, harvest energy, and dispose of waste products in order to maintain their delicate metabolic equilibrium. Organisms typically possess an entire arsenal of physiological regulatory mechanisms which keep the conditions for their metabolism, such as their temperature, internal acidity (pH), and blood sugar levels within viable limits. These homeostatic mechanisms allow organisms to robustly cope with variability in their environments, and help to facilitate their ecological generalization (Futuyma, 1998). Natural cognition shades-off into and is intrinsically connected to the basic processes that govern life itself (Godfrey-Smith, 2002). That is, cognitive organisms assess and assign values to internal and external changes based on their current state of homeostasis, their past experiences, and their own predispositions (Lyon, 2006a). From a biogenic perspective, natural cognition is best viewed as an extension of these basic homeostatic processes, which helps to facilitate organisms to cope with environmental challenges and to maintain their organization. A biogenic perspective subsequently differentiates between different kinds of adaptive behavior, such as ontogenetic adaptation, phenotypic plasticity, and sensorimotor coordination, in order to distinguish basic cognitive behaviors from other forms of adaptation to get clearer on what separates cognition from life itself and other forms of biological adaptation.

(3) *Sensorimotor behavior*. In this thesis, I adopt a biogenic view to cognition that also incorporates the views of EEC[12]. A central claim of EEC is that sensorimotor behavior forms the phylogenetic and ontogenetic foundation for cognitive processes (e.g. Anderson, 2005; Keijzer, 2001; 2009; Ziemke, 2008). Sensorimotor behavior is ubiquitous in the animal kingdom and is also exhibited by organisms that lack a brain or a nervous system, such as single-celled organisms. Sensorimotor behavior provides organisms with an extension of homeostatic processes: sensorimotor behavior allows organisms to optimize their homeostasis by actively seeking out environments that best suit their metabolic requirements. The capacity of organisms to engage in normative, goal-directed sensorimotor behaviors allows these organisms to deal more adequately with the variability in their environments and to extend their ecological generalization. According to Christensen and Hooker (2000) this gives rise to self-directedness in organisms: “Self-directedness is a capacity for integrative process modulation which allows a system to ‘steer’ itself through its world by anticipatively matching its own viability requirements to

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[12] Lyon (2006b) notes that embodied/embedded cognition is not by default biogenic and that biogenic approaches do not necessarily endorse EEC. In fact, anthropocentric interpretations of EEC are quite common, as well as biogenic oriented perspectives that are based on a cognitivist' perspective on cognition.

interaction with its environment" (p.5) (see also Christensen, 2004). The biogenic approach to cognition taken in this thesis homes in on the mechanisms that give rise to goal-directed sensorimotor behavior and discusses how these organisms use sensorimotor behavior to attain their adaptive goals.

The main goal of this thesis is to specify the biological principles involved in natural cognition, or biocognition, and to anchor the notion of biocognition in the biological mechanisms that govern the sensorimotor behaviors of organisms. On this view, biocognition becomes an intrinsic feature of the basic biological set-up of all free-moving organisms. This biogenic approach also facilitates the theoretical integration of psychology with biology by providing a common conceptual understanding of natural cognition as a form of biological adaptation that involves sensorimotor coordination. In the next chapter, I start with an investigation into the minimal requirements for biocognition. I argue that bacterial chemotaxis provides a good starting-point for understanding biocognition as a form of sensorimotor coordination, and that sensorimotor coordination can serve as a "mark of the cognitive" for natural cognitive systems.

2. The Lower Bound:
Principles of Minimal Cognition

A modern molecular biologist might paraphrase the poet Pope by saying,
The proper study of mankind is the bacterium.

David Koshland (1977)

2.1 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, 2002; 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[13] was manipulated so that it remained stuck in an iterative, automatic behavioral loop;

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

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, 2006; 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, Giurfa & Brembs & *2006*, 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[14] How to proceed with this task? Davidson made a

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[14] 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, 2002; 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

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 (2002, 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, 2003a; Lyon, 2006a; 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, 2004; Lengeler *et al.*, 2000; Lyon, 2006a; 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, 2006b), 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

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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 loses 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.

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.

2.2 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[15] (see also, Beer, 2004; Bitbol & Luigi, 2004; Luisi, 2003; Lyon, 2004). Next, we introduce the work of Moreno and collaborators regarding their ideas on what sets cognition apart from life.

2.2.1 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

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[15] 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, 2004.

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.

2.2.2 Nervous systems and the Cognitive Domain

Moreno and collaborators (e.g. Moreno, Merelo & Etxeberria, 1992; Etxeberria, Merelo, & Moreno, 1994; Moreno, Umerez, & Ibañez,, 1997; Barandiaran & Moreno, 2006; 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, 2004; Lyon, 2006a 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.

2.3 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, 1977; Boyd & Simon, 1982).

2.3.1 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[16] (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 2).

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

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[16] 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).

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)[17].

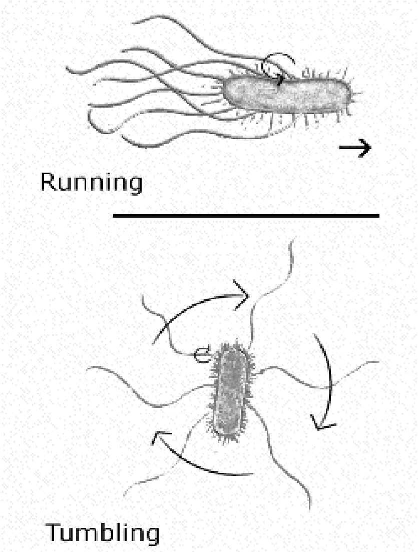

Figure 2. Running and tumbling behavior in *E. Coli* (drawing by Daan Franken).

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

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[17] Recent computer modeling work on *E.coli's* chemotaxis behavior suggests that its tumbling behavior is not as random as was previously assumed. Using computer simulations, Vladimirov, Lebiedz & Sourjik, (2010) predict that an additional navigational fine-tuning mechanisms exists in *E. coli* that affects the degree of reorientation during tumbling behaviors: When these bacteria are traveling up a gradient of chemicals tumbling angles are slightly below average, while when traveling down a gradient tumbling angles are slightly larger than average. As Vladimirov *et al*., (ibid.) put it: Taken together, our results suggest that in addition to extending the run length while swimming up the gradient, *E. coli* uses an auxiliary mechanism of tumbling angle tuning according to the swimming direction. This fine tuning of tumble is mediated by the same adjustment of tumbling frequency that underlies the conventional chemotaxis strategy of *E. coli*. Since both navigation mechanisms arise from the same basic mechanism of altered motor switching, evolutionary optimization of the basic mechanism depends on both the effect from the tumble frequency and the number of flagella that reverse per tumble. The previously unrecognized mechanism shown here is expected to be shared by other peritrichously flagellated [i.e. having multiple flagella distributed across its entire surface] bacteria with similar chemotactic behavior, and it seems to represent yet another level of evolutionary optimization of the chemotaxis system" (p.4, my brackets).

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.

2.3.2 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 address some of the dynamic principles that govern 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 3). 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 3).

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).

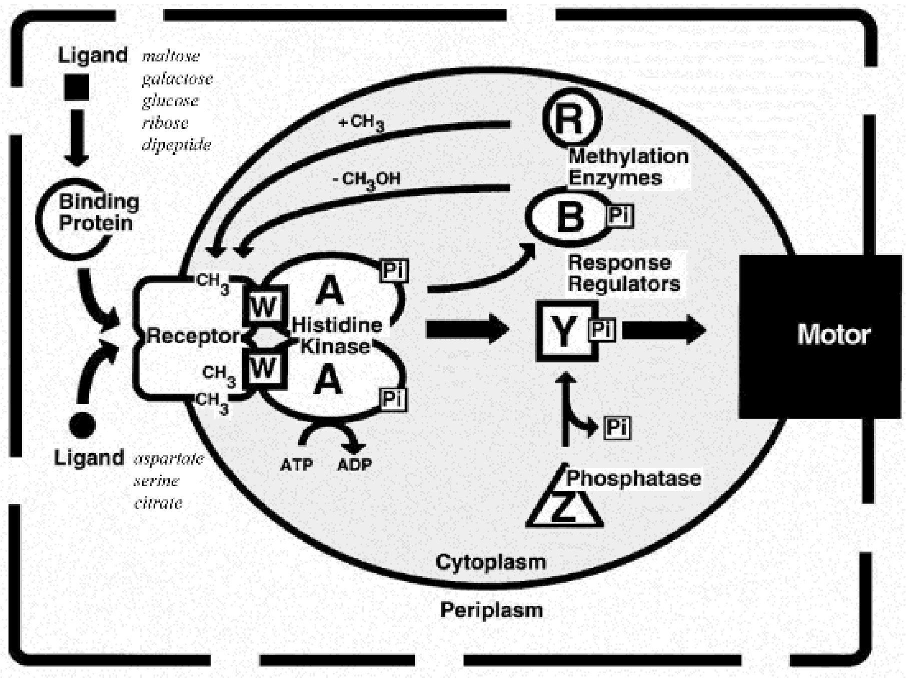

Figure 3. Schematic representation of the protein complexes and their interactions in the TCST system of the *Escherichia coli* bacterium (taken from Falke *et al.*, 1997, used with permission of the first author).

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 3). 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 adaptation. As Tyson, Chen and Novak (2003) frame it in their discussion of the mathematical modeling 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 strength, its steady state response R is independent of S. Such behavior is typical of chemotactic systems, which respond to an abrupt 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).

2.4 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, 2006a). 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.

2.4.1 From Metabolic Adaptation to Minimal Cognition

The earliest forms of ontogenetic adaptation in unicellular organisms were probably governed by metabolic reactions[18]. 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).

An 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 abundant in the environment, the lac operon system becomes disinhibited, 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 is 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 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

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[18] In this chapter, "metabolism" is interpreted as the sum of processes that continuously maintains functional cell integrity.

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 a bacterium or a 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 originally metabolism related, but later evolved to serve these other purposes (Alexandre & Zhulin, 2001; Bourret *et al*., 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 than 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. Analogous to Dobzhansky, Maturana could have said that nothing in biology makes sense except in the light of metabolism or autopoiesis. In our view, metabolism and cognition remain intrinsically connected even when they are clearly different kinds of processes. Metabolism is based in chemistry while 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.

2.4.2 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 formed 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, 1996). 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 spatial- and temporal dimensions". (p. 117). From this perspective, minimal cognition is not so much a centralized property of the 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 with 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.

2.5 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 mechanistic-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. Brooks, 1999; Clark, 1997; O'Regan, & Noë, 2001). We elaborate on each of these implications.

2.5.1 Anthropocentrism and the 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, Snoep, Treur, Westerhoff, & Wijngaards, 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 provides 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 anthropomorphic 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 was probably 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 such as 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 overprivileging 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, 2006a) perspective on cognition may eventually lead to less biased, more natural descriptions of these complex behaviors, as well as their determinants.

2.5.2 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, in addition to 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 with 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, 2006a) 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). In 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.

2.6 Conclusion

In this article, we have attempted to clarify 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.

3. The Middle Ground:
Biological Principles of Cognitive Organization

How complex or simple a structure is depends critically upon the way in which we describe it. Most of the complex structures found in the world are enormously redundant, and we can use this redundancy to simplify their description. But to use it, to achieve the simplification, we must find the right representation.

Herbert A. Simon (1962)

3.1 Introduction

So far I have established that biocognition extends widely across the biological domain, being based in a sensorimotor organization that is already present in bacteria. This chapter investigates how such minimal forms of cognition are related to more elaborate forms, and ultimately to human cognition, by delineating the fundamental organizational principles of biocognitive systems. Biocognition is shaped and constrained by principles of biological organization. That is, biological systems are highly optimized by evolution and fundamental organizational features such as modularity and near-decomposability are therefore ubiquitous in nature (e.g. Callebaut & Rasskin-Gutman, 2005; Simon, 1962). These and other basic principles of biological organization also bear on the organization of natural cognitive systems: Biocognitive organization is co-determined by phylogenetic, ontogenetic, and epigenetic factors, such as an organisms' genetic make-up, its morphological organization, and its sensorimotor experience, respectively. The goal of this chapter is to examine some fundamental principles of biological organization such as modularity, epigenetic organization, and bow-tie organization, and to use these principles as guidelines to obtain organizational principles of biocognition. These principles of biocognitive organization also help to make clear how bacterial cognition scales up to human cognition.

The key concept that makes the transition from bacterial to human cognition thinkable is *modularity*. Modularity is a major biological principle that is also relevant to understanding the organization of cognitive systems. Although most cognitive scientists seem to agree that cognitive systems are modular to a certain degree, consisting of many functionally specialized processes, cognitive modularity remains a rather controversial topic. In the cognitive sciences, there is no consensus on as to what constitutes a cognitive module, on which level(s) of description cognitive modules are plausibly distinguished, and how cognitive modularity is related to mechanisms of cognitive development and evolution. For a long time these issues are debated and cognitive modularity continues to be a central topic in the modern cognitive science literature (e.g. Altenberg, 2005; Atran, 2001; Barrett & Kurzban, 2006; Bechtel, 2009; Buller, 2005a; Garcia, 2007; 2010; Geary & Huffman, 2002; Griffiths & Machery, 2008; Velichkovsky, 2005).

The dissonance in cognitive science on the topic of modularity sharply contrasts with the way in which the notion of modularity is used in modern-day biology. In this broad field, modularity has become a central research theme that serves as a nexus between evolutionary biology and developmental biology, yielding new research disciplines such as 'evo-devo', i.e. evolutionary-developmental biology (e.g. Callebaut & Rasskin-Gutman, 2005; Schlosser & Wagner, 2004). Some theorists argue that this alternative, more fecund approach to modularity can also help to provide an alternative view on cognitive modularity (Griffiths, 2007; Griffiths & Machery, 2008). Following up on and extending this work, this chapter investigates how four major biological organizational principles co-determine the organization of natural cognitive systems in order to obtain a more biologically plausible view on cognitive modularity and to provide additional biological principles that help to bridge the gap between minimal cognition and human cognition.

This chapter is structured as follows: In section 3.2, I discuss the still dominant cognitivistic interpretation of cognitive modularity. I mainly focus on Evolutionary Psychology (3.2.1) as the most pure and influential example and examine its main problems. Next, I discuss the distinction between vertical and horizontal cognitive modularity (3.2.2). The vertically modular view as advocated by cognitivists is regarded problematic, while the horizontally modular view is still underdeveloped; this chapter further develops the horizontally modular view and also develops additional biocognitive organizational principles. In the remainder of this chapter I examine four major biological organizational principles, namely: (1) modularity, (2) hierarchical organization and reuse as a way to achieve organizational complexity, (3) epigenetic organization, and (4) bow-tie architecture. In each case, I will first describe how the principle operates in a general biological context. Subsequently, I will discuss how the principle can be applied to the biocognitive domain by developing four biocognitive organizational principles (see table 1). In section 3.3, I examine how the notion of modularity itself is used in developmental biology, evolutionary biology, and evo-devo (3.3.1). Biological modules are distinguished at different levels of biological organization: from metabolic pathways and gene-protein networks to variational modules in the genotype-phenotype map and morphological modules. In section 3.4, I discuss hierarchical organization in connection to reuse as a second major biological organizational principle. Reuse is a key principle that supports the evolution and development of complex hierarchical systems. Next, in section 3.5, I deal with epigenetic organization as a third major biological organizational principle. Epigenetic mechanisms facilitate the ecological specialization of organisms by the context-dependent modulation of genetic-expression, so that organisms can flexibly adapt their phenotype to the meet the demands of local conditions. Section 3.6 focuses on bow-tie architecture as a fourth major biological organizational principle. Bow-tie architecture characterizes the global connectivity architecture in complex biological networks such as gene networks, metabolic networks and the vertebrate immune system. Lastly, in the conclusion I summarize the main points of this chapter.

1. **Modularity***: Biocognitive modules are bi- or multistable sensorimotor feedback control mechanisms that facilitate the sensorimotor coordination capacities of organisms (section 3.3.1).*
2. **Hierarchical Organization & Reuse**: *Biocognitive organizations are typically organized hierarchically with nested modules on phylogenetic and ontogenetic levels of sensorimotor organization; reuse of existing features is an important way to achieve cognitive complexity in development and evolution (sections 3.4.2 & 3.4.3).*
3. **Epigenetic Organization**: *Biocognitive organization derives to a large extent from epigenetic factors in which, genetic, physical, morphological, sensorimotor, and environmental factors mutually interact and constrain one another, modulating experience-dependent gene expression to sustain a flexible cognitive organization (section 3.5.1).*
4. **Bow-tie Architecture**: *Biocognitive control systems are bow-tie architectures that combine phylogenetically conserved core systems with peripheral and more flexible sensorimotor structures. Cognitive bow-tie architecture optimizes trade-offs between efficiency, metabolic costs of neuronal wiring, and cognitive flexibility (section 3.6.1).*

Table 1. Biocognitive organizational principles.

3.2 Modularity in Cognitive Science

Cognitive modules are usually viewed as domain-specific computational units in the brain that can be differentially impaired. Cognitive modularity is often posited in relation to computational tractability problems such as the frame problem (see Sterelny & Griffiths, 1999). The frame problem is best known as the epistemological problem concerned with how an agent models change in an environment when performing a certain action (Pfeiffer & Scheier, 1999). The frame problem originated in AI and is known in a variety of forms, all of which involve computational intractability issues due to combinatorial explosion (Sterelny, 2003, p.206). To prevent combinatorial explosion, an agent needs to know which aspects of the environment are relevant in relation to its action-effects so that it can minimize its search-space. According to Fodor (1983), cognitive modularity tackles the frame problem by imposing restrictions on input conditions so that the complexity of environmental input is reduced (pp.116-117). That is, a modular mind divides and restricts its range of inputs to specific domains of information that have limited search-spaces. Cognitive modules are then only triggered by certain preset and well-constrained environmental inputs, preventing combinatorial explosion.

Fodor's (1983) "The Modularity of Mind" discusses the classic and most influential cognitivistic interpretation of cognitive modularity. Fodor (Ibid., p.41) argues that the human mind is a three-tier system that consists of peripheral transducers, modular input systems and central systems. The peripheral transducers convert incoming stimuli into a format suitable for further processing, while the modular input systems - the main target for Fodor's modularity hypothesis – are domain-specific information-processors that make inferences about the information provided by the transducers. The modules in turn feed this information to the central systems, which are non-modular general-purpose mechanisms that integrate information from modular resources. Fodorian modules adhere to nine criteria; the most notable ones being “domain specificity” and “informational encapsulation” (see Barrett & Kurzban, 2006; Coltheart, 1999; Seok, 2006; Sperber, 2001). Fodorian modules are domain specific in the sense that they are responsive only to information in certain specific stimulus domains, so that these modules do not interfere and compete for central cognitive resources like memory and intelligence (Fodor, 1983, p.21). Furthermore, Fodor’s modules are informationally encapsulated in the sense that they do not process information available in other modules or in central systems.

Fodor’s characterization of cognitive modularity is rather narrow, which is why this view has become heavily criticized (Barrett & Kurzban, 2006; Brase, 2002; Garcia, 2007; Rockwell, 2005; Seek, 2006). The main criticism is that Fodor’s criteria are too strict, and that instead other less restrictive criteria for cognitive modularity need to be used. Fodor’s criteria for cognitive modularity are violated by the dynamic dispositions of the human brain: For example, fMRI research has revealed that most neocortical areas are better characterized as domain-dominant rather than domain-specific. Even a prototypical language ‘module’ such as Broca's area not only deals with language production, but also mediates learning by imitation and contributes to action-sequencing, motion-imagery, and movement preparation (Prinz, 2006; Uttal, 2001). In fact, cortical areas are usually involved in many different functions in different informational domains (Anderson, 2008). Given this extensive overlap found in most cognitive processes, informational encapsulation and domain-specificity seem to be far too stringent criteria to be applied to cognitive modules. Moreover, Fodor’s assumption that impaired modules display specific breakdown patterns that result in clear-cut dissociations has not been confirmed empirically. In clinical reality, co-morbid patterns seem to be the rule rather than the exception (see Karmiloff-Smith, Brown, Grice, & Paterson, 2003).

Since Fodor's stringent criteria for modularity are so easily violated many authors have suggested that a cognitive module is better characterized by its ‘functional specialization’ or its ‘computational autonomy’ (e.g. Barrett, 2005; Barrett & Kurzban, 2006; Pinker, 1997; Shettleworth, 2000; Sperber, 2001; Tooby & Cosmides, 2005); these interpretations of cognitive modularity are also frequently used by evolutionary psychologists.

3.2.1 Darwinian Modularity in Evolutionary Psychology

The cognitive modules postulated by Evolutionary Psychology[19] (henceforth EP) are 'Darwinian modules'. EP holds that Darwinian modules are solutions dedicated to specific adaptive problems encountered by our distant ancestors. Like Fodorian modules, Darwinian modules are specific-purpose computational units in the brain that are responsible for certain cognitive operations. Unlike Fodorian modules, however, Darwinian modules run from input to decision-making to output. Darwinian modules can allegedly be traced back to certain recurrent adaptive problems faced by our Pleistocene ancestors in the "environment of evolutionary adaptedness" or EEA[20] (e.g. Buller, 2005b; Carruthers, 2006; Sperber, 2001; Tooby & Cosmides, 1990; 2000). Darwinian modules represent innate bodies of knowledge stored in the genetic program; there are sets of genes that specifically encode for the developmental onset of Darwinian modules (e.g. Pinker, 1997). Standard examples of cognitive modules postulated by evolutionary psychologists include the 'cheater-detection' module, a module for altruistic behavior, and others for face recognition, incest avoidance, numbers, theory of mind, jealousy, kin detection, and alliance formation, to name but a few examples (see also Buller, 2005a; Buller & Hardcastle, 2000; Panksepp & Panksepp, 2000; 2001).

Darwinian modules do not neatly map onto the anatomical modules of the brain, but are mostly seen as widely distributed computational modules. Given that our genetic make-up hasn't changed much since the Pleistocene, it is often held by evolutionary psychologists that we are still equipped with hunter-gatherer brains that are trying to cope with a modern world. On this view, the brain is organized much like a Swiss-Army knife: the neonates brain comes pre-equipped with an array of specific-purpose tools that are solutions to very specific adaptive problems (Carruthers, 2006; Sperber, 2001). Some evolutionary psychologists hold that our cognitive architecture is massively modular. On this view, the human mind is for the most part made up out of specific-purpose systems that have been sorted by natural selection. Tooby and Cosmides (2005) argue that folk-psychological, general-purpose aspects of cognition such as learning, memory, and judgment, are best explained as expressions of constellations of cooperating Darwinian modules. Darwinian modules can be triggered in novel situations which show a high positive correlation with situations in the EEA, and continuously re-organize and re-route their inputs and outputs in order to cope with novel cognitive problems (Tooby &

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[19] Buller (2005b) distinguishes between evolutionary psychology as a general field of inquiry and Evolutionary Psychology (capitalized) as a research paradigm; here, the latter use of EP is maintained.

[20] The Pleistocene ranges from roughly 1.8 million years to 11.000 years ago, and according to many evolutionary psychologists this time period has had the most significant impact in the shaping of the human brain and typically human cognitive functions (Pinker, 1997). According to Cosmides and Tooby (1990), the EEA is "a statistical composite of the adaptation relevant properties of the ancestral environment encountered by members of ancestral populations, weighted by their frequencies and their fitness consequences (pp. 386-387).

Cosmides, 2005, p.33). According to Tooby & Cosmides (2005), this flexibility of Darwinian modules enables the human mind to solve domain-general problems and novel problems that never occurred in the EEA, such as for example driving a car or using a computer.

EP's interpretation of cognitive modularity is also heavily criticized (Brase, 2002; Buller, 2005b; Buller & Hardcastle, 2000, Hagen, 2005; Sterelny & Griffiths, 1999). A major criticism is that EP is 'phylogeny-minded' and centered on a gene-based view of cognitive modularity. That is, proponents of EP often endorse a hard distinction between ultimate and proximate factors; a dichotomy that also lies at the roots of the nature/nurture debate (Barrett & Kurzban, 2006; Lickliter & Honeycutt, 2003a; Panksepp & Panksepp, 2001). Since the works of Tinbergen[21] (1963), who drew on Ernst Mayr's distinction between ultimate and proximate causes, this distinction between ultimate and proximate causation has become widely influential in the cognitive sciences and it has played an important role in EP's theorizing about cognitive modularity. Lickliter and Honeycutt (2003a) argue that this classic dichotomy has lead evolutionary psychologists to decouple proximate and ultimate factors and to focus on ultimate causation: the phylogenetic determinants of cognitive modularity and the genetic basis for cognitive modules. Lickliter and Honeycutt (2003b) claim that even EP proponents that advocate a weaker form of interactionism still commit what they call the "phylogeny fallacy" by holding on to this principled distinction, downplaying the role of developmental factors. However, the dichotomy between proximate and ultimate factors has since long been abandoned by most biologists who argue that ultimate and proximate causes cannot be teased apart and that they are better interpreted as extremities along a continuum (Barrett & Kurzban, 2006; Futuyma, 1998). Modern-day biology shows that the phenotype of organisms is not a simple linear expression of a genetic program in response to environmental triggers, rather, the phenotype of organisms is the product of a complex of self-organizing processes that depends on the continuous interplay between the developmental system, gene-action, and epigenetic factors[22] (Ho, 1998). Epigenetic factors intervene between genotype and the generation of the phenotype and are evenly important in determining cognitive organization. The indirect relation between genotype and phenotype severely complicates the assumed straightforward relation between genes and cognitive modules postulated by

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[21] Proximate causation is related to *how* questions regarding the operations of developmental mechanisms that shape the phenotype of an individual organism, whereas ultimate causation deals with *why* questions regarding the evolutionary factors that have shaped the organization of the genotype on the population level (Mayr, 1961). Following Ernst Mayr, Tinbergen (1963) famously distinguished between two proximate causes of animal behavior - causation (internal/external factors) and ontogeny (development) - and two ultimate causes - function (survival/reproductive value), and evolution (phylogenetic origin) (Pisula, 1998).

[22] 'Epigenetics' (literally: 'above' or 'in addition to' the gene) broadly defined refers to the regulatory processes apart from those on the level of primary gene-action that lead to persistent phenotypical changes throughout development (see Jablonka & Lamb, 2005; see also section 3.5).

EP (Paterson, Brown, Gsödl, Johnson, & Karmiloff-Smith, 1999). As Karmiloff-Smith (2006) puts it:

> *We have seen that simple, direct mappings between genes and cognitive-level modules are not sustainable. In fact, genes are more likely to contribute to much more general levels such as developmental timing, neuronal migration, neuronal type/size/density/orientation, myelination, lamination, ratio of gray matter to white matter, firing thresholds, neurotransmitter differences, and so forth, any or all of which may be atypical in developmental disorders. The neonate brain starts out highly connected, not with domain-specific higher level modular processing; this emerges gradually over developmental time* (p. 48).

Developmental cognitive scientists such as Annette Karmiloff-Smith (2006) argue that the cognitive system of neonates becomes progressively modularly organized throughout development and that cognitive modules are mostly local adaptations that gradually emerge and self-organize during ontogeny rather than being hardwired adaptations to an ancestral environment. For example, Karmiloff-Smith (2006) claims that children are not born with a full-fledged face recognition module, as proponents of EP would have it, rather, face-recognition is a specialization of a more general object recognition ability that becomes modularized during development. Research shows that face recognition is one of the first cognitive abilities mastered by newborn infants; neonates quickly learn how to recognize their mother's face, within a matter of hours, possibly minutes after birth (Pascalis & Slater, 2003). At birth, human infants already show a preference for faces as opposed to other shapes and figures (Bushnell, 2001). Face recognition in newborns is mediated by subcortical structures, but from about two months on cortical areas become increasingly involved (Tzourio-Mazoyer *et al*., 2002). In adulthood, face processing is mediated by the fusiform face area (FFA), a discrete region in the human extrastriate cortex in inferior temporal cortex, which is dedicated to facial processing; (e.g. Grill-Spector, Knouf & Kanwisher, 2004, Kanwisher & Yovel, 2006; Paterson, Heim, Friedman, Choudhury & Benasich, 2006), among other visual tasks (see Gauthier, Skudlarski, Gore, Anderson, 2000; Grill-Spector, Sayres, Ress, 2006; Haxby, Gobbini, Furey, Ishai, Schouten & Pietrini, 2001). In infants, lesions in FFA not only impair face recognition but also degrades performance on other cognitive skills, such as object recognition. Conversely, in adults lesions in FFA result in a disorder known as prosopagnosia, the selective impairment of face recognition apparently without affecting other cognitive abilities, such as object recognition (Kanwisher & Yovel, 2006). According to Karmiloff-Smith, this shows that face recognition as a cognitive ability becomes progressively modularized during development as it becomes mediated exclusively by FFA. The gene-based view on cognitive modularity therefore provides a highly restricted view of the determinants of cognitive modularity that underestimates the role of the proximate factors in determining the modularization of cognitive abilities.

The so-called "grain-problem" also severely complicates EP's assumption that Darwinian modules bear a one-to-one relation to the adaptive problems they are meant to solve (Atkinson & Wheeler, 2003; 2004; Sterelny & Griffiths, 1999, pp. 328-332). That is, whereas evolutionary psychologists claim that Darwinian modules are solutions to specific adaptive problems, such as ‘fear of heights' or 'fear of snakes', these adaptive problems can also either be subdivided into a host of nested, finer-grained adaptive problems, or they can be viewed as expressions of a single, generalized fear response module. Atkinson and Wheeler (2003) argue that by taking human problem solving as the criterion for natural selection EP's approach becomes arbitrary; natural selection operates at many descriptive levels or grains not just on the level of human problem solving. Sterelny and Griffiths (1999) argue that there is no one-to-one mapping between cognitive modules and certain specific adaptive problems; a niche may contain many overlapping adaptive problems. The grain problem is illustrative of the difficulties involved to determine on which level(s) of explanation is cognitive modularity is plausibly distinguished.

The many persistent theoretical problems surrounding some of EP's major claims (see Panksepp & Panksepp, 2000, 2001, for an overview) have led some scholars to argue that EP has failed as a research paradigm (Buller, 2005a). Buller (2005a, 2005b) claims that, given the many theoretical problems regarding EP's central claims, that the evidence for the existence of highly specialized Darwinian modules is inconclusive at best. Many authors propose that the wide array of Darwinian modules postulated by EP can be explained away by considering that the cognitive skills they represent are the product of the complex interactions between the emotional system and a handful of domain-general cortico-cognitive functions (Brase, 2002; Buller & Hardcastle, 2000; Meisenberg, 2001; Panksepp & Panksepp, 2000, 2001). What seems to be clear though, is that EP’s tendency to posit a cognitive module for each and every cognitive ability generates too many false positives, and that it is best to apply Ockham’s razor to EP’s version of massive modularity.

In sum, the cognitivist’ interpretation of cognitive modularity is deeply problematic. Some theorists argue that the continuing terminological disagreements only hamper the development towards a more pragmatic account of cognitive modularity and that a fundamentally different theoretical perspective is required for understanding cognitive modularity (e.g. Buller, 2005a, 2005b; Rockwell, 2005). According to Griffiths (2007), a more biologically oriented approach to cognitive modularity provides a promising alternative (see also, Griffiths & Machery, 2008). The horizontally modular view might provide such a more biologically plausible approach.

3.2.2 Vertical vs. Horizontal Cognitive Modularity

A fundamental critique of the cognitivist interpretation of cognitive modularity comes from the field of EEC, which provides a radical departure from cognitivism (see chapter 1). How does this change in perspective on what constitutes cognition bear upon understanding its modularity? This switch in perspective is so fundamental that the notion of modularity as it was conceived of in classical cognitivism seems at odds with it (Bechtel, 2009). Some authors even abandon the notion of cognitive modularity altogether, at least in the classical cognitivist sense (Thelen & Smith, 1994). Susan Hurley (1998;

2001; 2008) differentiates between vertical and horizontal modularity[23] (Figure 4). Vertical modularity is a Fodorian input→inner processing→output picture to cognition, which wedges cognition in between input and output buffer zones. Horizontal modularity, by contrast, involves an entangled network of intimately coupled, task-specific sensorimotor processes which extend from input to output back to input as dynamic feedback loops that are spread out over brain, body and environment. The horizontal modular view supports a decentralized view of cognition that provides a way to decompose the mind based on sub-personal mechanisms that is rooted in adaptive perception-action feedback loops, and can be used to frame ontogenetic and/or phylogenetic hypothesis about cognitive decomposition.

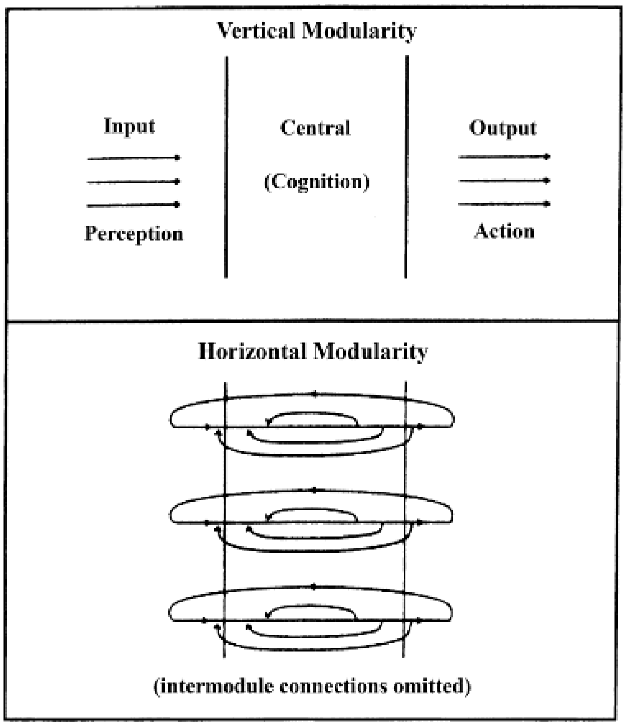

Figure 4: Vertical versus horizontal modularity. Adapted from Hurley (1998, p.407).

Hurley's (2005; 2008) shared circuits model offers an elaborated horizontally modular view of how cognitive functions such as imitation, deliberation, and mind-reading are based in five task-specific perception-action layers. In the shared circuits model, each

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[23] Hurley's (1998; 2001) distinction between horizontal and vertical modularity does not correspond with the way in which Fodor talks about horizontal and vertical modularity. According to Fodor (1983), horizontal modules are general-purpose mental faculties such as memory, attention, perception and judgment, while vertical modules are domain-specific cognitive skills such as language and mathematics. Hurley's version of horizontal modularity is similar to Brooks' subsumption architecture, except that in Hurley's version higher layers are dedicated to off-line functions that can be temporarily decoupled from overt behavior.

horizontal layer is dedicated to a certain general-purpose task such as spatial perception, object recognition, acquisition-type behavior, fight/flight behaviors, imitative responses, and so on. On Hurley's view, cognitive abilities are the emergent result of the coordinated interaction between a handful of layered, environmentally situated, horizontal sensorimotor structures (Hurley, 2001). A horizontally modular, or layered view of cognitive modularity such as advocated by Susan Hurley seems to be a more biologically plausible approach. The horizontal modular view, however, is still a preliminary and tentative view that remains largely unspecific about biological constraints. A biogenic view of cognitive organization can elaborate on this view of horizontal modularity by providing a more biologically plausible view on cognitive modularity and also by providing additional biological organizational principles, which is exactly the purpose of the remainder of this chapter. In the following sections, I examine how modularity and other key biological organizational principles such as hierarchical organization and reuse, epigenetic organization, and bow-tie organization are understood in different sub-disciplines of biology to develop more biologically plausible picture of (bio)cognitive organization. I start with an examination of how the notion of modularity is employed in developmental and evolutionary biology.

3.3 Modularity in Biological Development and Evolution

Herbert A. Simon (1962) advanced the view that the architecture of complex systems, whether they be physical, chemical, biological, economical, or social ones, share a common property, namely: "near-decomposability". Simon argued that nearly-decomposable systems are typically hierarchically organized assemblies of stable sub-systems or modules, of which the components display rich and fast-paced intra-component linkages while the inter-component interactions are of weaker intensity usually by about an order of magnitude or two (Simon, 2002). The human body is an example of such a richly nested, nearly-decomposable system that is build up out of many modular parts such as organs, which are built up from specialized cells that consist of sub-structures such as mitochondria, which are in turn built up from molecules and so on. According to Simon (1969), evolution employs an incremental construction method[24], which explains the

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[24] Simon (1969 pp.188-190) explains the relation between near-decomposability and evolution in his well-known watchmaker's parable about Tempus and Hora, two watchmakers who are in the business of assembling watches that consist of 1000 components each. Both watchmakers use their own strategy to construct the watches: whereas Tempus uses a plain linear method, adding one component at a time into a single assembly, Hora first creates stable subassemblies comprised of 10 components each before integrating them. In the story, both watchmakers are frequently interrupted by phone calls, and it turns out that Hora's method is much more resistant to these interruptions, whereas Tempus finds himself starting from scratch after each phone call; his assembly falls apart each time he is interrupted. The gist of the parable is that the construction method employed by Hora is much more resistant against interruptions, and that his modular construction method therefore provides a more robust means to fabricate watches than the non-

abundance of nearly-decomposable systems in nature. That is, nearly-decomposable systems have gradually evolved from the agglomeration of stable smaller systems: by adding sub-assemblies these systems could form progressively larger stable assemblies; natural selection only sorted stable system configurations that improved overall fitness.

Simon's view that near-decomposability is one the hallmarks for robust evolutionary design is well accepted nowadays, and modularity[25] has become a major research theme in modern-day biology. Many authors argue that modularity fosters evolvability (e.g. Altenberg, 2005; Hansen, 2003, 2006; Wagner & Altenberg, 1996): "an organism's ability to produce heritable, selectable phenotypic variation" (Kirschner & Gerhard, 1998, p.8420). Modularity reduces covariation among traits and confers evolvability by allowing natural selection to attune local optimizations on each character independently without interfering with global system stability and integrity (Kitano, 2004; Schlosser & Wagner, 2004). Modular design promotes variation, integration, and stability of novel system functions, and also accelerates the rate of evolutionary adaptation by promoting functional specialization (Calabretta, Nolfi, Parisi & Wagner, 1998; Calabretta, Nolfi, Parisi & Wagner, 2000; Calabretta, Di Ferdinando, Wagner & Parisi, 2003; Schlosser & Wagner, 2004; Simon, 2002; Wimsatt & Schank, 2004). Another way in which modularity promotes evolvability is that it serves as a fail-safe mechanism: modularity creates redundancy so that when one module breaks-down other modules can compensate by taking over the loss of function (Kitano, 2004).

In modern-day biology, modularity has become a central research theme that has elicited syntheses in various sub-disciplines, such as developmental and evolutionary biology (e.g. Schlosser & Wagner, 2004; Callebaut & Raskinn-Gutman, 2005). Biological modules are distinguished at different levels of biological organization, from metabolic-pathways, modules of gene-regulation, gene networks, to organ rudiments such as limb buds (Bonner, 1988; Lewontin, 1978; Riedl, 1978; Wagner, Mezey, & Calabretta, 2005; Winther, 2001). Very much in line with Simon, according to Bolker (2000), a general definition of a biological module is a semi-independent, internally tightly integrated unit (a structure, a process, or a pathway) that can be delineated from its surrounds or context in which it is integrated by much weaker inter-component connections (p.773).

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modular one handled by Tempus. According to Simon (1969), evolution, much like Hora, employs this modular construction method.

[25] The terms near-decomposability and modularity are often used interchangeably. Near-decomposability and modularity both refer to the relation between quasi-independent elements in complex systems. As Simon himself put it: "In a nearly-decomposable system, the short-run behavior of each of the component subsystems is approximately independent of the short-run behavior of the other components;" and, "in the long run the behaviour of any one of the components depends in only an aggregate way on the behaviour of the other components" (Simon, 1969, p.198). However, according to Zhang and Gao (2010), modularity is a special case of near-decomposability in which "the interdependencies between modules are specified by design rules (p.171)"; see Zhang and Gao (2010) for a more detailed discussion on the relation between modularity and near-decomposability.

In line with this rough definition, a general distinction is often made between (i) structure-oriented and (ii) process-oriented perspectives on biological modularity (Callebaut, 2005; Schlosser, 2004): (i) Structure-oriented perspectives on biological modularity focus on the relatively independent structural features of organisms, such as arthropod segments, limbs, bodily organs, and modules of the nervous system (Altenberg, 2005; Bonner, 1988; Leisse, 1990; Winther, 2001). The independence of structural modules is relative in the sense that there can be strong functional inter-dependencies between structural modules (Watson & Pollack, 2005); (ii) Process-oriented perspectives on biological modularity focus on semi-autonomous processes such as metabolic pathways, gene-regulatory interactions, and psychological traits (Breuker, Debat & Klingenberg, 2006; Callebaut & Rasskin-Gutman, 2005). According to Schlosser and Wagner (2004), a process module is an integrated dynamic organization that displays quasi autonomous, context-insensitive behavior. Process modules also need to function in an integrative manner, which is why they are only 'quasi' autonomous (Wimsatt & Schank, 2004; Winther, 2005). Process modules may map directly onto structural modules but usually there is not a straightforward one-to-one mapping (Callebaut, 2005).

In developmental biology, modularity is often used to designate the semi-independent functional units of development. Developmental biologists distinguish different functional parts in embryonic development, each with their own characteristic onset, spatial location, and developmental trajectory. Developmental modules are distinguished at different levels of biological organization, from modules of gene-regulation and gene-networks, to morphogenetic modules (Bonner, 1988; Hall, 2003; Schlosser & Wagner, 2004; Wagner & Altenberg, 1996). Morphological modules such as limb buds and organ rudiments often serve as the paradigmatic examples of developmental modules (e.g. Raff, 1996). These so-called "histogenetic fields" are tissue-producing fields in embryonic development that give rise to the morphological modules in adult form (e.g. Bolker, 2000; Lewontin, 1978). Morphogenetic fields in embryonic development are governed by the dynamic expression of constellations of genes which specify positional gradients for developmental modules along the embryonic anterior-posterior and rostral-caudal axis (Callebaut, 2005; Redies & Puelles, 2001; Wagner *et al.*, 2005). Developmental modules are distinguished by their quasi-independent, context-insensitive behavior (Schlosser & Wagner, 2004). According to Schlosser (2004, p.523), morphological modules are context-insensitive in the sense that they have the propensity to retain an invariant input-output relation despite a variety of operational conditions and environmental perturbations (see also Breuker *et al.*, 2006). Differently put, developmental modules are internally integrated by the dynamic covariation between components and relatively independent of the context in which they are embedded. Because of their context-insensitivity, developmental modules are highly robust to parameter changes and uncertainty (Kitano, 2004). The fruit-fly eye is illustrative of the context-independence of developmental modules. Halder, Callaerts and Gehring (1995) targeted the mis-expression, or ‘ectopic expression’ of the ‘eyeless’ gene [26], a master control gene for eye morphogenesis, and succeeded in inducing ectopic eyes to grow on the wings, the antennal segments, and middle leg of the fruit-fly Drosophila. These topologically misplaced eye structures demonstrate their resistance against contextual perturbations by fully retaining their typical structural organization despite being expressed in an abnormal location and in the wrong kind of tissue (see also, Wagner & Altenberg, 1996).

Evolutionary biologists use the notion of modularity to explain morphological evolution. In evolutionary biology, the modules of central interest are variational modules. Variational modules [27] are the units of natural selection. Variational or evolutionary modules are distinguished on different levels of biological organization, from modules of genetic regulation, signaling modules, to positional modules such as body segments (see Schlosser, 2004). Variational modularity is a property of the genotype-phenotype map and can be seen as an inference about its statistical structure (Mezey, Cheverud, & Wagner, 2000; Wagner & Altenberg, 1996). The genotype-phenotype map specifies the relation between genotypic and phenotypic variation; it forms a complex hierarchical system composed of genes, gene-reactions, reaction products, and feedback effects organized in epigenetic networks, composed of second-order effects of genes and their interactions, and governed by information that is not specified at the genetic level (Callebaut, 2005; Klingenberg, 2005; Wagner *et al.*, 2005).

Variational modules are clusters of pleiotropic[28] effects in the genotype-phenotype map (Wagner & Altenberg, 1996). Wagner and Mezey (2004) define a variational module as: “a collection of phenotypic traits that are variationally integrated through the pleiotropic effects of genes and independent of other such clusters because of the relative lack of pleiotropic effects among them” (p.341). Given that pleiotropy occurs mainly within variational modules, any changes that might occur because of mutations are limited

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[26] The eye morphogenetic field in Drosophila is under control of the ‘eyeless’ (ey) gene, a master control gene for eye morphogenesis (Halder *et al.*, 1996; see also section 3.1). Eyeless or Pax-6 has its homologues in both invertebrates and vertebrates, and is employed by a wide variety of organisms such as flies, mice, humans, and also nematodes (Wagner & Altenberg, 1996). Nematodes lack eye-like structures; *Pax-6* here serves a role in the shaping of the head. Allman (1999, p.68) suggests that this function reflects a phylogenetically more ancient role for *Pax-6.*

[27] Variational modules often do not neatly map onto developmental modules. For example, whereas each tooth germ is an instance of a developmental module, canines, front teeth, and molars all constitute different instances of variational modules (Wagner *et al.*, 2004).

[28] A gene exerts pleiotropic effects when its expression has multiple phenotypic effects, which occurs for example when a single gene is expressed in different tissues (Futuyma, 1998; see Wagner & Zhang, 2011) for a recent review on the significance of pleiotropy in the genotype-phenotype map).To exemplify, universal pleiotropy in the genotype-phenotype map would imply that every gene is correlated to every phenotypic variable; a single mutation at the genetic level would then (mal)affect the entire phenotype. In contrast, a complete lack of pleiotropy in the genotype-phenotype map would imply that each gene maps only to one unique phenotypic trait; this would therefore constitute an extreme case of genetic modularity. According to Callebaut (2005) the modular make-up of the genotype-phenotype map ranges somewhere between these extremes.

to the variational module in question rather than (mal)affecting other traits. This way, variational modules can be optimized independently of other modules, which fosters evolvability. Pleiotropy also facilitates the integration of characters that belong to the same functional unit. As Klingenberg (2005) explains:

> *Selection will tend, on the one hand, to extend the pleiotropic effects of genes to the sets of traits serving particular functions, and on the other hand, to break up pleiotropic complexes of traits that are involved in different functions. As a result of this adaptive process, separate sets of loci will have effects on the sets of traits associated with different functions. The genetic modularity will match the subdivision of morphological structures into functional units. The genetic modules are distinct sets of loci, each internally connected by a network of pleiotropic effects, which will map directly to functional modules, sets of traits related by shared functions. The crucial point of this view is that modularity is the outcome of selection for variation that can accommodate groups of traits serving different functions (p.18).*

Accordingly, Wagner and Altenberg (1996) distinguish two ways in which the individuation of variational modules in the genotype-phenotype map can take place: (1) modularization by integration, which occurs when traits become integrated into a single module due to an increase in pleiotropic effects; pleiotropic effects are then extended between sets of traits that accommodate a certain adaptive function, and (2) modularization by parcellation, which allows sets of traits that serve different functions to change independently due to the brake up of pleiotropic effects.

There are different views on the origins of variational modularity. The extrinsic view is that modularity is a generic design principle and necessary consequence of variation and natural selection (Wagner & Altenberg, 1996; Lipson, Pollack & Suh, 2002). According to this line of thought, modularity is an evolved property and biological systems are characteristically composed of modular elements that combine in a hierarchical, nearly-decomposable fashion (Wagner *et al*., 2005). The intrinsic perspective holds that modularity is the outcome of the developmental system and therefore an intrinsic feature of organisms. The main idea here is that the developmental system produces patterns of variation and constraints, and biases evolution into certain directions in morphospace; a hypothetical space of all possible and impossible morphologies (Klingenberg, 2005). On this latter view, modularity occurs as a side effect of evolutionary dynamics, arising indirectly as the outcome of physical self-organizing processes (Altenberg, 2005; Calabretta, Nolfi, Parisi, & Wagner, 2000, Callebaut, 2005; Kauffman, 1995). Although these differing views on the origins of modularity are sometimes taken as antagonistic, they are compatible as ultimate and proximate determinants of modular organization in biological structures (Barrett & Kurzban, 2006). Indeed, current evidence vindicates both the intrinsic and the extrinsic views (Klingenberg, 2005). However, on a more detailed level it is still unresolved which mechanisms, be it intrinsic or extrinsic ones, explain the origins of modularity. Wagner *et al*. (2005) promote mechanistic plurality with respect to this issue. They suggest that at least seven distinct mechanisms promote evolutionary modularity and argue that potentially more mechanisms could be identified in the future.

3.3.1 Evo-Devo

In the last three decades, developmental biology and evolutionary biology have partially merged into a single field dubbed "evolutionary developmental biology", or "evo-devo" for short. Evo-devo examines how changes in development relate to evolutionary changes (Baguñà & Garcia-Fernàndez, 2003; Breuker, Debat & Klingenberg, 2006; Hall, 2003; Klingenberg, 2005; Wagner *et al.*, 2005). In the nineteenth century, Ernst Haeckel first recognized the connection between development and evolution. However, his biogenetic law of recapitulation - *ontogeny recapitulates phylogeny* - was soon discredited by experimental morphologists and biologists who demonstrated that there is no simple isomorphic relation between ontogeny and phylogeny (Bolker, 2000). With the coming of evo-devo, there is a revived interest in the important parallels that can be drawn between developmental and evolutionary changes. The modules of central interest in evo-devo are the genetic regulatory toolkits, which are now found to be common to most multicellular organisms, from sponges to vertebrates (Baguñá & Garcia-Fernández, 2003). Regulatory modules such as homeobox genes are the basic building blocks of evolution and provide an interface between phenotype and genotype (Klingenberg, 2005). Homeobox genes do not encode for proteins but rather serve as transcription factors that act as switches causing genes to be expressed or repressed. Homeobox genes such as Hox determine axial differentiation of body segments and appendages (Futuyma, 1998). Some of these so-called "developmental-evolutionary toolkits" have been conserved for over 500 million years (Hall, 2003; Carroll, 2008).

The developmental system with its conserved genetic toolkit is not just the main source for generating morphological diversity, but it also comes with inherent constraints on variability. *Negative constraints*, such as phylogenetic constraints[29], reduce evolvability and make it difficult to attain certain (maladaptive) morphologies. For example, the phylotypic stage in embryonic development is an early developmental stage at which all

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[29] Phylogenetic constraints are adaptive characters that limit the variability of organisms. Futuyma (1998, p.671) lists a number of such phylogenetic constraints: (1) Local physical constraints, such the respiratory system of insects (tracheae), whose functionality limits the size of these organisms. (2) Selective constraints, some traits may not have evolved in a certain lineage because of certain selective disadvantages. (3) Functional constraints, some traits may not have evolved in a certain lineage because they impair the functionality of other features; these are a special kind of selective constraints. (4) Developmental constraints, such as the correlation between phenotypical features through pleiotropy, or the absence of genetically based phenotypic variation. Ontogenetic constraints partially overlap with phylogenetic constraints such as absence of dissociability or correlation between developmental modules through pleiotropy (Futuyma, 1998). Universal constraints such as gravity or the mixture of gases in the atmosphere also limit the variability of organisms. For example, flying elephants and man-sized single-cellular organisms are 'forbidden' phenotypes because of universal constraints.

vertebrate embryos bear a close morphological resemblance to each other (Futuyma, 1998). The phylotypic stage is an embryonic developmental pattern that is heavily constrained at the middle stage (the phylotypic stage) and exhibits more divergence at the early and later stages, forming a hourglass pattern (see Raff, 1996). The phylotypic stage is marked by a lack of modularity due to strong pleiotropic effects, which makes this stage highly vulnerable; any slight deviations at this stage of embryonic development are detrimental and most often lethal (Galis & Metz, 2001). The phylotypic stage is highly conserved because of strong stabilizing selection, which makes it resistant against evolutionary changes (Galis & Metz, 2001, p.195; Kalinka *et al.*, 2010). The matter whether the phylotypic stage truly exists was long regarded controversial (Hall, 1997; Richardson *et al.*, 1997; Bininda-Emonds, Jeffery & Richardson, 2003), although converging evidence now vindicates the view that a developmental hourglass pattern indeed exists at least among vertebrates, drosophilids, arthropods and cnidarians (Kalinka *et al.*, 2010; Domazet-Lošo & Tautz, 2010; Salazar-Ciudad, 2010).

Positive constraints such as heterotropy and heterochrony, bias evolution into certain directions of morphospace, the space of all possible morphologies (Brusca & Brusca, 2003; Klingenberg, 2005; Rasskin-Gutman, 2005). Evo-devo investigates how the developmental system with its conserved regulatory toolkit produces patterns of morphological variability and constraints in the evolution of biodiversity (Carroll, 2008). Evo-devo emphasizes the central generative role for developmental modules in the evolution of novel phenotypes: changes in the interaction patterns in genetic regulatory networks are an important factor in macro-evolution (Baguñá & Garcia-Fernández, 2003). Evo-devo therefore challenges some of the central tenets of the Modern Synthesis[30], such as the neo-Darwinian view that novelty in evolution is merely due to gene duplication, mutations, and gene diversification, and that only natural selection is responsible for phenotypical diversity (Futuyma, 1998). Griffiths (2007) argues that by taking a multi-leveled stance on development and evolution evo-devo has problematized the idea that the unit of selection is the gene, and has complicated the view that morphology is shaped in a one-sided manner by selection-pressures only. Evo-devo has revealed that simple changes in the timing, site, or activity level in regulator modules can cause radical changes in specific morphological features independently of others, which accounts for some of the abrupt, discontinuous changes seen in evolution (Shubin, Tabin & Carroll, 2009). Evo-devo therefore provides an import addition to more conventional views on evolution. Other present research in evo-devo aims for an alternative view of homological relations, morphological novelty, genotype/phenotype divergence, and developmental dynamics in general (Artieri & Singh, 2010; Breuker *et al.*, 2006; Carroll, 2008; Müller, 2007).

To sum up, biological modules are relatively autonomous structure or process units that are tightly integrated internally and much weaker connected externally. The biological

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[30] The Modern Synthesis or Evolutionary Synthesis was an interdisciplinary effort that spanned the 1930s-1940s, which aimed to integrate Darwin's theory of natural selection with Mendelian genetics.

notion of modularity is highly flexible and broadly applicable to quasi-independent organizational units on different levels of biological organization, from metabolic pathways to limb buds. It is also clear that this interpretation of modularity is highly fruitful, and has supported the merger of developmental and evolutionary biology. So how can this interpretation of modularity help to develop a more biologically plausible view of cognitive modularity? In the next section, I argue that like developmental modules, (bio)cognitive modules are best viewed as feedback control systems.

3.3.2 Cognitive Modules as Sensorimotor Feedback Control Systems

Feedback control is a common biological mechanism. Positive feedback amplifies signals, which can force a system to bifurcate and to settle into a new equilibrium, another steady-state (Yi, Huang, Simon & Doyle, 2000). Positive feedback therefore often - though not necessarily - leads to bi- or multi-stability, which results in switch-like behaviors. For example, feedback induced bi- and stability and threshold regulation is common in gene-expression where it involves the on- or off-switching of transcription factors (Smits, Kuipers, Veening, 2006; Smits, Veening, Kuipers, 2008). In contrast, negative feedback has damping effect which forces a system to return to its current attractor state when perturbed, which is characteristic behavior of homeostatic systems such as circadian clocks (Hammerstein, Hagen, Hertz & Herzel, 2006). Negative feedback connects the output of a system with its input in a closed-loop; by attenuating the difference between the actual output and the desired steady-state output the system is able to maintain equilibrium (Kitano, 2004). Negative feedback dampens fluctuations in system parameters due to perturbations.

Feedback control is also an important feature of biological modules such as developmental modules. Developmental modules display quasi-independent, context-intensive behavior, which is due their propensity to retain an invariant input-output relation even when facing environmental perturbations (see also Schlosser, 2004; Breuker *et al.*, 2006). Developmental modules are highly robust to parameter changes and uncertainty due to feedback control (Kitano, 2004). Biocognitive modules can be viewed as a special kind bi- or multistable feedback control systems that facilitate the sensorimotor capacities of organisms. For example, we have seen in chapter two that minimal cognition can be viewed as the higher order regulation of sensorimotor behaviors. *E. coli*'s chemotaxis cognitive module is a behavioral bi-stability[31] that consists of two

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[31] A better known example of a behavioral multi-stability is provided by the horse's four distinct gaits, which are commonly referred to as walking, trotting, cantering, and galloping (Kelso, 1995). As horses speed up, they discontinuously shift their gait patterns; with a preference for a certain gait pattern within a particular speed range (Thelen & Smith, 1994). Horses prefer a certain gait pattern based on minimizing their energy consumption (Kelso, 1995). Gait transition dynamics are primarily determined by the speed of the horse, but are also sensitive to a variety of other internal and external factors, such as heart-rate, oxygen consumption, terrain characteristics, and temperature. According to Rockwell (2005) the gaits of the horse's ambulatory system can be viewed as attractors, or basins of attraction in a dynamic horse-environment system. Gait

attractors: a running behavior and a tumbling behavior; the context-dependent action-selection between these two behavioral states gives rise to chemotaxis. The bi-stable running/tumbling behaviors of *E. coli* are governed by positive feedback from *E. coli*'s receptors and TCST-pathway, which amplifies the bacterium's sensory-input so that it is able to detect a wide range of subtle differences between superimposed chemo-attractant levels (Sourjik & Berg, 2002). Negative feedback from the methylation pathway resets the receptors of the bacterium to their default state, which allows the bacterium to be sensitive to the relative value of stimuli rather than to their absolute value (Berg, 2000). Due to the rate-difference between the fast-paced two-component signaling pathway and the much slower methylation pathway, the bacterium is able to compare the current state of affairs with that of previous ones so that it can modulate its behavior accordingly. The chemotaxis module regulates the bacterium's action-selection by modulating its relative propensity to run or to tumble. Behavioral switching is based on contextual factors which facilitates the sensorimotor coordination of the bacterium. Cognitive control over behavioral bi-stability provides these organisms with an extension of basic homeostatic processes, enabling them to optimize the external conditions for their metabolism by navigating to niches that best support growth and survival. Besides chemotaxis, organisms such as bacteria use many other sensorimotor coordination modules that are sensitive to other contextual factors, such as phototaxis (light), aerotaxis (oxygen), thermotaxis (temperature), osmotaxis (osmolarity), gravitotaxis (gravity), and redox taxis (reduction potential) (e.g. Alexandre, Greer-Phillips & Zhulin, 2004; Taylor, Watts & Johnson, 2007). Throughout evolution, the modularization of cognition facilitated the increased physicochemical context-sensitivity of microbial sensorimotor behavior. This allowed these microorganisms to better distinguish and adaptively respond to a greater variety of stimuli, which must have conferred important selective advantages.

Control systems such as nervous systems are necessary for basic locomotion strategies at the level of multicellular organisms, such as hydrostatic propulsion, head-tail undulations, and locomotor limb movements. According to Christensen, (2007) the first level of cognitive control in Metazoa is provided by 'central pattern generators' (CPGs). CPGs are control systems responsible for the generation and regulation of stable behavioral patterns by generating rhythmic contractions across a bodily surface. CPGs are composed of pre-motor interneurons, which generate oscillations, coupled to motoneurons which stimulate the muscles to generate rhythmic patterns (Tsakiris *et al.*, 2005). Feedback control over multi-stable behavioral patterns through CPGs characterizes the sensorimotor behaviors of many Metazoa, such as the lamprey, the worm *C. Elegans*, and cnidarians such as hydra and jellyfish (see chapter 5; Jung, Kiemel & Cohen, 1996; Tsakiris *et al.*, 2005;). This shows that there are fundamental similarities between the basic behaviors exhibited by these organisms: all are feedback control strategies that revolve on the modulation of behavioral multi-stabilities; these forms of organismal motility are rooted in

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transitions can be viewed as steady-state transitions or bifurcations which allow the horse's ambulatory system to swiftly settle into another behavioral stability (Rockwell, 2005).

sensorimotor coordination. According to IJspeert (2003), CPGs can serve as modular templates that can be modulated by higher control and sensory feedback. Such templates or modules can be reused and redeployed throughout evolution to come to serve different adaptive purposes and to support a greater variety of behaviors, conferring survival and competitive advantages (Lichtneckert & Reichert, 2007; p.291). With the evolution of centralized nervous systems, the hierarchical control dimension of sensorimotor coordination could be expanded in ways unprecedented.

3.4 Hierarchical Organization & Reuse

Simon (1962) argued that hierarchical, nearly-decomposable organization is characteristic of biological systems. This kind of organization can be distinguished along phylogenetic and ontogenetic dimensions. The development of the vertebrate brain is an illustrative example of the nested hierarchical modularity on the ontogenetic level. In embryonic development, the neural tube is topologically organized in dissociated histogenetic fields of neural tissue (Leisse, 1990; Mountcastle, 1997; Allman, 1999). At the early stages of embryonic development, all chordates[32] possess a dorsal, hollow nerve cord called the neural tube, which grows rostral bulges termed the rhombencephalon (hindbrain), the mesencephalon (midbrain), the prosencephalon (forebrain). This tripartite modular division of the brain is one of the hallmarks of chordate embryonic development (Martin, 2003) (see figure 5).

These bulges are discrete neuroepithelial domains or histogenetic modules which are the product of the dynamic expressions of gene constellations that form mosaic-like expression patterns along both the longitudinal (anterior-posterior) axis and transverse (dorsal-ventral) axis of the neural tube (Kandel, Schwartz & Jessell, 2000). Throughout embryonic development, the hindbrain, midbrain, and forebrain give rise to further secondary and tertiary divisions into finer-grained, nested modules (Redies & Puelles, 2001). For example, the forebrain or prosencephalon subdivides into telencephalon (cerebral hemisphere) and diencephalon (thalamus and hypothalamus); rhombencephalon subdivides into metencephalon (pons, cerebellum) and myencephalon (medula) Later in development, telencephalon also subdivides into a number of morphological modules, and also gives rise to the neocortex, which is for the most part organized into six horizontal layers of cortical sheets of about 1-3 millimeter in thickness. Layers II-VI of the cortex are composed of minicolumns: iterative modular sub-structures that each contain about 80-100 piramidal neurons (Allman, 1999; Kandel *et al.*, 2000; Mountcastle, 1997).

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[32] The phylum chordata includes vertebrates and two invertebrate or protochordate taxa: urochordata (ascidians or sea squirts) and cephalochordata (amphioxus or lancelets), which, at least at some stage in embryonic development possess a neural tube, a notochord, pharyngeal gill slits, and a tale (Wada, 2001; Prescott, 2007).

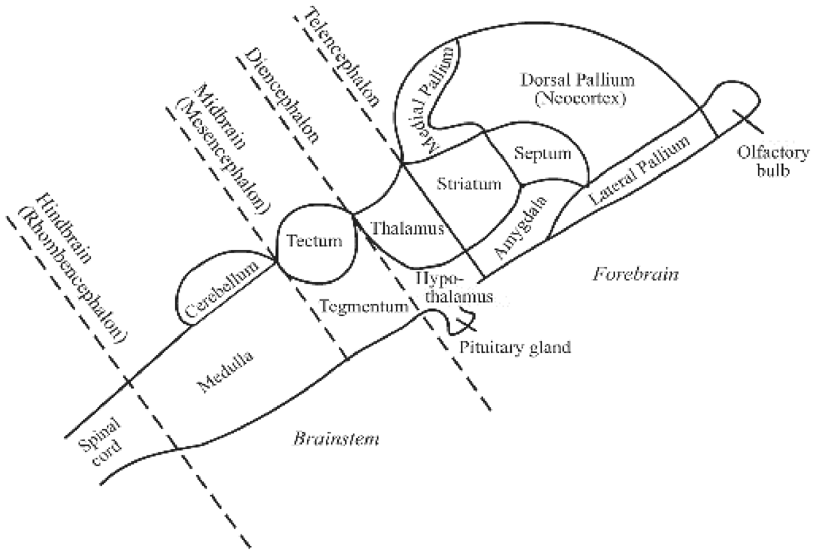

Figure 5. A depiction of a generalized vertebrate brain and its major morphological modules. The vertebrate brain plan is composed of hindbrain, midbrain, forebrain and spinal cord, and is characteristic of all vertebrates (from Prescott, Redgrave, & Gurney, 1999).

This kind of cortical organization characterizes the brain of most mammals (Leisse, 1990). Cross-species analysis shows that the long conserved morphological modules that make up the vertebrate brain plan, such as basal ganglia, cerebellum, diencephalon, telencephalon, and also its underlying genetic modules, are highly conserved among mammals, not only in form, but also in development (e.g. Deacon 1990; Northcutt 2002; Redies & Puelles, 2001).

A classic but questionable view of hierarchical brain evolution is provided by MacLean's (1973; 1978) 'triune brain hypothesis', which presupposes that the human brain is a 'layered cake' made up out of distinct structures that mediate different aspects of behavior, corresponding to distinct stages in evolution. According to the triune brain hypothesis, the phylogenetically oldest layer is 'R-complex' or 'reptilian brain', which is made up by the brain stem and cerebellum, which mediates homeostatic functions such as breathing, balance, posture, and reproductive behaviors and repetitive behaviors. The next layer is the limbic system or the 'paleomammalian brain' which is responsible for emotional behaviors such as attachment, value judgments, sexual behavior, and long-term memory. The third and phylogenetically youngest layer is made up by the neocortex or the 'neomammalian brain', which is associated with language skills, abstract thought, and voluntary action.

The triune brain hypothesis is refuted by modern research which shows that mammals do not possess augmented reptilian brains but rather that all vertebrates share a common brain plan (Allman, 1999). This basic design for the vertebrate brain is already found in the earliest fossils of Agnatha or the jawless fish *Myllokunmingia fengjiaoa* that inhabited the earth's oceans roughly 530 million years ago (Shu *et al.*, 1999). Genetic evidence suggests that the division of forebrain, midbrain, and hind brain is a phylogenetically ancient feature that is governed by a highly conserved genetic toolkit - Super-Hox - that was present in the last common ancestor of all bilateral symmetrical organisms, urbilateria (Butts, Holland & Ferrier, 2008; Hirth, Kammermeier, Frei, Walldorf, Noll, & Reichert, 2003; Lichtneckert, & Reichert, 2007). Contrary to the triune brain hypotheses, it is therefore not the case that forebrain and midbrain were simply added to the hindbrain in different phylogenetic stages. Rather, throughout evolution, the vertebrate brain has undergone many subdivisions, specializations, and differential enlargements of the rostral parts of the neural tube, which has given rise to its nested hierarchical modular design (e.g. Allman, 1999). For example, it is hypothesized that the six-layered mammalian cortex evolved from the tri-layered reptilian dorsal cortex by adding layers and by modifying connections to sensory regions, in particular auditory projections (Striedter, 2005; Puelles, 2001). This form of reusing and re-modifying old parts for new purposes is an important principle in biology; in the next section I elaborate on the importance of reuse as a biological organizational principle.

3.4.1 Reuse as a Way to Achieve Biological Complexity

A now popular view among evolutionary biologists is that evolution proceeded mainly by the differentiation and subsequent specialization of existing structures as opposed to by creating novel structures out of the blue (e.g. Butler & Hodos, 2005; Carroll, 2008; Krubitzer & Kaas, 2005; Raff, 1996). Reuse of developmental modules is thought to play an important role in macro-evolution (e.g. Wagner & Mezey, 2004). That is, evolutionary modules are generally not created *de novo*, rather, old parts are reused in different contexts so that they can attain new functionalities (Rasskin-Gutman, 2005). According to (Carroll, 2008), evo-devo shows that evolution proceeds not so much by gene duplication and changes in DNA sequence but primarily through co-option of core mechanisms of genetic regulation. The finding that genetic regulatory modules such as HOX are conserved for such a long time, and the fact that they are distributed widely across long diverged animal taxa was surprising for many biologists at the time of their discovery, given their expectation that the genetic make-up of organisms would exhibit as much variation as their phenotypical features (Breuker *et al.*, 2006). Throughout evolution, genetic regulatory circuits have been frequently co-opted and re-used in different contexts. As Brakefield (2006) explains:

> *Many differences in complex morphological traits are not the result of the presence or absence of particular genes but are based on changes in the mechanisms of gene regulation affecting when and where a gene is expressed. Thus, there is a limited genetic tool kit and much of morphological diversity evolution is about old genes performing new tricks. Although existing genetic pathways can be co-opted and subsequently elaborated upon to do something different, and specific genes can take on additional*

> *tasks at new times during development and in different tissues via gene duplication and divergence, de novo evolution of new pathways appears to be rare* (p.362).

Reuse of developmental modules is a key mechanism for generating morphological novelty: redeployed modules can be expressed in different contexts so that they can take on new adaptive roles. Raff (1996) distinguishes between three ways in which modules are reused: (i) dissociation, and (ii) duplication and divergence, and (iii) co-option: (i) Dissociation refers to the spatial, temporal, or relational alteration between existing modules by for example heterochrony, i.e. changes in the rate or timing of developmental processes, and heterotopy[33], i.e. changes in the topological expression or spatial patterning of developmental processes (Futuyma, 1998). Dissociation occurs when a module that serves a certain function becomes disconnected from the mechanisms it is associated with and performs the same or another function in a different context; the dissociability of developmental modules allows evolution to optimize each character independently (Hansen, 2003; Futuyma, 1998). (ii) Duplication involves identical repetitive modules, whereas divergence involves slightly different versions of the original module that serve other adaptive functions. Well-known examples of duplication and divergence are serial homologues, such as feathers, arthropod segments, and tooth germs. Duplication of developmental modules creates redundancy, which can serve as a "breathing space" so that modules can be redeployment to serve other adaptive functions (Elbe, 2005; Rasskin-Gutman, 2005; Wimsatt & Schank, 2004). Duplication and divergence can occur on both evolutionary and developmental timescales. (iii) Co-option, or exaptation[34] occurs when an existing structure or process module is recruited for a new and different adaptive function. Genetic regulators often serve different roles in multiple independent developmental processes and developmental stages. Due to their dual role in development and evolution, genetic regulators provide the key for understanding and relating developmental to evolutionary changes. Slight changes in the expression patterns of regulator genes can yield profound changes at the phenotypic level, which is why modifications in regulator genes play a key role in macro evolution. For example, Shubin, Tabin and Carroll (2009) discuss evidence that the modification and co-option of pre-existing genetic regulatory circuits underlies the evolution of morphological features such as animal eyes, tetrapod limbs, and fish fins. Some

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[33] An example of heterochrony is allometry, i.e. changes in the differential growth rate of body parts, such as for example the positive allometric growth of the neocortex during the evolution of hominids (Roth & Dicke, 2005). A well-known example of heterotopy are the two additional “digits” of the giant panda; a thumb at the radial side of its hand and a “pinky finger” at the ulnar side of its hand. The bones in the additional fingers come equipped with their own set of muscles and consist of enlarged sesamoids, bones embedded within a tendon, which develop as a response to kinetic stress (Müller, 1990, p.113).

[34] Gould and Lewontin (1979) famously distinguished between two types of exaptations: (i) Co-opted adaptations, such as lungs, which originally evolved as a swim bladder to regulate buoyancy, and only at a later stage in evolution became exaptated to serve the function of a respiratory organ; and (ii) Spandrels, features that serve no direct adaptive purposes and originally appeared as by-products of other adaptations, but which only at a later stage came to serve a certain adaptive function(s).

authors argue that this kind of reuse of genetic regulatory circuits is perhaps the most important source of generating novel morphological traits in evolution (e.g. Carroll, 2008).

3.4.2 Hierarchical Cognitive Organization

The organization of the nervous system is long since viewed as a hierarchical architecture that incorporates different levels of sensorimotor control (e.g. Prescott *et al*., 1999). Such a perspective was already presented in the work of John Hughlings Jackson in the late nineteenth century. He proposed that the nervous system is a three-layered, modular organization consisting of sensorimotor mechanisms of which the higher levels provide re-representations of the lower ones. Following Hughlings-Jackson, Bernstein (1967) proposed an influential stratification of brain functions based on a hierarchical organization of the human movement system. Bernstein´s six levels[35] of coordination of movements reflect a hierarchy of control systems that deal with movement coordination, from lower level sensorimotor functions, such as the regulation of muscle tone to higher level control functions such as consciousness. Recent research dovetails with Bernstein's view but also expands it. Hierarchical organization shows up in research on many different cognitive functions, such as attention (Velichkovsky, 2005), working memory (Sneider & Logan, 2006), action-representation (Grafton & Hamilton 2007), sensory integration (Marrelec *et al*., 2008), reinforcement learning (Botvinick, Niv & Barto, 2009), executive control and the temporal control of behavior (Koechlin & Jubault, 2006). Cognitive organization thus exhibits a deeply nested hierarchical[36] architecture which is the result of its evolutionary and developmental background.

According to Christensen (2007), the hierarchical architecture of cognition in Metazoa evolved by progressively adding of layers of control to a basic sensorimotor

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[35] Velichkovsky (2005) provides an overview of Bernstein´s six levels of coordination of movements, which proceeds from lower level sensorimotor functions to higher level executive functions: (1) The lowest rubro-spinal level mediates so-called 'paleokinetic regulations', which involve elementary behavioral functions such as the regulation of muscle tonus as well as reflexes mediated by the brain and spinal cord, (2) The thalamo-pallidium level deal with 'synergies'. Synergies are coordinations of large muscle groups and the generation of different rhythmic and cyclic patterns of locomotion involving muscular-articular links that allow organisms to move as a coordinated whole, (3) The pyramido-striatum level gives rise to what Bernstein refers to as the 'spatial field', which governs exteroceptive perception enabling goal-directed behavior in an environment, (4) The parieto-premotor level deals with more sophisticated 'object actions' or manipulation of objects involving procedural memory, (5) The associative cortices support 'conceptual structures', which involves the integration of information from the different sensory-modalities and also enables the formation of symbolic representation, language, and self-awareness, and finally, (6) The sixth prefrontal cortex level copes with 'meta cognitive coordinations', and involves reflective consciousness (p.357).

[36] According to Prescott *et al.* (1999), the vertebrate nervous system combines features of both hierarchical and heterarchical design (which allows bottom-up and top-down causal relations), which is why they use the more neutral term 'layered' to describe its organization. I here use the notions of 'hierarchy' and 'layered' interchangeably; this weaker notion of hierarchy I use allows room for two-way interactions between components and decentralized control, as opposed to exclusive top-down, centralized control.

architecture. These layers can be viewed as control modules that provide different levels of sensorimotor control. Christensen argues that throughout evolution, cognitive architectures became increasingly hierarchically organized due to different selection pressures that spurred the evolution of high order mechanisms incorporating different levels of sensorimotor control. In short, Christensen's (2007) account proposes that: (1) External articulation pressures such as predator-prey cycles and other ecological factors favor selection for functional diversification through modularization; (2) Progressive modularization subsequently leads to high order coordination problems, which results in an increase of internal articulation pressures, favoring selection for mechanisms that support internal coherence; (3) Hierarchical design provides an efficient solution for internal coordination problems by facilitating higher order coordination of modules; (4) High order control itself is also subject to these selection pressures and leads to successively more complex forms of control. Higher layers of sensorimotor control govern the strategic control of behavior through higher level modulation of motor output subserving long term behavioral goals (Christensen, 2007).

3.4.3 Reuse as a Way to Achieve Cognitive Complexity

We have seen that reuse is an import biological principle for achieving organizational complexity. There is also considerable support for the view that reuse serves a key role in cognitive evolution and development in particular in the evolution of language and grammaticalization (e.g. Croft, 2000; Gould, 1991; Lass, 1990). For example, Hauser, Chomsky and Fitch (2002) argue that the language capacity derives accidentally from exaptation of a computational mechanism for recursion; this recursion ability presumably evolved for reasons other than language. In recent years, the idea that re-use is a fundamental organization principle in cognitive evolution and development has gained popularity and a number of different - but largely compatible - hypotheses about re-use have appeared (Anderson 2006, 2007a, 2007b, 2008, 2010; Dehaene 2005, Dehaene and Cohen, 2007; Gallese's 2008, 2010; Hurely, 2008). Anderson's (2006, 2007a, 2007b, 2008, 2010) "massive redeployment hypothesis" suggests that re-use or exaptation is the norm in cognitive evolution rather than the exception. Anderson (2007a/b, 2008) argues that cognitive evolution is mainly driven by re-use of existing brain functions in order to minimize metabolic costs of the brain; so that neural circuits that initially evolved to serve a particular adaptive purpose are reused for other adaptive purposes without losing their original functionality. The massive redeployment hypothesis postulates that differences in cognitive functions are due to differences in the co-activation and co-operation patterns between different, sometimes widely scattered local neural circuits each with their own functional capacity. By redeploying local neuronal circuits and combining them with other circuits new kinds of functionality can be obtained (Anderson, 2010).

Based on the premise that reuse is a pervasive mechanism in cognitive organization, Anderson (2010) makes three predictions and regarding the functional topography of the brain and also reports evidence for these predictions based on fMRI studies: (1) neuronal circuits are poly-functional and typically re-used in a wide variety of cognitive contexts. In line with this prediction, Anderson (2010) found that a typical cortical region is involved in *nine* different cognitive functions in different task domains; (2) phylogenetically older brain areas are more likely to have been frequently co-opted and redeployed for various other cognitive functions than more recently evolved brain areas. In support of this, Anderson (2007) found that area's in the back of the brain such as the occipital lobe in general participate in a greater variety of cognitive functions than phylogenetically younger area's in the front of the brain such as the frontal lobe; (3) there is a correlation between the phylogenetic age of a cognitive function and its degree of localization. That is, evolutionary more recent cognitive functions such as language utilize more widely scattered brain areas than evolutionary older functions such as attention. In support of this, Anderson (2007a, 2008, 2010) reports evidence that language activates the most widely scattered cortical regions, followed by presumably evolutionary older cognitive functions such as reasoning, mental imagery, and attention.

Critics to Anderson's massive redeployment hypothesis point out that neuronal circuits need not have fixed functions that are reused in different contexts, but rather that neural circuits are highly plastic and that throughout development these circuits can come to serve different functions depending on epigenetic input. On this view, neuronal circuits do not compute a fixed, local function that can be connected in different constellations of other modules, rather, the neural circuit itself is multi-functional and can be used throughout development different ways depending on context (Dils & Flusberg, 2010; Dekker & Karmiloff-Smith, 2010). Be that as it may, Anderson (2006, 2007a, 2007b, 2008, 2010) has made a compelling case that reuse of brain circuits is at least an important factor in the evolution of cognition.

A complementary, developmental view on cognitive reuse is provided by Dehaene's (2005; Dehaene & Cohen, 2007) "neuronal recycling hypothesis", which, unlike the massive redeployment hypothesis, targets culturally acquired cognitive abilities such as reading and arithmetic. Dehaene and Cohen (2007) claim that higher level, cultural aspects of cognition must find their "neuronal niche", in circuits that are already well-suited for the job. That is, learned cognitive functions are assigned to those brain circuits that are sufficiently plastic and already closely fit the functional requirements to mediate these cognitive functions. The neuronal recycling hypothesis presumes that cultural cognitive abilities such as reading and arithmetic basically invade and reuse pre-existing brain circuits without disrupting their original functionality, and in the process acquire the functional constraints and inherent biases of these cortical circuits. According to Cohen and Dehaene (2007), neuronal recycling explains the fact that there is little cross-individual and cross-cultural variability in the cerebral topography of acquired abilities such as reading, which is mediated by the visual word form area (VWFA); a cortical area dedicated to recognition and processing of written words, among other functions. VWFA appears in the same location in the brain - in the fusiform gyrus which is located in the left occipital-temporal cortex - regardless of the language or writing system used by participants, including braille. Cohen and Dehaene (2007) claim that during reading acquisition, VWFA becomes functionally specialized and fine-tuned for detecting orthographic regularities, i.e. the sets of symbols and rules about how to write a certain language, in the subject's script, whether they use Chinese, English, or any other language; with only slight cross-cultural invariances depending on the complexity of the orthography in question. VWFA is well-equipped for the job of visual word recognition because it is made up by a hierarchy of neurons, so-called "local combination detectors", with increasingly larger receptive fields and attuned to increasingly more complex word fragments; from line intersections and letter shapes to morphemes and words. Dehaene and Cohen (2007) argue that the function of the evolutionary precursor of VWFA was related to object and scene recognition, and that this area therefore already harbored the necessary ingredients for word recognition. On this view, VWFA is not a Darwinian module that is selected and hardwired for word recognition as proponents of EP would have it, rather, the existing functionality of this area is reused as a 'neuronal niche' for word recognition, which rides piggyback on the cognitive functions for which it was originally selected.

A third hypothesis on cognitive reuse focuses on how existing sensorimotor organization is reused for the development of higher level social cognitive functions such as language and Theory of Mind. Gallese's (2008) "neural exploitation hypothesis", posits that higher cognitive abilities such as language, abstract thought, and empathy build on brain mechanisms that originally evolved for sensorimotor integration. Gallese's account on cognitive reuse centers on the mirror neuron system; a cluster of neurons that is presumably located mostly in the human frontal and parietal brain regions, such as premotor cortex, posterior parietal cortex, supplementary motor area, and Broca's area (Gallese, 2008; Keysers & Gazzola, 2007; Keysers & Fadiga, 2008; Molenberghs, Cunnington, & Mattingley, 2009). This system has received much attention since its discovery in the premotor cortex of the macaque monkey in the early nineties (see Di Pellegrino *et al.*, 1992). Research shows that mirror neurons do not only discharge when the monkey performs a certain goal-directed hand action such as grasping an object, but also when the monkey is observing the experimenter performing similar such actions[37]. It has been demonstrated that similar such mirror neuron systems are present in other primates, including humans (see Mukamel *et al.*, 2010), and also in song birds (Prather *et al.*, 2008). Some researchers have suggested that the mirror neuron system provides its owner with a sense of "action understanding", which facilitates observational learning and learning by imitation by priming the execution of the observed action (e.g. Van Gog *et al.*, 2009).

According to Gallese's (2008) the mirror neuron system originally evolved for sensorimotor integration but is reused during human cognitive development for the benefit of

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[37] According to Gallese (2008) a particular class of mirror neurons, so-called F5 or parietal mirror neurons not only code the goal of executed/observed motor acts, but also the action intention by encoding the anticipation of the ultimate goal-state of the motor act.

various higher level cognitive functions such as language and thought, in order to understand and to anticipate the behavior of others (e.g. Arbib, 2005; Gallese & Lakoff, 2005). Gallese argues that the premotor cortex of which the mirror neuron system is part, is responsible for providing temporal structure or “phase structure” to motor actions by coordinating actions into goal-directed actions sequences. Gallese (2008) speculates that the premotor system can function according to two modes of operation: (1) the circuit is either used on-line for action execution or imitation, or for off-line purposes such as imagination or action perception, where action execution is inhibited; (2) the premotor circuits are decoupled from action execution and action perception, and its computational role in providing temporal structure is reused by non-sensorimotor parts of the brain such as dorsal prefrontal cortex to facilitate the hierarchical, recursive structure that characterizes language and thought.

Very much in line with the neural recycling hypothesis, the neural exploitation hypotheses postulates that parts of the mirror neuron system serve as a neuronal niche that underpins many higher level social cognitive skills. Although some researchers have cast doubt on the role of the mirror neuron system in empathy (e.g. Decety, 2010) and action-understanding (e.g. Csibra, 2008; Hickok, 2009), evidence for the role of the mirror neuron system in other social cognitive functions such as language is more compelling (e.g. Arbib, 2010; Corballis, 2010; Fogassi & Ferrari, 2007). More research is required to find out whether and if so in which ways the mirror neuron system has been co-opted by other cognitive systems. What seems to be clear though is reuse is pervasive feature in biology and also an important organizational aspect in both cognitive development and cognitive evolution.

3.5 Epigenetic Organization

In modern-day biology - and evo-devo in particular - there is a growing research interest in the epigenetic mechanisms that mediate between the gene expression patterns of organisms and environmental factors. The term 'epigenetics' (literally: ‘above’ or ‘in addition to’ the gene) was coined by Conrad Waddington[38] in the nineteen-forties to refer to “the branch of biology which studies the causal interactions between genes and their products which bring the phenotype into being” (Waddington, 1942, p.218). Since Waddington, the meaning of the term ‘epigenetics’ has altered, and biologists now use the

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[38] Waddington (1977) described the role of epigenetic factors in development with his well-known metaphor of the ‘epigenetic landscape’, which depicts the developmental system as a marble rolling down a sloped, progressively undulated landscape, with increasingly steep ridges and deep valleys, as a means to illustrate the way in which the developmental route of cellular decision-making is canalized by the epigenetic product of gene-environment interactions. The metaphor illustrates that the relation between the genotype and phenotype of organisms is not straightforward, but mediated by epigenetic mechanisms that co-determine the developmental trajectory.

term in a variety of ways[39] (See Ho & Burggren, 2010). Jablonka and Lamb (2009) use the notion of epigenetics in a broad sense, much in line with Waddington's usage of the term, to refer to "the regulatory mechanisms (epigenetic control systems) that can lead to inducible, persistent, developmental changes" (p.10). For example, epigenetic mechanisms play a crucial role in determining the identity of cells: all cells in the human body share the same genetic information, yet some cells become kidney cells, whereas others become neurons, or skin cells etc.. With few exceptions, it is epigenetic factors that determine the identity of cells (Jablonka & Lamb, 2008). Besides determining cell fate, epigenetic control systems mediate a plethora of other processes such as the construction of the cytoskeleton (Kirschner & Gerhard, 1998), and synaptogenesis and synaptic pruning in brain development (Elman *et al.*, 1996). Epigenetic control mechanisms are found on different levels of organization: molecular, cellular, morphological, behavioral.

3.5.1 Chromatin Marking

A textbook example of an epigenetic mechanism is chromatin marking. Chromatin is the stuff that chromosomes are made up of; this includes the complex of the DNA double helix that is coiled around cores of histone proteins – the nucleosomes - the repeating organizational units that are together organized much like "beads on a string" (Sweatt, 2009). Chromatin marks are proteins or molecules such as methyl groups attached to the chromatin, which cause alterations in folding patterns of the chromatin structure affecting the likelihood of gene transcription. Chromatin marking patterns constitute a kind of structural chromosomal memory that allows for the context-dependent modification of genetic expression of eukaryotic cells. There exists a wide variety of chromatin marking mechanisms (see Bártová *et al.*, 2008; Hernández-Muñoz, 2010; Spivakov & Fisher, 2007); some are transient while others persist during mitosis and meiosis.

Two forms of chromatin marking are DNA methylation and histone modification. DNA methylation involves coavelent bonds between small methyl groups that are directly attached to the cytosine–guanine (CpG) dinucleotides of the DNA. DNA methylation typically suppresses gene expression, although it is sometimes also associated with transcriptional activation (see Cohen, Zhou & Greenberg, 2008). Histone modification alters higher order chromatin structure by affecting connections between histones and between histones and DNA (McClung & Nestler, 2008). These histone tags modulate the physical three-dimensional structure of the chromatin, either decondensing it so that the

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[39] Unlike Waddington, many molecular and evolutionary biologists often restrict the use of the term epigenetics to the context of stable transgenerational effects. Youngson & Whitelaw (2008, p.234) further distinguish between 'transgenerational epigenetic effects' and 'transgenerational epigenetic inheritance', the former more lenient definition refers to "all processes that have evolved to achieve the non-genetic determination of phenotype", while the latter more strict definition refers to "mitotically and/or meiotically heritable changes in gene function that cannot be explained by changes in gene sequence". According to Youngson and Whitelaw (2008), the latter more strict explanation is more common among molecular biologists.

accessibility of DNA to the transcriptional machinery is increased, or by enhancing chromatin condensation so that the transcriptional machinery is blocked and genetic expression is silenced (Albertini, 2009; see Figure 6).

Along with DNA, histone proteins are the major constituents of chromatin. Histones are organized in octamers (two copies of histones: H2A, H2B, H3 & H4) (Barrett & Wood, 2008). Each histone consists of a protein core and a protruding N-terminus 'tail' that is composed of amino acids. Histone tagging occurs predominantly on lysine residues on the N-terminus tails of histones and includes acetylation, phosporylation, methylation, and ubiquitylation (Sweatt, 2009). Histone modification is associated with both post-transcriptional activation and repression of gene activity (Franklin & Mansuy, 2010). According to Gräff and Mansuy (2008), epigenetic marks such as post-translational histone modifications often act in concert, giving rise to complex feedback cycles between histone tags and gene expression. At present, researchers have only just begun to identify and characterize the broad set of epigenetic mechanisms, and much more research is needed in order to fully map all the bi-directional relations that exist between the epigenome and gene expression (Franklin & Mansuy, 2010; Day & Sweatt, 2010, 2011).

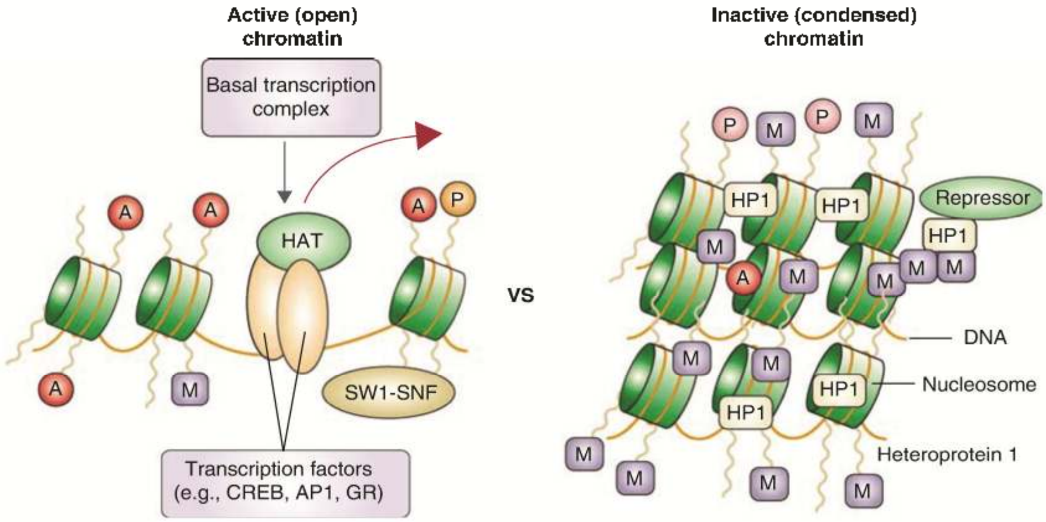

Figure 6. Different states of chromatin. Chromatin can either be open (i.e. active, allowing gene expression) or condensed (i.e. inactive, repressing gene expression). This (reversible) change in state is mediated by the modifications to core histone proteins. Histone acetylation (A) is associated with chromatin relaxation and the binding of transcription factors and co-activators, such as HATs (histone acetyl transferases) and SWI-SNF proteins that mediate the movement of nucleosomes along a strand of DNA. Histone methylation (M) results in condensed chromatin and transcriptional repression (figure and subscript from McClung & Nestler (2008) with permission from the first author)

Kirschner and Gerhart (1998, p.8422) argue that epigenetic mechanisms, like those in the immune system or the vertebrate brain, are so-called “exploratory mechanisms”. Epigenetic mechanisms facilitate the ecological specialization of organisms by the context-dependent modulation of genetic-expression, so that they can flexibly adapt their phenotype to meet the demands of local conditions. Epigenetic mechanisms like chromatin marks can have dramatic effects on the development of organismal morphology. For example, the phenotypes of worker bees and honey bee queens are radically different in terms of their physiology and anatomy despite being genetically identical. The phenotypical differences are induced epigenetically by the modification of gene activity through nutrition. That is, the queen larva is fed large amounts of royal jelly, which results in the selective modification of its DNA through methylation (Maleszka, 2008). According to Jablonka and Lamb (2008), epigenetic factors also include physico-chemical properties such as temperature, gravity, uterine effects, and tissue characteristics, which can all have a significant impact on the unfolding of the phenotype. For example, the different gravitational conditions that occur in terrestrial and aquatic environments produce different phenotypes such as by affecting bone density and muscle tissue development through epigenetically induced changes in gene expression (see Krubitzer, 2009). Furthermore, in many reptiles, fish, and amphibians, incubation temperature is the control parameter that determines the sex of the hatchling (Geary & Huffman, 2002). It is thus the complex interplay between genetic and epigenetic factors that gives rise to the phenotype of organisms, rather than a genetic program that is induced by environmental triggers (e.g. Futuyma, 1998; Ho, 1998).

According to Jablonka and Lamb (2008, 2009) ‘soft inheritance’ by epigenetic processes that persist across generations play an important role in evolution. Jablonka and Lamb’s epigenetic approach supports aspects of the controversial Lamarkian view of evolution, which implies that at least some acquired phenotypic characteristics are heritable. The transgenerational epigenetic transfer of acquired traits (e.g. physiological, morphological or behavioral) relies on non-Mendelian forms of inheritance, i.e. evolutionary changes that do not rely on changes in the DNA sequence. However, although the effects of transgenerational epigenetic inheritance are well documented in plants and mice, Morgan and Whitelaw (2008) claim that the evidence of transgenerational epigenetic effects in humans is still meager. Ho and Bruggren (2010) argue that although current research on epigenetic transgenerational transfer is booming, more specialized research techniques are required to further investigate the role of epigenetic transfer in order to properly distinguish epigenetic effects from other factors. Nevertheless, it seems clear that the study of epigenetics is becoming one of the major themes in modern-day biology and that epigenetics is now recognized as another major biological organizational principle.

3.5.2 Epigenetic Determinants of Cognitive Organization

The study of epigenetics in biology has fueled a recent surge of research interest for the epigenetic determinants of cognition (e.g. Covic, Karaca & Lie, 2010; Franklin & Mansuy, 2010; Ginsburg & Jablonka, 2009; Gräff & Mansuy 2008; Ma *et al.*, 2010; McGowan, Meaney & Szyf, 2008; McQuown & Wood, 2010; Roth, Lubin, Sodhi & Kleinman, 2009; Sweatt, 2009; Trompet *et al.*, 2010). The epigenetic approach probes how environmental influences bear on cognitive development through the context-dependent modification of genetic expression by processes such as chromatin marking, and how this (dis)regulates cognitive processes such as memory and learning. Epigenetic forms of genetic regulation such as histone modification play a key role in regulating synaptic plasticity, which facilitates memory formation and learning in both vertebrates and invertebrates (Gräff & Mansuy, 2008). Whereas the epigenetic marking patterns that determine cell identity are static, (i.e. when stem cells differentiate they persistently 'remember' their phenotype), the epigenetic processes employed by the nervous systems are highly dynamic and transient; for example, DNA methylation and demethylation can alternate within a matter of 100 minutes (Franklin & Mansuy, 2010).

According to Levenson & Sweatt (2006), the epigenetic tagging of chromatin is a phylogenetically ancient form of cellular memory that has been co-opted by the nervous system to subserve long-term memory formation. Two major forms of synaptic plasticity, long-term depression (LTD) - a persistent decrease in synaptic transmission that weakens synaptic connections -, and long-term facilitation (LTF) - a persistent increase in synaptic transmission that strengthens synaptic connections -, are both for an important part mediated by histone acetylation (Franklin & Mansuy, 2010; McClung & Nestler, 2008). Research targeting the role of histone acetylation in LTF and LTD has been pioneered by Guan *et al.* (2002) who used cultured sensorimotor neurons of the giant marine snail and model organism *Aplysia californica*. Guan *et al.* (2002) found that LTF and LTD in the sensorimotor neurons of *Aplysia* are mediated by the (hyper)acetylation and deacetylation of specific histones, which leads to reversible changes in chromatin structure and gene expression: Repeated pulses of the excitatory neuromodulator 5–HT (serotonin) administered to the sensorimotor synapse initiates a signaling cascade that results in the (hyper)acetylation of histones H3 and H4, which decondenses the chromatin allowing the transient activation of the immediate response gene C/EBP (CAAT box enhancer binding protein). This promotes the synthesis of proteins required for increasing synaptic strength and the growth of new synapses required for LTF. Conversely, repeated pulses of the inhibitory neuropeptide FMRFamide administered to the sensorimotor synapse initiates a signaling cascade that deacetylates specific histones so that the chromatin condenses and the process of C/EBP gene expression is blocked; this subsequently leads to a reduction in neuronal activity and a weakening of synaptic connections, supporting LTD. According to Guan *et al.* (2002) their results show that the mechanisms underlying short-term and long-term synaptic plasticity are temporally and mechanistically distinct. That is, the sensorimotor neurons of *Aplysia* integrate inhibitory and excitatory signals on two levels: short-term plasticity is regulated locally, confined to the stimulated synapse, while long-term plasticity relies on the synthesis of new proteins and involves the restructuring of the chromatin through histone (de)acetylation in the cell nucleus to alter gene expression; this affects the plasticity of all synapses of that neuron.

Histone modification, DNA methylation and other chromatin remodeling events also turn out to be commonly employed by the mammalian nervous system for the benefit of cognitive processes such as memory and learning (Day & Sweatt, 2010, 2011; Feng, Fouse, & Fan, 2007; Franklin & Mansuy, 2010; Gupta *et al.*, 2010; McClung & Nestler, 2008; Riccio, 2010; Sweatt, 2009). Different forms of chromatin marking have been found to mediate cognitive abilities in mammals such as novel taste learning, object recognition, spatial and contextual memory, and conditional learning (see Gräff & Mansuy, 2008). In a groundbreaking study investigating changes in chromatin structure during induction of long-term memory formation in rats, Levenson *et al.*, (2004) found that contextual fear conditioning (the association of a novel context with a noxious stimulus, in this case three electrical footshocks) induced the transient acetylation of histone H3 in hippocampus, which facilitated the transciption of genes necessary for LTP. Histone acetylation is a reversible process that is catalyzed by enzymes called histone acetyltransferases (HATs), while deacetylation of histone tales is promoted by deacetylases (HDACs) (Sweatt, 2009). Levenson *et al.*, (2004) found that HDAC inbititors (sodium butyrate) enhanced LTP in the rat hippocampus *in vitro* and long term contextual fear memory *in vivo*, and that manipulation of these enzymes can either disrupt or enhance memory formation. Levenson *et al.*, (2004) also found that latent inhibition, which occurred by pre-exposing the rats to the novel context two hours prior to receiving a shock does not lead to the acetylation of histone H3. Instead, latent inhibition blocks associative contextual fear memory and resulted in acetylation of histone H4. According to Levenson *et al.*, (2004) this suggests that specific types of memory consolidation require specific patterns of histone modifications. More recent studies vindicate this claim but also indicate that different forms of histone modification and DNA methylation often exhibit extensive crosstalk resulting in mutually enhancing feedback loops that regulate synaptic plasticity and memory consolidation (Day & Sweatt, 2010; 2011; Franklin & Mansuy, 2010; Roth, Roth & Sweatt, 2010).

Sensorimotor experience is an important epigenetic factor that determines brain and cognitive organization. The adult human brain contains in the vicinity of 10^{10} neurons and some 10^{14} synaptic connections; these gargantuan numbers venture way beyond the information carrying capabilities of the genome and are largely dependent on epigenetic shaping. The epigenetic sensitivity of the cortical phenotype allows the brain to flexibly adapt to local demands and ongoing conditions. For example, many studies on visually deprived juvenile animals show that patterns of sensory activity transduced by the visual system fundamentally co-determine the organization of the cortical phenotype of the developing visual cortex through modifications in the transcriptional levels of experience-regulated genes (see White & Fitzpatrick, 2007). This susceptibility to sensorimotor experience is especially strong during transient critical periods[40] of cortical plasticity in

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[40] There is converging evidence that epigenetic mechanisms co-mediate these critical periods of cortical plasticity in cognitive development, and that critical periods of heightened plasticity are down-regulated later in development due to organizational changes in the epigenome (Fagiolini,

post-natal development. During a critical period, neocortical circuits display a heightened susceptibility to sensory experience; the degree and duration of epigenetic sensitivity in cortical development differs from one cortical region to the next (White & Fitzpatrick, 2007).

The tight interplay between epigenetic factors such as sensorimotor experience and other factors such as morphological and genetic ones is best illustrated in the development of the cortex. Early in prenatal brain development regulatory genes such as Pax that control the regional patterning in the developing cortex, give rise to a number of distinct histogenetic "cortical fields" such as primary visual area (V1) and somatosensory area (S1); each with their own neuroanatomical and topographic organization, functional characteristics, and connectivity patterns (Krubitzer, 2009). According to Larsen and Krubitzer (2008), the phenotype of the cortical field, i.e. its size, internal organization, connectivity patterns and functions, are determined by the tight interplay between three factors, which mutually constrain one another: (1) genetic factors, i.e. the spatiotemporal expression of genes in the cortex, (2) extrinsic (morphological) factors, i.e. variability in peripheral morphology and receptor distribution (which is dependent on both genetic and epigenetic factors), and (3) epigenetic factors such as physical stimulus properties (i.e. kinetic energy, photons, gravity) and sensorimotor experience. Epigenetic factors such as sensorimotor experience modulate experience-dependent gene expression to sustain flexible cortical organization. Larsen and Krubitzer (2008) argue that the boundary between genetic, extrinsic, and epigenetic factors is rather fuzzy given that all factors mutually interact and constrain one another, which is why their individual contribution is difficult to isolate from other factors.

Situated variables are also important epigenetic determinants of cognitive organization. Research shows that 'environmental enrichment', i.e. increased levels of social complexity, toys, physical exercise, maternal care, and multisensory stimulation, has an important beneficial impact on cognitive development, most notably on memory, learning, and emotional and stress reactivity (Baroncelli *et al*., 2010). An initial study that targets how environmental effects modulate gene expression focuses on the role of maternal behavior. In a seminal paper, Weaver *et al*. (2004) report evidence that differences in maternal care styles in rats lead to persistent changes in genetic expression in their young, which ultimately affects their ability to respond to stress in adulthood. Offspring of nurturing mothers that extensively lick and groom their pups and arch their backs during nursing to help the pups feed, showed behavioral differences in coping with stress due to a significant difference in numbers of hippocampal glucocorticoid receptors

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Jensen & Champagne, 2009; Sweatt, 2009). For example, Putignano *et al*. (2007) found that changes in posttranslational histone modifications (H3 and phosphoacetylation and H4 acetylation) are associated with the activation and closure of a sensitive period in the visual cortex of juvenile mice, and that this form of plasticity is down-regulated in older mice.

as compared to offspring of mothers with a more inattentive nurturing style. Rat pups reared by inattentive mothers showed a strong stress response in adulthood due to decreased glucocorticoid receptor expression in hippocampus; this is because of more extensive DNA methylation of the glucocorticoid receptor gene, which silences the expression of that gene so that fewer glucocorticoid receptors are produced. Glucocorticoid receptors are part of a negative feedback loop that dampens the effects of corticosterone stress hormones. The offspring of nurturing mothers show a more modest responses to stress because of a high expression of glucocorticoid receptors in hippocampus, which provide negative feedback on the hypothalamic-pituitary-adrenal system and leads to decreased sensitivity to stress and more socially adept behaviors in adulthood. Weaver *et al.*, (2004) argue that their research shows that behavioral effects such as maternal care are causally related to epigenetically regulated changes in DNA expression in their offspring, which leads to an altered brain in adulthood that responds differently to stress; an effect that can persist across generations because of stable epigenetic marks.

Other studies show that complex environmental enrichment elicits strong positive effects on brain development by inducing the secretion of neurotrophic factors, which positively influences cortical thickness, synaptic density, and synaptic thickening in occipital cortex and hippocampus (see Baroncelli *et al.*, 2010). According to Fischer *et al.* (2007), the positive effects of environmental enrichment are at least for an important part mediated by chromatin remodeling. Fischer *et al.* found that environmental enrichment induces hippocampal and cortical acetylation and methylation of histones H3 and H4 in mice, which leads to a ‘rewiring’ of neural networks. Chromatin remodeling also induces recovery from neurodegenerative diseases and clinical disorders, such as Alzheimer’s desease, depression, and PTSD (Franklin & Mansuy, 2010; Gräff & Mansuy 2008; Hendriksen, Prins, Oliver & Oosting, 2010). This research suggests that positive clinical benefits can be obtained by artificially modulating chromatin remodeling for example by using HDAC inhibitors. All this shows that the epigenetic mechanisms give rise to a highly plastic phenotypical organization, which suggests that cognitive organization is much more flexible than was previously assumed. Although much progress has been made in recent years, experts in the field argue that much more research is needed to fully map the wide variety of epigenetic regulation mechanisms that mediate cognitive organization (e.g. Franklin & Mansuy, 2010)

3.6 Bow-Tie Architecture

We have seen that biological systems exhibit a number of shared organizational principles such as modularity, hierarchical or ‘layered’ organization, and epigenetic organization. Bow-tie architecture provides a way to understand how these organizational features are related and integrated in a global control architecture. In modern-day biology, research endeavors are increasingly focused on understanding the workings of global system functions. Systems biology is such an integrative, multidisciplinary, systemic approach that aims to discover the organizing principles that govern biological functions as they emerge out of the interaction between components. In recent years, systems biology has revealed a universal organizational feature of biological systems dubbed 'bow-tie architecture' (figure 7).

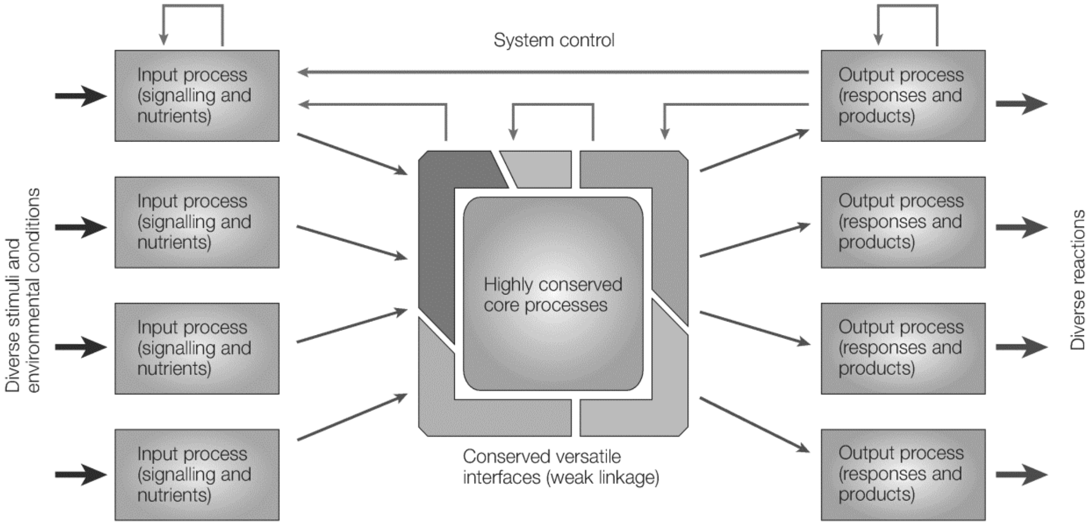

Figure 7. Bow-tie architectures are global control systems that interface a core of closely coupled, phylogenetically conserved processes with an array of flexible input and output processes that fan-in and fan-out the core. Bow-tie architecture provides a form of "plug and play" modularity around the core through versatile interfaces, which promotes robustness and fosters evolvability (from Kitano, 2004).

Bow-tie organization is a statement about the global connectivity structure between the nodes in complex networks. That is, in complex biological networks the nodes are usually not fully interconnected but typically organized around a versatile core system. The core system operates through a fixed set of protocols[41] , and is characteristically flanked by an array of widely diversified and redundant input and output processes, together forming a 'bow-tie' structure (Kitano, 2004). Bow-tie architecture is found at different levels of organization such as in gene-protein networks (Li & Chen, 2010), metabolic networks (Ma & Zeng, 2003; Zhao *et al*., 2006; Zhao *et al*., 2007), the immune system (Kitano & Oda, 2006; Tieri *et al*., 2010), signal-transduction systems (Oda & Kitano, 2006), and also in many engineered systems such as power grids and the world wide web.

Perhaps the best studied bow-tie architectures are metabolic networks. According to Csete and Doyle (2004), the topology of metabolic networks is typically organized as a

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[41] In the context of bow-tie architecture, Csete & Doyle (2004) use the term 'protocols' to refer to: "the rules and interfaces by which modules interact; these protocols are organized within a global framework referred to as the 'architecture' (p.446)

bow-tie that is comprised of a conserved core of activated carriers and precursors, which is flanked by an array of widely diversified input networks of nutrients that ‘fan-in’ the core and an array of reaction-products that ‘fan-out’ the core (Zhao *et al*., 2006); or as Csete and Doyle (2004) describe the bacterial metabolic bow-tie:

> *Bacterial metabolic networks are a striking example of ‘bow-tie’ organization and illustrate the flexibility that such a structure provides. [...] a myriad of nutrient sources are catabolized, or ‘fan in’, to produce a handful of activated carriers (e.g. ATP, NADH and NADPH) and 12 precursor metabolites, which are then synthesized into roughly 70 larger building blocks (e.g. amino acids, nucleotides, fatty acids and sugars). The precursors and carriers can be thought of as two ‘knots’ of separate bow ties that are both fed by catabolism, but whereas the former ‘fan out’ locally to the biosynthesis of universal building blocks, the latter fan out to the whole cell to provide energy, reducing power and small moieties* [i.e. molecule parts]. *The building blocks then further fan out into the complex assembly of macromolecules by general-purpose polymerases (p.446, my brackets).*

Bow-tie architectures are often hierarchically organized structures made up out of several nested bow-ties. For example, Zhao *et al*., (2006) found that the topology of the metabolism of bacteria such as *E. coli* consists of a hierarchy of bow-tie control systems that are integrated in the global metabolism. Likewise, Csete & Doyle (2004) distinguish several nested bow-ties that make up the global metabolism, which is itself also organized as a bow-tie. Several authors argue that this nested hierarchical bow-tie pattern is the result of evolutionary optimizing processes, and that this type of recurrent bow-tie organization is an efficient way of biological organization that enhances robustness. According to Kitano (2004), bow-tie architecture is a universal characteristic of evolved systems due to its robust design. Robustness refers to the way in which biological systems maintain their functionality when facing internal or external perturbations (see Kitano, 2007): bow-tie structures are global feedback control mechanisms that are robust in the sense that they are able to generate a wide variety of functional states, which promotes stability and sustains phenotypical flexibility. This kind of design promotes adaptability in the short run, and also fosters evolvability in the long run (Csete & Doyle, 2004; Kitano & Oda, 2006; Zhao, Yu, Luo, Cao & Li, 2006). Kitano (2004) argues that bow-tie architecture comes with inherent fragilities, in particular to rare, unexpected perturbations, which can lead to catastrophic system failure; such as when certain processes such as pathogens or toxins disrupt the workings of the core mechanisms. According to Kitano, this robust yet fragile trade-off is a key aspect of all biological systems.

The cores of biological bow-tie architectures are typically phylogenetically conserved features that are highly constrained and show little or no variability throughout evolution, such as developmental-evolutionary toolkits, the basic vertebrate brain plan, or bacterial two-component-signal-transduction-systems (Csete & Doyle, 2004). Consider for example the bow-tie core of metabolism: Ma and Zeng (2003) found that the connectivity structure of the global metabolic network of 65 fully sequenced organisms form a bow-tie architecture. Ma and Zeng (ibid.) refer to the central knot of this metabolic bow-tie as the "giant strong component", which constitutes a robust core of closely coupled and phylogenetically conserved modular processes. Ma and Zeng claim that the giant strong component in metabolism is highly constrained in the sense that it is robust against mutations because of the high degree of interconnectedness between the modules that make up the network core (see also, Zhao *et al*., 2006).

According to Csete & Doyle (2004), the benefit these conserved cores of bow-tie architectures is that they facilitate high variability in the more peripheral parts of the bow-tie structure, the flexible input and output processes that interface with the core (p.448). These peripheral mechanisms can therefore be more susceptible to epigenetic modulation, which allows the bow-tie control system to flexibly adapt to local conditions. This type of organization is highly adaptive and capable of generating a great variety of functional states (Kitano, 2004). For example, the vertebrate immune system with its limited set of tools such as *T*-cells and *B*-cells, is capable of generating an almost indefinite amount of responses against invading antigens (Buller & Hardcastle, 2000 p.317).

Bow-tie architecture is also highly efficient: additional mechanisms can simply be added to the input or output part of the existing machinery without having to invent entirely new input-output pathways (Csete & Doyle, 2004). Bow-tie architecture provides a form of "plug and play" modularity around the core through versatile interfaces (Csete & Doyle, 2004). That is, the core mechanisms can be reused over and over again by different processes. For example, the bacterial signal transduction system, TCST, is comprised of a conserved core of shared circuitry - a transmitter, the protein histidine kinase (CheA) and a response regulator, the protein aspartate kinase (CheY) - that interfaces an array of receptor inputs with a host of output processes, such as mechanisms of gene transcription, signal-transduction and flagellar regulation. TCST is a highly versatile signal-transduction system that has been co-opted by many different processes and is a highly conserved feature that is also used by archaea, plants, and fungi (Koretke, Lupas, Warren, Rosenberg & Brown, 2000). Kitano and Oda (2006) argue that adding new functions to the input and output sides of the bow-tie core is another important way to enhance robustness; new input or output systems can easily be modified added to the existing machinery without threatening the stability of the core (Tieri *et al*., 2010). According to Kitano (2006), these features make bow-tie architecture highly evolvable.

3.6.1 Centralization in the Nervous System & Action-Selection

In order to make a case that bow-tie architecture is also a important feature of biocognitive design we first must consider the high metabolic costs that comes with neural tissue and the evolutionary trend towards increased centralization that marks the evolution of nervous systems (e.g. Arendt *et al*., 2008). The evolution of brains and nervous systems is subjected to strong selection pressures that yield trade-offs between adaptive benefits and energy costs (See for a review: Niven & Laughlin, 2008). That is, bigger brains come with many additional cognitive benefits but also at the expense of high metabolic costs (Isler & van Schaik, 2006; Laughlin, 2001). Given the high metabolic expenditure of brains the principles of "using least wire" and limiting connections and energy consumption are important organizational constraints on the evolution of complex nervous systems and brains (Cherniak, 1994; Niven & Naughlin, 2008). Also, neural processing constraints set limits to brain size and connectivity patterns: as brain size increases, the percentage of interconnectedness necessarily declines. Maintaining a high degree of interconnectedness is highly inefficient in large brains as it requires increasingly longer axons which ultimately results in diminished computational speed (Ringo, 1991). Prescott (2007) argues that centralized brain mechanisms are 'forced moves' in the evolution in cognitive architectures due to strong selective pressures to limit the connection costs in brain wiring. Whereas distributed forms of action-selection such as reciprocal inhibition requires a high degree of neuronal connectivity, centralized systems only require a fraction of these connection costs.

According to Prescott (2007), centralized brain mechanisms also evolved to accommodate the need for specialized action-selection structures that co-ordinate different action subsystems that compete against each other for behavioral control. In order for complex multicellular animals to exhibit adaptive behavior, they need to be able to swiftly resolve conflicts between multiple competing actions systems. For example, animals need to feed, drink, take care of their offspring, and watch out for predators, and these behaviors compete for access to limited cognitive resources. When priority conflicts between different behavioral subsystems occur, higher order action-selection is required to overcome these conflicts, enabling fast and flexible switching between competing actions. In order to determine which action is the most urgent at any given moment, the organism has to take into account a number of intrinsic and extrinsic factors, so that the most appropriate action gains precedence over the others. Prescott (2007) argues that centralized brains provide specialized integrative structures that facilitate action-selection by coordinating different action subsystems based on higher order contextual information that is provided by integrating exteroceptive (e.g.. visual, auditory, olfactory) and interoceptive (e.g. somatosensory, proprioceptive) sensory information.

The honeybee brain (*Apis mellifera*) already exhibits this kind of centralized organization. Central convergence of multi-sensory information occurs in neuropils in the honey-bee brain, so-called "mushroom bodies", relatively large central structures that each contain approximately 130000 tightly packed neurones, called "Kenyon cells", which together make up about one third of the honey bee brain (Grünewald, 1999). Mushroom bodies make up the integrative core of honeybee brain providing an interface between sensory information from different stimulus domains and general purpose response output neurons (Giufra & Menzel, 2003). According to Giufra and Menzel (2003, p.38), these mushroom bodies in the honeybee brain facilitate the higher order sensory integration of domain-specific sensorimotor information which is required for complex non-elementary forms of learning such as context-dependent learning, categorization, the ability of having a notion of 'sameness' and 'difference', abstraction, relational learning, and navigation according to mental maps (Menzel & Giufra, 2006).

In the vertebrate brain, dedicated action-selection mechanisms such as the basal ganglia constitute a core control system for regulating sensorimotor coordination (Humphries & Prescott, 2010). The basal ganglia contribute to behavioral coordination by resolving conflicts between competing behavioral alternatives (Redgrave *et al*., 1999; Prescott, 2007). The basal ganglia or basal nuclei are composed of a small set of highly interconnected subcortical nuclei which can be subdivided into input nuclei, intrinsic nuclei, and output nuclei: The striatum forms the input nucleus, the subthalamic nucleus, the external segment of the globus pallidus, the substantia nigra pars compacta, and the ventral tegmental area together make-up the intrinsic nuclei, and the internal segment of the globus pallidus, the substantia nigra pars reticulata, and the ventral pallidum form its output nuclei (Martin, 2003). The basal ganglia have many input and output connections to structures all throughout the brain: afferent connections arrive from all areas of the cerebral cortex (except for V1), brain stem, and the limbic system, and efferent connections project to the frontal lobe cortex relayed via the thalamus, and also to premotor areas of midbrain and brainstem (Prescott, Redgrave & Gurney, 1999; Humphries & Prescott, 2010). The basal ganglia-thalamocortical circuit forms a complex set of feedback loops that regulate the inhibition and facilitation of movements, thought and emotions. The tonically inhibitory influence of the output nuclei is modulated by two parallel pathways that originate in the striatum and terminate in the cortex: a ‘direct’ pathway (which travels directly from the input nuclei to the output nuclei of the basal ganglia) provides positive feedback and facilitates motor movements by stimulating thalamocortical activity, and an ‘indirect’ negative feedback pathway (which is mediated by the intrinsic nuclei of the basal ganglia) that further inhibits the thalamocortical circuit, putting the brakes on behavior (see Redgrave *et al*., 1999). According to Prescott (2007), the role of basal ganglia is to resolve conflicts between different action subsystems by selecting desired actions and to inhibit other competing actions so as to enable fast switching between behaviors:

> *Neural signals that may represent ‘requests for access’ to the motor system are continuously projected to the striatum, which is the principle basal ganglia input nucleus, from relevant functional sub-systems in both the brainstem and forebrain of the animal. Afferents from a wide range of sensory and motivational systems also arrive at striatal input neurons. This connectivity should allow both extrinsic and intrinsic motivating factors to influencing the strength of rival bids. The level of activity in different populations of striatal neurons (channels) may then form a “common currency” in which competing requests for actuating systems can be effectively compared. The main output centers of the basal ganglia (parts of the substantia nigra and pallidum) are tonically active and direct a continuous flow of inhibition at neural centers throughout the brain that either directly or indirectly*

> *generate movement. This tonic inhibition appears to place a powerful brake on these movement systems such that the basal ganglia seem to hold a 'veto' over all voluntary movement. Intrinsic basal ganglia circuitry, together with feedback loops via the thalamus, appears to be suitably configured to resolve the selection competition between multiple active channels and selectively disinhibit winning action sub-systems whilst maintaining or increasing inhibition on competing channels (p.23).*

Neurodegenerative disorders such as Parkinson's disease and Huntington's disease both in different ways disrupt the workings of the basal ganglia, which results in slowed and impoverished movements, and rapid involuntary movements, respectively (Martin, 2003).

According to Prescott (2007), the evolution of the basal ganglia was only one among of the many 'forced moves' in evolution that favor centralized action-selection mechanisms. He argues that other structures along the neuraxis such as the medial reticular formation (mRF) in the core of the brainstem, and the forebrain also provide substrates for action-section; these are also convergence zones for interoceptive and exteroceptive sensory information that bias action-selection and action-planning.

3.6.2 Cognitive Bow-tie Architecture

My hypothesis is that bow-tie architecture is also a pervasive feature of biocognitive organization. We have seen that bow-tie architectures are control mechanisms that are typically organized around a core of closely coupled, and highly conserved modular processes, which provide a versatile interface for a wide variety of input and output processes. In the previous section, we have also seen that in the vertebrate brain, dedicated action-selection mechanisms such as the basal ganglia constitute a neuronal core control system for regulating sensorimotor coordination through higher order action-selection. This highly optimized organization effectively forms a cognitive bow-tie module: The basal ganglia make-up its conserved core, while the peripheral input and output parts of the bow-tie organization are formed by multimodal sensory inputs that fan into the core, and a variety of actions and action-plans that fan out of the core.

Bow-tie architecture can provide a way to understand how biocognitive organizational principles such as modularity, hierarchical organization and reuse, and epigenetic organization are related and integrated in a global biocognitive control architecture. Cognitive bow-tie modules are feedback control modules that govern action-selection by regulating an entangled network of intimately coupled sensorimotor processes. Bow-tie modules consist of a phylogenetically conserved neuronal core system, which is flanked by peripheral, more flexible sensory-input and motor output connections, which extend from input to output back to input as dynamic feedback loops that are spread out over brain, body and environment. The core action-selection system is a convergence zone for multisensory information, and operates as an action-selection mechanism that is biased by contextual information provided by integrating sensory inputs.

In complex organisms such as vertebrates, cognitive bow-tie architecture is a hierarchically structured or layered sensorimotor organization that is made up of a handful of loosely coupled, horizontally modular bow-tie units. The cores of the cognitive bow-tie architecture are phylogenetically conserved, hierarchically organized neuronal core systems, which govern progressively higher levels of sensorimotor control. Different structures along the neuraxis such as the medial reticular formation (mRF) in the core of the brain stem, the basal ganglia, and the fore brain provide such substrates for action-section that supplement each other and provide different forms of contextual information. Cognitive bow-tie architecture forms an economical solution for coordinating a wide variety of sensory systems, motor systems, emotional systems, memory systems, and involves reusing and sharing efficient resources such as centralized control systems. The core mechanism are robust, evolutionary stable, highly constraint organizational units, while the peripheral mechanisms are only softly constrained42, forming flexible sensory input and motor output pathways that are more susceptible to epigenetic modulation. This combination of evolutionary stable core systems and highly flexible peripheral systems optimizes the relation between adaptability in the short run, and evolvability in the long run.

Looking at natural cognitive systems in terms of bow-tie architecture also provides an alternative view on the biological significance of consciousness, which also exhibits all the aspects of cognitive bow-tie architecture. According to several authors, consciousness is a highly conserved cognitive function that evolved as an efficient solution to integrate and coordinate information from multiple resources such as sensory information, motor information, bodily/emotive states such as pain and pleasure, and past-experiences (Cabanac, Cabanac & Parent, 2009; Damasio, 1999). Consciousness facilitates executive functions such as voluntary action, and allows organisms to flexibly cope with novel situations (e.g. Baars, 1988; Christensen, 2007). Merker (2005) claims that consciousness was another 'forced move' in the evolution of the vertebrate nervous system; a biological solution that evolved in mobile animals “to the neural logistics problems inherent in the control of orientation to their surroundings” (p.90). According to Merker (2005, 2007), selection pressures such as neuronal connectivity economy led to the transition to consciousness in

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[42] Soft constraints are probabilistic constraints that can be violated as they are contingent on many different parameters that may affect the developmental trajectory, such as genetic, morphological, physiological, and epigenetic factors (Elman *et al*., 1996; Griffiths & Stotz, 2000). According to Geary and Huffman (2002), the degree to which the organizational features of brain and cognition are inherently constrained or softly constrained is a function of cost-benefit trade-offs between inherent constraints and flexibility during evolution: characters that exhibit a high degree of inherent organizational constraint correlate with information patterns and ecological conditions that remain invariant over the course of evolution, while adaptivity to more variable information patterns demands characters that exhibit low constraints and high plasticity. Geary and Huffman (ibid.) argue that the flexible aspects of cognitive and brain organization facilitates rapid adjustment to changing information patterns and ecological conditions. The costs of flexibility come in a poor initial ability to discriminate between relevant and irrelevant information patterns, and a longer period of cognitive development. Conversely, highly constrained characters allow the fast processing of evolutionary significant information and efficient discrimination between relevant and irrelevant information patterns, but comes at the cost of poorer adaptability to rapidly changing information patterns and changing ecological circumstances (p.668).

animal evolution. That is, the evolution of complex multicellular organisms such as vertebrates led to an increasingly wide variety of sensory systems, motor systems, emotional systems, memory systems, and these systems needed to be coordinated for the benefit of adaptive behavior; this involves a large brain that has the resources for multimodal synthesis. An economical solution for this coordination problem involves reusing and sharing efficient resources such as centralized control systems.

According to Merker (2005), this is exactly the function of consciousness: multimodal integration of interoceptive, exteroceptive, and proprioceptive information for the benefit of motivated behavior and goal related action-selection; while leaving out the detailed information of sensory preliminaries and motor control, which can be left to be dealt with by lower control systems. Merker (2005) speculates that the core circuitry of consciousness resides in the "core control system of the upper brainstem", which involves a set of structures such as the ventral tegmental area, the midbrain reticular formation and the zona incerta that are widely interconnected to virtually all parts of the brain (p.102; see also Merker, 2007). Very much like the basal ganglia, this architectural design involves the "multisystem convergence from many parts of the brain onto a laminar scheme for topographic integration of the principle spatial modalities within a common efferent framework" (p.94). This description also fits nicely with the features of bow-tie architecture. Looking at consciousness in terms of bow-tie architecture provides a still preliminary but biologically plausible explanation of consciousness as a core control function that evolved to facilitate the synthesis and coordination of exteroceptive and interoceptive sensory information to facilitate the coordination of goal-directed, voluntary action. In the next chapter, I will go deeper into the role of consciousness in sensorimotor behavior and voluntary action.

3.7 Conclusion

In this chapter, I investigated how fundamental biological organizational principles such as modularity, hierarchical organization and reuse, epigenetic organization, and bow-tie architecture pertain to biocognitive organization by developing four principles of biocognitive organization: First, cognitive modules in natural cognitive systems share important features with other biological process modules such as feedback control. Biocognitive modules are sensorimotor feedback control mechanisms that modulate the dynamics of behavioral multi-stabilities to facilitate the sensorimotor coordination capacities of organisms. Biocognitive modules form an entangled network of intimately coupled, sensorimotor processes which extend from input to output back to input as dynamic feedback loops.

Second, cognitive modules are hierarchically organized or 'layered' sensorimotor control systems that reuse components on evolutionary and developmental levels to achieve organizational complexity. Biocognitive systems are sensorimotor control systems that evolved through modularization, and progressive hierarchical organization by reusing existing components to expand their existing sensorimotor organization.

Third, we have discussed that many evolutionary psychologists endorse a hard-lined distinction between ultimate and proximate factors, which leads to an overestimation of the importance of the phylogenetic determinants of cognitive organization. Instead, modern-day biology has revealed that the phenotype of organisms is the product of a complex of self-organizing processes that depends on the continuous interplay between the developmental system, gene-action, and epigenetic factors. This has important consequences for thinking about biocognitive organization. Biocognitive organization derives to a large extent from epigenetic factors in which, genetic, physical, morphological, sensorimotor, and situated factors mutually interact and constrain one another, modulating experience-dependent gene expression to sustain a flexible cognitive organization.

Lastly, I discuss how these organizational features are integrated in a global functional control architecture, dubbed 'cognitive bow-tie architecture'. Cognitive bow-tie architecture optimizes trade-offs among efficiency, metabolic costs of neuronal wiring, and cognitive flexibility. Cognitive bow-tie architecture combines versatile core elements that can be reused by peripheral sensorimotor input and output pathways, which are more flexible and more susceptible to epigenetic modulation. Biocognition in complex organisms such as vertebrates is a hierarchically structured bow-tie organization, consisting of multiple, layered sensorimotor modules that are epigenetically shaped by re-using, changing, and re-organizing existing features.

Cognitive bow-tie architecture can provide a new principle to understand how other biocognitive organizational principles such as modularity, hierarchical organization and reuse, and epigenetic organization are related and integrated in a global control architecture. It is a matter of empirical investigation to settle the matter in which ways bow-tie architecture is implemented in the organization of natural cognitive systems.

4. The Upper Reaches:
On the Alleged Illusion of Conscious Will

> *The particulars of the distribution of consciousness, in so far as we know them, point to its being efficacious. It is very generally admitted, though the point would be hard to prove, that consciousness grows more complex and intense the higher we rise in the animal kingdom. That of a man must exceed that of an oyster. From this point of view, it seems an organ, superadded to the other organs which maintains the animal in the struggle for existence; and the presumption of course is that it helps him in some way in the struggle, just as they do. But it cannot help him without being in some way efficacious and influencing the course of his bodily history (pp.141-142).*
>
> William James (1890)

4.1 Introduction

If the lower bound of the biocognitive spectrum is represented by bacterial chemotaxis then human consciousness can be situated along its upper reaches. William James (1890) already argued that consciousness is a biological mechanism that evolved because it confers certain important adaptive benefits for organisms, such as by regulating the actions of the brain and nervous system. A modern biological perspective on consciousness is provided by Damasio and Meyer (2009) who argue that consciousness is a behavioral regulatory mechanism that provides an extension of basic homeostatic processes. According to Damasio and Meyer, consciousness enables organisms to integrate information about bodily states, such as feelings and emotions, external events, past-experiences, which allows them to flexibly cope with novel situations (see also, Damasio, 1999). In a similar vein, other authors have argued that consciousness contributes to cognition by: (i) optimizing valence judgments by integrating information from different sensory domains and bodily/emotive states, such as pain and pleasure (e.g. Cabanac, Cabanac & Parent, 2009), (ii) governing executive functions, such as self-monitoring, executive control, contextual learning, coping with novelty, and resolving ambiguity problems by relating global system information to context (Baars, 1988; 1997), (iii) optimizing neuronal logistics by limiting connection costs in the brain through multimodal integration of sensory and bodily signals so as to enable fast and efficient control of behavior (Merker, 2005), (iv) facilitating volitional movement (Pierson & Trout, 2005). This biological perspective on consciousness thus suggests that consciousness is an action-based (bow-tie) mechanism that augments cognition by providing higher order regulatory functions.

In modern-day cognitive science, however, the view that consciousness is action-based is not at all widely accepted. There is still considerable controversy regarding the causal role of consciousness in our everyday behavior. Many authors claim that the subjective, first-person aspects of consciousness do not exert a direct causal influence on our actions. This epiphenomenalist' view was famously worded by Thomas Huxley (1901) as follows:

> *The consciousness of brutes and men would appear to be related to the mechanism of their body simply as a collateral product of its working, and to be as completely without any power of modifying that working, as the steam whistle which accompanies the work of a locomotive engine is without influence upon its machinery. Their volition, if they have any, is an emotion indicative of physical changes, not a cause of such changes* [...] *The soul stands to the body as the bell of a clock to the works, and consciousness answers to the sound which the bell gives out when it is struck* [...]. *If these positions are well based, it follows that our mental positions are simply the symbols in consciousness of the changes that take place automatically in the organism; and that to take an extreme illustration, the feeling we call volition is not the cause of a voluntary act, but the symbol of that state of the brain, which is the immediate cause of that act. We are conscious automata* (pp. 240-244; my brackets).

Very much in line with Huxley's classic automaton theory of consciousness, many modern authors claim that there is strong empirical evidence to support the claim that conscious will provides us with a false sense of authorship of our actions (Wegner, 2002; Wegner & Wheatley, 1999; Caruthers, 2007). Recently, some renowned cognitive neuroscientists have argued that the subjective experience of our conscious will is fundamentally misguided, and that there is empirical evidence to support the claim that conscious will is in fact an illusion created by the brain (e.g., Gazzaniga, 1998; Nørretranders, 1998; Roth, 2003; Wegner, 2002, 2003). This ‘‘illusion-claim’’ is based on the finding that neuronal activity that sets-up a consciously willed action, occurs prior to the conscious decision to engage in that action (e.g., Libet, 1985). We are normally not aware of this discrepancy, so the claim goes, because the brain retrospectively fabricates a coherent story that is accessible to subjective experience. Introspection is thus asserted to provide us only with access to an illusory causal path from thought to action (Wegner, 2003); the causal efficacy of conscious will is therefore only apparent (Nørretranders, 1998; Roth, 2003; Wegner & Wheatley, 1999). The illusion-argument holds that it is unconscious neuronal activity that causes us to act, and that we merely become conscious of the outcome of these unconscious processes. Our conscious mind is therefore mislead into thinking that it exerts a causal role in the initiations of our actions, so the claim goes; the real causal mechanisms reside on the neuronal level and we only become aware of their outcome after the fact. The view that the causal role of consciousness in our actions is an illusion created by the brain is still a widely endorsed hypothesis that is also often discussed in popular science books. This view obviously clashes with the biologically oriented perspective that consciousness evolved as a means to guide and control our actions. The aim of this chapter is to provide an alternative view on the causal efficacy of conscious will that better strokes with the biologically-oriented perspective which holds that consciousness facilitates volitional behavior.

The empirical evidence supporting the illusion-claim is partly based on the classical, pioneering experimental work by physiologist Benjamin Libet. His research suggests that a conscious decision to engage in an action is preceded by neuronal activity that sets up this action. However, Libet's work has been controversial from the start; his experiments have also been claimed as evidence supporting precognition, retro-causality, "quantum-consciousness", and dualism (Bierman, 2003; Hameroff, 1998a, 1998b; Eccles & Popper, 1977; King, 1997; Penrose, 1989; Radin, 2003; Wolf, 1989, 1998). Over the last 20 years or so, criticisms related to Libet's own interpretations of his data have accumulated, and other, less radical interpretations have been suggested that appear equally compatible with Libet's data (e.g., Churchland, 1981a; Glynn, 1990; Gomes, 1998; Pockett, 2002). Given these criticisms and alternative interpretations, can Libet's findings still be seen as supporting the illusion-claim? In this article, we contest the empirical and theoretical validity of this illusion claim, and discuss the notions of 'self-organization' and 'self-steering' to provide an alternative perspective on the causal mechanisms that support conscious will, using the language of dynamic systems theory. In the final sections, we provide a tentative theoretical picture of conscious will as an instance of self-steered self-organization, based on recent empirical work that targets self-organizing processes in the brain. We conclude that the subjective experience of conscious will is not a misguided one, but rather that the neuronal mechanisms that govern conscious will are still poorly understood.

4.2 The Libet-Experiments

Benjamin Libet is regarded as a true pioneer in the empirical study of human consciousness. Two of his experimental approaches have been much discussed over the years. The first approach, which we refer to as the 'back-referral experiments' (Libet *et al.*, 1964; Libet *et al.*, 1967; Libet *et al.*, 1979), is based on the assumption that there exists a substantial delay before cerebral processes achieve what Libet (1985) calls "neuronal adequacy"—i.e., according to Libet (1991), the brain requires a considerable neuronal build-up period, up to 500 ms, in order for us to become conscious of peripheral stimuli. Still, the subjective timing of the sensory experience appears to be without a significant delay, which is due to an alleged back-referral mechanism (e.g., Libet *et al.*, 1979). Based upon the findings of these back-referral experiments, Libet and his collaborators came up with their much discussed second experimental approach, the 'readiness potential' or 'RP-experiments' (Libet *et al.*, 1982; Libet *et al.*, 1983; Libet, 1985). The readiness potential (RP) is an electrophysiological indicator for cortical movement preparation. It normally precedes a voluntary motor act by approximately 500–1500 ms (Libet *et al.*, 1982; Haggard & Eimer, 1999). The appearance of these preparatory cerebral processes at such surprisingly long times before spontaneous acts led Libet to question whether the conscious intention to act occurs equally far in advance of the actual movement. Libet argued that if the RP-onset occurs before the time of a conscious decision to perform a certain action, consciously willed decisions therefore also require a substantial build-up period to achieve "neuronal adequacy."

In order to test this hypothesis, Libet *et al.* (1983) devised an experiment to time objectively subjects' awareness of their "urge to move" when performing spontaneous movements, and to relate this subjective timing to the onset of the RP. This was achieved by instructing his subjects to fix their gaze on the circular screen of a cathode ray oscilloscope (CRO). The CRO had a spot of light that revolved clock-wise near the circumference of the screen with numbers at each five second position, similar to an ordinary clock. While the RPs were recorded on the subjects' scalps, the subjects were directed to abruptly and spontaneously flex the wrist or fingers of the right arm, at any time after the spot on the CRO completed one full revolution. Before the start of the experiment, the subjects were asked to remember the clock position at the moment they were aware of an "urge" or a "feeling to make movement." The results of the RP-experiments showed that preparatory neuronal processes, measured in the form of RPs, preceded the awareness of the conscious intent by about one third of a second. The onset of the averaged RP was found to be about 550 ms before the arm-movement, whereas the subjects reported their "urge to move" only 200 ms before the action, 350 ms after the RP-onset. Libet (1985) concluded from these RP-experiments that although conscious will does not appear to control the initiation of actions, it still acts as a veto-mechanism: as his subjects were aware of an "urge to move" 200 ms before the act itself, the veto to move or to refrain from this act was under conscious control during a brief 100–200 ms time-window just before the act was executed. To Libet then, conscious will does not initiate behavior but is a binary control device that censors unconsciously generated actions.

As said before, although Libet's views have been criticized heavily over time (e.g., Churchland, 1981a,b; Flanagan, 1997; Glynn, 1990; Gomes, 1998, 2002; Keller & Heckhausen, 1990; Pockett, 2002), some have adopted his experiments as evidence in favor of the idea that conscious will is merely "an illusion created by the brain" (e.g., Gazzaniga, 1998; Nørretranders, 1998; Roth, 2003; Wegner, 2002, 2003). For instance, neuroscientist Gerhard Roth (2003) recently concluded the following from Libet's RP-experiments:

> *These studies demonstrate that the 'act of will' occurs several hundred milliseconds after the onset of the . . . readiness potential. This means that the 'act of will' cannot cause voluntary actions and that the freedom of the 'act of will' is an illusion. (pp. 129–130)*

On this view, even Libet's (1985) conscious veto would only be an epiphenomenon of unconscious neuronal activity (Dennett & Kinsbourne, 1992; Gomes, 1998). Recently, however, other interpretations of Libet's work have been offered, which also provide an alternative perspective on the validity of the illusion-claim (e.g., Glynn, 1990; Gomes, 1998; Pockett, 2002).

4.3 Other Interpretations of the Libet-Experiments

Many have questioned the ecological validity of the Libet-experiments: Can Libet's finding that neuronal activity precedes a conscious willed decision be generalized to normal, everyday conscious decisions? Keller and Heckhausen (1990) and Gomes (1998, 2002) argue that conscious intent was "artificially imposed" by Libet's experimental set-up: Libet *et al*. (1983) instructed their subjects to pay attention to an "urge" or a "feeling to move," and to initiate the willed act when this feeling occurred. However, Keller and Heckhausen (1990) claim that unconscious motor responses to a particular sensory stimulus can be detected through a mechanism of selective attention. The "urge to move" in the RP-experiments, then, could have functioned as an internal stimulus to which the subjects responded by executing the predefined act. While subjects were prepared to make a movement, introspective attention thus "picked up" neuronal activity that is normally unconscious. The ecological validity of the Libet-experiments is therefore rather questionable (Gomes, 1998).

Another much discussed problem related to the Libet-experiments deals with whether the conscious decisions were made by the subjects on every single trial of the RP-experiments, or only once, at the beginning of the experiment. For example, van de Grind and Lokhorst (2001) argue that when the subjects were given instructions on how to act in the experiment, they also consciously prepared themselves to participate in the experiment, thereby activating or "pre-programming" the appropriate response (see also Flanagan, 1997; Gomes, 1998; Joordens, van Duijn, & Spalek, 2002; Keller & Heckhausen, 1990; Zhu, 2003). After that, automatic unconscious processes took over, initiating pre-set, automatic movements on each trial. On this view, conscious will only guides behaviors in a global manner and monitors when it is time to stop or initiate unconscious "motor programs" (van de Grind & Lokhorst, 2001).

This view is further corroborated by recent research that also suggests that the role of conscious will in behavior is indeed an active one (e.g., Baars, 1997; Elsner & Hommel, 2001; Jahanshahi & Frith, 1998; Jeannerod, 2000). Given the limited capacity of the conscious system, the bulk of processes need to be automatic and unconscious. By far the majority of our actions are thus prepared and executed automatically, which guarantees a fast and accurate execution of the act. Conscious control on the other hand operates at a much slower pace, but prevents us from getting "stuck in set" by solving failures that occur at the automatic levels, by creating the context for understanding an action, and by rearranging the means to achieve a certain goal if necessary (Flanagan, 1997; Jahanshahi & Frith, 1998; Jeannerod, 1997). Conscious will therefore appears to provide a meta-level of behavioral control that creates, edits, and selects global action plans, which in turn enables us to engage in more strategically complex behaviors (e.g., Baars, 1997;

Jeannerod, 2000). On this view, it is not necessary to assume a direct conscious cause for every single voluntary movement. By far most of our actions are automatically controlled and executed but have to be understood in a broader context in which conscious will influences behavior by setting up the automatic action-routines in advance.

With this alternative interpretation in mind, Libet's findings of the appearance of RPs before the conscious initiation of an act are hardly surprising. However, although these alternative interpretations of Libet's findings and of conscious will appear to resolve most of the counterintuitive consequences of Libet's (1985) conclusions, they still do not exclude the illusion-claim. After all, it could still be argued that even though conscious will appears to globally set-up and activate "motor programs" (van de Grind & Lokhorst, 2001), even such a global conscious decision would be preceded by preparatory neuronal activity (Gomes, 1998). On this view, the genuine causal processes that support conscious will would thus only reside on the neuronal level, and not on the conscious one. The preparatory neuronal activity that sets up a willed action would also give rise to an after-the-fact illusory subjective experience of a causally effective will (e.g., Nørretranders, 1998; Roth, 2003; Wegner, 2002). In sum, although critics to Libet's work have provided a convincing case against the validity of his main claims, we need to dig deeper into the background assumptions of the illusion-claim in order to reveal its theoretical incoherencies.

4.4 The Input-Output Paradigm

Although behaviorism is no longer fashionable in the modern cognitive neurosciences, some of its theoretical assumptions still appear to be of influence today. In particular, the stimulus-response paradigm, or 'input-output model', has remained quite tenacious (e.g., Anderson, 1995; Freeman, 1999b). The behaviorists looked upon perception and action as two separate mechanisms, and acquired associations between stimulus and response were seen as deterministic, one-way causal constructs. Action was thus regarded as a linear and reflexive effect of perception, while feedback loops between action and perception were disregarded (Hurley, 2001). The cognitivists elaborated on this behaviorist model by wedging "cognition" in between the "perception" and "action" boxes (Hurley, 1998). This way, the behaviorist reflex paradigm became incorporated into cognitivist psychology. Because of the influence of the input-output model, psychological phenomena are still sometimes explained in a strict, linear causal manner (Anderson, 1995).

Behavior is then captured in terms of the classical Newtonian picture of causality: events are placed on an imaginary time-line, succeeding each other in a discrete, and conveniently arranged linear sequence (Freeman, 1999a). These linear causal models abstract away from their context, and characteristically require a "first cause": one discrete occurrence at the origin of a discrete causal cascade of events. The influence of the input-output paradigm and linear causal thinking can also be recognized in Libet's work. In order to account for his results, Libet (1985) placed the RP-onset at the beginning of the linear causal chain, as to constitute the first cause. The RP-onset is followed by the conscious veto, which in turn leads to the execution of the act itself. From a strict linear causal perspective, it seems that the RP-onset actually causes the consciously willed decision, and that therefore the causal work is performed by the first event in the sequence, the RP-onset, effectively robbing conscious will of its causal powers. Libet's notion of the "conscious veto" attempts to escape from this epiphenomenalistic threat by restoring the idea that conscious will still matters to the behavioral outcome just prior to the execution of the act. However, this apparent "veto solution" results in a rather artificial conception of conscious will as a reactive veto-mechanism that only has a say in whether or not unconsciously generated actions can proceed—a solution that does not convincingly restore the idea of a causally potent conscious will (Dennett & Kinsbourne, 1992; Gomes, 1998). Unfortunately, the view that conscious will only guides our global behavior and not every single action we take (Flanagan, 1997; Keller & Heckhausen, 1990; van de Grind & Lokhorst, 2001) also succumbs to this strict, linear causal way of thinking, as it simply places the conscious decision at the beginning of the linear time-line, before the RP-onset. This theoretical move is incomplete because it results in a fruitless, never-ending discussion: What comes first, the conscious decision to initiate a certain action, or the preparatory neuronal activity that sets-up and causes the conscious decision? It has become apparent that linear causal models cannot provide a satisfying answer to this discussion, and that a fundamentally different approach is required. In the remainder of this paper, we develop an alternative perspective on the causal efficacy of conscious will.

4.5 Self-Organization

During the last few decades, self-organization has been increasingly recognized as an important subject of scientific inquiry (e.g., Haken, 1987), and researchers from various scientific disciplines now study it. 'Self-organization' is generally defined as a process that, given certain boundary conditions, gives rise to increasing order in a particular system by spontaneous synchronization of system parts, without a central executive that helps to set-up this self-organization (Jantsch, 1980). Heylighen (2001) discusses (ferro)magnetization as a conservative example of self-organization[43]: potentially magnetic materials can be seen as to consist of a collection of tiny, individual magnets called "spins," which represent local magnetic domains. At very high temperatures these spins show no coherence, i.e., their individual orientation is random so that they cancel each other out. However, when the material cools down and reaches a material specific transition temperature, the so-called "Curie point," the individual spins spontaneously begin to organize and to align themselves. When the material solidifies, the given system reaches a

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[43] Other relatively well-known examples of self-organization include (1) the hexagonal Rayleigh Bénard cells, characteristic convection rolls that form in uniformly heated liquids (Jantsch, 1980), and (2) the Belousov-Zhabotinski reaction, a complex prolonged chemical reaction.

so-called "attractor state," locking the collective spin-dynamics in-place, and thereby providing that material with "macroscopic" magnetic properties (Heylighen, 2001)[44].

Self-organization is more complex in so-called "dissipative structures" or "far-from-thermodynamical-equilibrium-systems." These dynamical systems can be described in terms of changes in the values of a set of interdependent variables (e.g., Port & van Gelder, 1995), which together constitute a high-dimensional statespace or phase-space, with each variable counting as a distinct dimension. The function of the dynamics of the system are depicted as a trajectory through an n-dimensional state-space containing attractors and repellents. The attractor minima correspond to states of minimum energy and maximum stability, while the repellent maxima represent states of maximum energy and minimal stability in a given system. The trajectory of the system can then be drawn and settle into multiple kinds of attractors that may vary in complexity. Self-organization can be seen to operate as an attractor in a dynamical system. Under the proper boundary conditions (i.e., a particular temperature or energy level), systems can then be drawn into self-organization (Heylighen, 1989). In complex, dynamic, open systems pumped with energy, like our atmosphere, selforganization can technically be seen as an entropy/extropy cycle that supports a net flow of order into the system—enabled, on the one hand, by maintaining extropy or order import and production; and, on the other hand, by dissipating or exporting the acquired thermodynamical entropy by, e.g., giving of heat. The amount of entropy that a system is able to disperse is then a boundary condition for its organizational growth (Jantsch, 1980). Besides maintaining the energy flow to sustain self-organizing processes, harnessing and utilizing this energy is what life forms do best. This makes self-organization not only a particularly relevant phenomenon for biology (e.g., Ben-Jacob, 1997; Ho, 1996), but also for the brain and behavioral sciences (Bressler, 2003; Haken, 1995; Jordan, 2003; Kelso, 1995; Krippner & Combs, 2000).

4.6 Self-Steered Self-Organization

A particularly complex form of self-organizing, namely, "self-steered self-organization" (Keijzer, 2003b), has strong connotations with intentionality and conscious will (see also Jordan, 2003; Kelso, 1995). Self-steering processes involve internal control parameters that modulate the dynamics of self-organizing patterns into a particular adaptive direction, characterizing dynamical biological processes such as metabolism, morphogenesis, and ontogenesis (Ben-Jacob, 1997). DNA, for example, can be seen as an internal control parameter that perturbs the self-steered dynamics of the morphogenesis of organisms, without offering a strict prescription of the overall outcome (Keijzer, 2001). The presence of self-steering systems allows the hierarchical organization of the body to remain relatively flat, making its organization with all its different, relatively autonomous subsystems more efficient (Aulin, 1979; Heylighen, 1989). The more complex organisms

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[44] Not all forms of self-organization lead to macroscopic order that displays novel so-called "emergent" system properties.

become, the more they rely upon internal, self-steering factors in order to maintain internal stability (Beer, 1974). Self-steering processes can therefore be said to constitute an evolutionary compromise in complex biological systems between the importance of internal stability on the one hand, and effective organizational design on the other.

The link between self-steered self-organization and conscious will becomes more salient in the so-called “bimanual phase transition paradigm” (e.g., Lee, 2004). For example, Kelso (1995) demonstrated that when subjects performed bimanual finger movements to a metronome, both the in-phase and the out-of-phase pattern of finger twiddling can be equally stably maintained at low frequencies. At higher frequencies the out-of-phase pattern soon becomes unstable, as subjects have a tendency to synchronize to the metronome. However, the conscious wish to maintain an anti-phase pattern results in a more prolonged stability of the out-of-phase pattern at higher frequencies, and thus prevents the phase change to the in-phase pattern. This implies that the conscious wish to maintain a certain behavioral pattern is accompanied by the stabilization and destabilization of the already inherent coordination dynamics. Kelso (1995) introduced “specific parametric influences” or “coordination variables” to refer to these intentional forces: intrinsic information that alters the dynamics of a system, steering it towards the intended pattern.

Although self-steering phenomena occur in many biological and psychological contexts (Keijzer, 2003b), the notion of ‘self-steering’ may help provide us with an alternative perspective on conscious will. On this tentative view, conscious will can be seen as perturbing the intrinsic behavioral coordination dynamics of brain, although it cannot directly override its inherent constraints. That is, intentional switching between behavior patterns is dependent on and constrained by the stability and strength of existing patterns. Conscious will could then be envisaged as a self-steering neural mechanism generated by the collective, self-organized activity of neurons, providing the brain with a tool to rapidly switch between existing coordination dynamics, and to stabilize them when necessary, in order to achieve a particular behavioral goal. As many such self-steering self-organizing processes take place within our body and brain, the self-steering influences that govern large-scale, self-organizing neural phenomena should not be regarded as particularly special or mysterious. Nevertheless, it is clear that the neuronal mechanisms that support conscious will are still largely beyond the grasp of contemporary cognitive neuroscience. The idea that neurons cooperate on a macroscopic level to sustain psychological functions is not a new one, however, and can be traced back to the works of Pavlov, Luria, and Wernicke (Bressler, 2003). Donald Hebb (1949) already spoke of “neuronal cell-assemblies” that act as a “diffuse structure comprising cells in the cortex and diencephalon . . . capable of acting briefly as a closed system” (p.73). Whereas the proper tools to understand these integration mechanisms were not present in those times, we believe that relatively novel concepts such as selforganization and self-steering may help pave the way for a better understanding of conscious will, including its causal efficacy. At least it allows for an alternative perspective on the illusion-claim, on which we elaborate in the next section.

4.7 Levels and Causality

As discussed earlier, the illusion-claim is rooted in the philosophical position that the genuine causal processes that underlie conscious will only take place at the neuronal level. On this view, the dynamics of self-organized, macroscopic neuronal patterns can, at least in principle, be understood and explained by a complete account of the causal processes at the level of neurons and synapses. The modern cognitive neurosciences, however, study a wide range of phenomena, from the workings of NMDA-receptors and ion-channel dynamics, up to neuronal oscillation rhythms, and, of course, behavioral and psychological events. In other words, it is an enterprise that spans an entire hierarchy of mechanisms across multiple levels of description[45] (Craver, 2002). That is, levels are domains at a particular spatiotemporal resolution scale, so that events at one level obey particular characteristic laws or regularities that cannot be found at other levels, which in turn allows a clear demarcation of such levels (Juarrero, 1999). Additionally, not only do levels form a particular kind of a part-whole relation, there is also the restriction that the components on the microscopic level "are organized tighter to produce the behavior of the mechanism as a whole" (Craver, 2002, pp. 7–8). In other terms, the microscopic parts of a level are constrained to behave in a certain way; order or organization is therefore another key component in distinguishing levels (Craver & Bechtel, 2006). A part-whole or stratified picture of 'levels' is common in most scientific disciplines (Bem & Looren de Jong, 2006). For example, it is generally acknowledged that the laws of thermodynamics capture regularities that do not occur at the atomic level (Freeman, 1990). However, it appears that in the cognitive neurosciences the influence of the input-output paradigm and linear causal thinking has hampered the assimilation of this mereological perspective. Linear causal frameworks in particular have problems dealing adequately with hierarchies of mechanisms, as they can only mold hierarchical relations into strict, linear cause and effect relations. According to Juarrero (1999), the category mistake to ascribe linear causal powers to each individual explanatory level is then easily made. Such a category mistake lies also at the root of the illusion-claim: neuronal activity is seen as causing conscious will, whereas they only form a constituency relation. Saying that neuronal activity causes conscious will is therefore very much like saying that H_2O molecules cause water. Instead, the notion of self-organization comes with a distinction between a macroscopy and a

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[45] In modern philosophy of mind, there is still much discussion over the question of whether or not neuronal phenomena and psychological ones are really part of different levels (e.g., Kim, 1998). A view along these lines can be found in Keijzer and Schouten (2005).

microscopy as two different levels of aggregation (Keijzer, 2003b)[46], and it is here that the circular nature of self-organizing phenomena becomes more apparent, as we will show in the next section. The notion of self-organization then provides a handle on better describing interlevel relations, and, as we will argue later on, a more natural understanding of the causal efficacy of conscious will.

4.8 Interlevel Constraints

Interlevel causation is a rather controversial topic in modern philosophy. One reason for this is that interlevel causation is often erroneously captured in terms of strict, linear cause and effect relations between levels (e.g. Craver & Bechtel, 2006; Juarerro, 1999). How then do higher-and lower-level phenomena relate if not in a strict linear, causal, bottom-up and top-down manner? Clark (1997) argues that on the one hand, the elementary units of a given system may constitute macroscopic patterns, while at the same time these patterns can be said to constrain their microscopic elements to behave in ordered patterns. This two-way or reciprocal relation between a micro- and a macro-level is then often captured in terms such as ‘‘circular causation’’ (e.g. Freeman, 1999a; Kelso, 1995), ‘‘continuous reciprocal causation’’ (Clark, 1997, p. 163), and ‘‘inter-level constraints’’ (Juarrerro, 1999). In this context, the so-called cooperative phenomena in physics are highly relevant. For example, both water and ice are made of the same micro-level components, which lack properties such as liquidity or solidity. Water and ice as macroscopic phenomena, in turn, each comes with different constraints on the organization of H_2O molecules. These constraints then sustain system properties that exhibit causal powers that cannot be found at the level of its individual parts (Craver & Bechtel, 2006). It is thus the organized interaction between a multitude of units that yields novel system properties.

Self-organization is also a process that imposes order or constraints on system parts. For example, Haken’s (1987) laser gives rise to coherency of emitted wavelengths that compels all elements to behave in a coherent manner. The self-organized coherent bundle of photons comes with novel system properties, such as the ability to cut through certain materials, whereas a bundle containing collectively out-of-phase photons lacks these properties. The photons are thus said to be ‘‘enslaved’’ into order by self-organization, so that all parts no longer behave independently but as a collective (Kelso, 1995). This self-organized coherency expands the state-space of the system, bringing along more degrees of freedom and additional causal powers for the system as a whole, while simultaneously constraining the number of possible microscopic states.

We believe that Haken’s (1987) laser, and self-organizing phenomena in general, provide a good analogy for thinking about the causal efficacy of conscious will, as there is a similar reciprocal relation between macroscopic neuronal states and their microscopic

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[46] The relation between self-organization and ‘levels’ is not a straightforward one. Not all macroscopic properties of self-organizing systems are generally regarded as being part of a new level of description.

neuronal constituents: Global macroscopic mental states are constituted by neurons on the microscopic level, while simultaneously these mental states organize the activity of the individual neurons (Keijzer, 2001). On this view, the relatively slow and coordinated mass-activity of large populations of neurons can act as a constraint device that imposes order onto the firing patterns of the individual neurons (see also Freeman, 1999a). The self-organizing neuronal states that underlie wake and sleep rhythms and synchrony patterns in the gamma band, for example, can thus be seen as harnessing the individual behavior of neurons into ordered patterns. These patterns in turn may exhibit properties that cannot be found at the micro-level, and new dynamic principles are thus required to understand these global patterns (Kelso, 1995). Conscious will, as a self-steering component of self-organizing neuronal processes, may similarly impose restrictions on existing coordination patterns, thereby acting as a ‘‘dynamic constraint mechanism’’ that steers self-organized patterns of neuronal activity. On this view, it no longer makes any sense to pinpoint a ‘‘genuine’’ causal origin of a chain of events that leads to a willed action on one particular level of neural organization. That is, neither macroscopic mental states nor microscopic neural states should be seen as harboring the ‘‘ultimate causes’’ for all of our actions. In the penultimate section we shall relate our tentative interpretation to modern and classical views on conscious will.

4.9 The Efficacy of Conscious Will

William James (1890) maintained that primary reflexes and involuntary movements evoke complex impressions of looks, feelings, sounds and kinesthetics, which leave a multimodal image in our memory. The mere thought of a movement’s sensible effects then becomes sufficient to result in the instant automatic triggering of the necessary actions to achieve those effects. James (1890) argued that consciously willed acts differ from voluntary ones, as the former require an additional conscious element that has to intervene in order to overcome competing inhibitory forces. This element, which James termed the ‘‘volitional mandate’’ or ‘‘mental fiat,’’ has the power to overrule conflicting goals that keep some of our desired acts from execution. In James’s (1890) classical ideo-motor theory, our ‘‘mental images’’ are directly linked to movement codes, which suggests that conscious thoughts and actions are fundamentally intertwined. Recent research subscribes to and elaborates on James’s introspective account, and shows that there is indeed evidence that cognitive codes of movement patterns, which make up a ‘‘motor program’’ and anticipated action effects, or goals, automatically form a bilateral association. When performing voluntary actions, we actively use this automatically formed relationship for goal formulation and selection (Elsner & Hommel, 2001). Research in developmental psychology shows that successful inhibition of competing actions is key in the development of consciously willed behavior (e.g., Diamond, 2000). However, there might be more to conscious will than mere inhibition and excitation of existing coordination dynamics. It is likely that it also operates as a particular kind of matching mechanism that compares goal-states with visual or kinesthetic feedback. The self-steering aspect of conscious will then comes into play when there is a mismatch between external feedback and the internal goal state. Conscious will can be seen to organize or self-steer behavioral patterns towards the goal-state by matching it with perception-action feedback (e.g. Lee, 2004).

However, consciousness only has access to global information in the brain, so it only has a global influence on our actions; specialized parallel systems deal with far more detailed and complex information (van de Grind & Lokhorst, 2001). Automatic control processes correct actions by means of simple feedforward processes when there is a mismatch between a present state and desired goal-state. When for some reason the goal-state is not reached, the representation of the desired state becomes available to higher-level control processes, which enables conscious access to the goal and awareness of the previous failure to reach that goal (Jeannerod, 2000). Conscious will can then override the unconscious systems and minimize the error between the goal-state and the sensory feedback, by reorganizing the behavioral patterns to reach the goal-state, thereby preventing us from getting ''stuck in set'' (Jeannerod, 1997). In this article, we argued that 'self-organization' and 'self-steering' are useful notions to come to a better understanding of the cooperative neuronal mechanisms that underlie conscious will, although of course more research is needed to corroborate such a view. At least it provides us with a more natural alternative to the illusion-claim that allows modern scientific views to converge with good old-fashioned common sense.

4.10 Conclusion

In this paper, we discussed the empirical and theoretical validity concerning the illusion-claim, and made explicit some of its main philosophical presuppositions. By analyzing each of these three corner stones of the illusion-claim, it has become apparent that:

1. The empirical evidence that is seen as vindicating the illusion-claim is not persuasive. Rather, the evidence points in favor of the common sense idea that the conscious will plays an active role in behavior, although consciousness does not provide us with an all-access view to all the specific details that are involved in the underlying processes of these willed actions.
2. The theoretical incoherencies of the illusion-claim are rooted in the behaviorist input-output paradigm, which, by the use of strict, linear causal models, induces the category mistake of looking at neuronal activity as the cause for conscious will.
3. The philosophical position that the genuine causal processes that underlie conscious will only take place at the neuronal level lies at the roots of the illusion-claim. However, as we have argued, this theoretical position is based on faulty premises. Instead, we showed that with the help of notions such as 'self-organization', a better understanding of the integration mechanisms in the brain can be obtained, and with that a more natural picture of the causal efficacy of conscious will. This serves not only as to satisfy philosophical

curiosity, but also for its pragmatic relevance: a better empirical and theoretical framework on the global integration mechanisms in brain functioning might also help advance the understanding and treatment of clinical disorders such as schizophrenia, and Parkinson’s disease (e.g., Jahanshahi & Frith, 1998). This marks the importance of conscious will as a serious object of scientific investigation, rather than a mere illusion created by the brain.

5. The Biocognitive Domain: Explicating Biocognition

Why don't plants have brains?
The answer is quite simple: they do not have to move, and moving is what brains are really for.

Lewis Wolpert (2000)

5.1 Introduction

This final chapter provides a meta-analysis of the views developed in the previous chapters and integrates these views by providing an explication of the notion ‘biocognition'. Concept clarification or explication is a central enterprise in philosophy of science (Kuipers, 2007). Concept explication provides a means to link theory to observation: by clarifying informal notions such as for example ‘intelligence’ or 'representation', precise conceptual or operational definitions of those concepts can be obtained, which can be used to guide empirical research (Chaffee, 1991). A traditional method of concept explication involves transforming a vague, informal concept, a so-called “explicandum”, into an exact and precise concept, a so-called “explicatum” (e.g. Carnap, 1950). Concept explication usually proceeds by systematically spelling out an explicandum’s denotations and connotations. The aim of concept explication is to yield a precise notion of an informal concept by deriving conditions of adequacy that need be satisfied by the explicatum; in addition, the explicatum also needs to satisfy clear-cut instances and exclude clear-cut non-instances of the concept (Kuipers, 2001, p.61). Discussing evident examples and non-examples (such as 'near-misses') helps to demarcate the explicatum. It is often the case that the explicatum needs to fulfill additional qualitative criteria in the form of certain desiderata, which help constrain and guide the explication endeavor[47] (Carnap, 1950).

In this chapter, I employ Kuipers’ (2007) evaluation methodology for concept explication to clarify the notion ‘biocognition’. Using this methodology, I derive three conditions of adequacy for biocognition. That is, biocognitive systems are by definition: (1) motile organisms, capable of (2) sensorimotor coordination, which is governed by an (3) internal sensor/effector signal-transduction mechanism. According to this explication, biocognition is a form of biological adaptation that is shared by motile organisms capable of sensorimotor coordination. Biocognition allows these organisms to optimize the external conditions for their metabolism by optimizing the search for more favorable environmental conditions.

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[47] For example, Carnap (1950) uses four desiderata that the explicatum needs to abide: (1) *similarity to the explicandum*, (2) *exactness*, (3) *fruitfulness*, and (4) *simplicity*.

According to these conditions of adequacy, plant behavior is excluded from the biocognitive domain, since plants are sessile organisms. However, plants are highly adaptive organisms, and a small minority of researchers has recently argued in favor of plant cognition. In section 5.3, I discuss the plausibility of plant cognition. In defense of the conditions of adequacy of this explication, I argue based on a case-study of the sun-tracking behaviors of *Lavatera cretica,* that plant behavior is based on phenotypic plasticity rather than biocognition. This explication stresses the central importance of motility and sensorimotor coordination in biocognition, the cost-benefit trade-offs that come with sustaining a motile lifestyle, and the importance of size in determining trade-offs between metabolic costs and adaptive benefits of biocognition. Lastly, in accordance with Kuipers' methodology, I evaluate the explicatum in terms of three general desiderata.

5.2 Explicating Biocognition

In this section, I use Theo Kuipers' (2007) evaluation methodology for concept explication to explicate the notion 'biocognition'. Based on the explication methodology of Carnap, Hempel, and others, Kuipers provides a methodology for concept explication in which 5 phases can be discerned:

(1) to propose an explicandum
(2) to provide a number of specific desiderata by stating conditions of (in)adequacy and by providing evident cases of (non)examples
(3) to propose an explicatum by stating an idealized explication proposal
(4) to evaluate the explication proposal by discussing its successes and problems
(5) to evaluate the explicatum in terms of 3 general desiderata: *precision*, *fruitfulness* and *simplicity*

Kuipers notes that when phase 5 does not yield a satisfactory result there is a second round: by resetting the specific desiderata and by further clarifying the explicatum by branching into sub-domains and by successive concretization, a more accurate characterization of the informal concept can be obtained. The explication method advances by providing an informal description of the explicandum, in this case the notion 'biocognition'.

5.2.1 The Explicandum: Biocognition

Biocognition is not a standard term in the cognitive science literature; it is used occasionally and inconsistently (see for example Bogdan, 1994; Martinez, 2003). I take the informal meaning of the notion 'biocognition'[48] to refer to the broad spectrum of extant and extinct biological forms of cognition, from bacterial chemotaxis to human reasoning. This affiliates biocognition with (1) adaptive behavior, (2) normativity, and (3) sensorimotor coordination:

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[48] The informal interpretation of biocognition I use best corresponds to the way in which it is used by the biocognition research group of the University of Alberta, who uses it to refer to the biological basis of cognition in organisms. See: http://www.psych.ualberta.ca/~csturdy/Biocognition_Home.htm

(1) Biocognition is the product of evolution by variation and natural selection. There is a deep phylogenetic continuity between species, which is reflected not only in their genetic make-up and morphology but also in behavior. Behavior and cognition are phenotypic traits, and they are shaped by evolution just as any other trait. Biocognition is a specific kind of biological adaptation[49]. Biocognition evolved because in some way it enhances fitness, that is, it confers adaptive advantages for organisms, such as by promoting their survival and progeny. Biocognition is a property term that refers to individual organisms, i.e. biocognition promotes the way in which individual organisms adapt to changing conditions in their environments, as well as to populations of organisms, i.e. biocognition maximizes fitness of members of a species or lineage.

(2) Biocognition is intrinsically connected to the homeostatic processes that sustain life. Homeostatic mechanisms allow organisms to robustly cope with variability in their environments. Organisms typically possess an entire arsenal of physiological regulatory mechanisms that help to keep the conditions for their metabolism such as their temperature, internal acidity (pH), and blood sugar levels within healthy limits. The function of biocognition is to enable organisms to coordinate the state of their internal milieu with that of their external environment by optimizing the external circumstances for their homeostasis. Biocognition is therefore inextricably linked to valence and normativity. Organisms assess and assign values to internal and external changes based on their current state of homeostasis, their past experiences, and their own predispositions (Lyon, 2006a). Biocognitive organisms engage in normative, goal-directed behaviors, optimizing their internal homeostasis by actively seeking out environments that best suit their metabolic requirements.

(3) Biocognition allows organisms to optimize the external conditions for homeostasis through sensorimotor coordination. Sensorimotor coordination allows organisms to escape the limitations and restrictions of local conditions and to seek out, select, and produce more favorable habitats. Sensorimotor coordination allows organisms to optimize the distribution of their population, which helps to spread the risks of extinction, promotes variation in social and genetic environments, and also reduces competition between parents and offspring (Danchin, Giraldeau & Cézilly, 2008). Advocates of embodied/embedded cognition argue that the phylogenetic and ontogenetic basis for cognition lies in sensorimotor behavior (e.g. Anderson, 2005; Beer, 2008; Brooks, 1999; Clark, 2008;

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[49] The notion of 'adaptation' has different meanings in biology; McFarland (1991) distinguishes between four different meanings: "Biologists usually distinguish between (1) evolutionary adaptation, which concerns the ways in which species adjust genetically to change in environmental conditions in the very long term; (2) physiological adaptation, which has to do with the physiological processes involved in the adjustment by the individual to climatic changes, changes in food quality, etc.; (3) sensory adaptation, by which the sense organs adjust to changes in the strength of the particular stimulation which they are designed to detect; and (4) adaptation by learning, which is the process by which animals are able to adjust to a wide variety of different types of environmental change." (p.22).

Keijzer, 2001). The biogenic approach to biocognition taken in this thesis extends this view to organisms that lack a brain or a nervous system. On this view, biocognition is a form of biological adaptation that is grounded in sensorimotor behavior and shared by prokaryotes and eukaryotes alike.

5.2.2 Specific Desiderata

Following Kuipers' methodology we can arrive at an idealized explication proposal of biocognition by formulating a number of specific desiderata (Kuipers, 2007). The explicatum needs to satisfy specific desiderata in the form of conditions of adequacy and also needs to satisfy evident examples. According to Kuipers (2001, p.263), conditions of adequacy are necessary but not sufficient conditions that all need to be fulfilled by the explicatum; these conditions correspond to certain desired features. Furthermore, the explicatum should exclude evident non-examples and violate conditions of inadequacy. Fulfilled conditions of inadequacy show that the explication is too narrow, whereas false positive examples and false negatives show that the explication is either too wide or to narrow, respectively (Kuipers, 2007, pp. xi-xii). Table 1 provides an overview of the specific desiderata of our explication of biocognition. The conditions of (in)adequacy and (non)examples are derived from the work in the previous chapters. In the next section, I discuss the conditions of adequacy of this explication in more depth.

Conditions of adequacy	*Conditions of inadequacy*
- Motile organisms	- Having a brain or nervous system
- Sensorimotor coordination	- Off-line cognition
- A sensor/effector signal-transduction mechanism	- Conditional learning
Evident examples	*Evident nonexamples*
- Chemotaxis in *E. coli*	- A compass
- Conditional learning in *Paramecium*	- A virus
- Sink-fishing behavior of *Aglantha digitale*	- Computers and A.I.
- Dead reckoning in honey bees	- The lac-operon system in *E. coli*
- Theory of Mind in chimpanzees	- Non-oriented motile behaviors
- Conscious will in humans	- Plant behavior

Table 2: Specific desiderata for biocognition.

5.2.3 The Explicatum: Conditions of Adequacy

Based on the conditions of adequacy biocognitive systems are by definition: (1) motile organisms, (2) capable of sensorimotor coordination, (3) which is mediated by a sensor/effector signal-transduction system. The explication therefore excludes: (i) sessile organisms such as plants and most fungi (see also section 5.3), and also (non)motile virtual and artificial systems[50], (ii) behaviors or forms of locomotion that do not involve sensorimotor coordination, and (iii), behaviors that do not rely on a direct coupling mechanism between sensors and effectors, such as for example behaviors based on phenotypic plasticity (see also section 5.3). Let's consider in more depth the conditions of adequacy:

(1) Biocognition is a property of vagile organisms, i.e. motile, free-moving organisms. Motility is a phylogenetically ancient feature that can be found across all three domains of life: Bacteria, Archaea, and Eucarya (Faguy & Jarrell, 1999; Woese, Kandler & Wheelis, 1990). Motility is subject to strong selection pressures that yield cost-benefit trade-offs between metabolic costs and adaptive benefits. On the one hand, basic locomotor behaviors confer many important adaptive benefits: it allows organisms to escape the limitations and restrictions of local conditions, and to seek out and select more favorable habitats, to hunt down and capture prey, to avoid predators, to spread the risks of extinction, and to seek new opportunities to procreate (Danchin, Giraldeau & Ceézilly, 2008). On the other hand, motility comes with high costs: active locomotion exposes organisms to threats such as predators and leads to a steep increase in energy expenditure. The metabolic costs for motility are relatively low but still significant for single-celled organisms such as bacteria and algae (Striebel *et al.*, 2009). However, in some species of small ciliates and flagellates, fast forms of motility can account for 10-100% of their energy expenditure, which is why these organisms limit their movements to short bursts (Crawford, 1992; Mitchell, 1991). Motility is also biosynthetically expensive. That is, in most bacteria the flagella are composed of 20.000 or so flagellin proteins, and their self-assembly is governed by the regulated expression of 50 or so genes (Chilcott & Hughes, 2000; Aldridge & Hughes, 2002; Metlina, 2004).

Motility in single celled organisms is often achieved by the use of flagella and cilia. Both flagella and cilia are extensions of the cell and structurally they are very similar. However, cilia are shorter and tend to occur in relatively larger numbers (in patches or tracts), while flagella are long and generally occur singly or in pairs (Brusca & Brusca, 2003). Beating cilia or rotating flagella provide both a propulsive force that can move an organism through a liquid. Such behavior can be controlled by electrical signaling and action potentials, all in a single cell. Motility by means of cilia and flagella imposes strong

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[50] This explication of biocognition excludes artificial forms of cognition such as computers and A.I., which obviously lack a biological origin. However, this does not implicate that computers and A.I. are not instances of artificial cognition, be it in very different ways. Whereas typical desktop computers rely on raw computing power and lack the embodiment and embeddedness of biological organisms, action-based robot architectures such as subsumption are often inspired by biological organisms and exploit principles from embodied/embedded cognition, such as sensorimotor coordination, perception-action coupling, and morphological computation (e.g. Brooks, 1999; Kassahun, Edgington, de Gea & Kirchner, 2007; Pfeifer & Iida, 2005; Prescott, Redgrave & Gurney, 1999). While these biologically inspired robots might mimic certain aspects of biocognition, the notion of biocognition as I use it is restricted to living organisms.

limitations on the size of the organisms involved. In large multicellular organisms, flagella and ciliary transport systems are ineffective for generating movement because of higher surface/volume ratios and higher Reynolds numbers[51]. It works well for single-celled bacteria that are as small as 1 μm and for protists like *Paramecium* that are 180 μm (Greenspan, 2007). It also works well enough for multicellular metazoa like flatworms, the size of which can be measured in millimeters (Trueman, 1975). The largest creatures driven by cilia are the comb jellies the size of which can be many centimeters (Brusca & Brusca, 2003). However, these latter cases are at the very limits of what cilia can do and they require specific adaptations and conditions that cannot be used more widely. All in all, cilia and flagella are only generally effective as a motility mechanism for creatures at or below the millimeter scale and sets a strong constraint on the size of motile animals (Keijzer, van Duijn, & Lyon, *submitted*).

Motile behavior at the scale of multicellular organisms is predominantly muscle-driven. To generate the coordinations of a multicellular body enabling muscle-based locomotion strategies such as hydrostatic propulsion, head-tail undulations, or locomotor limb movements, nervous systems are a necessity. The metabolic turnover for nerve tissue is high: energy consumption levels per unit of mass are almost an order of magnitude greater than most other tissues (Isler & van Schaik, 2006). The high metabolic costs of the nervous system are balanced out by important adaptive benefits. Nervous systems and sensory systems are subject to strong selective pressures that on the one hand minimize energy costs while on the other hand maximize reliable sensory information and robust adaptive behavior (Niven & Laughlin, 2008). These costs/benefit trade-offs play a key role in directing evolution. For example, the dramatic encephalization in the evolution of primates raised metabolic turnover even further. These costs needed to be compensated for by a smaller digestive system (Aiello & Wheeler, 1995), and more energy-rich diets (Snodgrass, Leonard & Robertson, 2009). The benefits of encephalization come in increased reproductive life-span, which is due to cognitive benefits such as more complex foraging skills and social cognition (Allman, 1999; Barrickman, Bastian, Isler & van Schaik, 2008). While modern nervous systems have various functions, such as housekeeping functions and sustaining higher cognitive functions, it is also evident that enabling an organism to move and to manipulate its environment in specific ways is the prime reason for the huge investment in these metabolically expensive organs (Allman, 1999). According to this explication,

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[51] Reynolds number is the ratio of inertial forces and viscous forces. At low Reynolds numbers, such as is the case at the scale of bacteria where Re is about 10^{-6}, viscous forces are dominant, whereas at high Reynolds numbers inertial forces become increasingly more dominant; for example, at the level of large whales the Reynolds number is 10^8 (Vogel, 2008). This has important consequences for the kinds of locomotion strategies that are effective at different scales of biological organization. Whereas fish and aquatic mammals have to deal with and make use of inertia and turbulence, which allows them to glide through the water, bacteria and larvae instead have to cope with the strong effects of the viscous forces of fluids, so that when cilliar or flagellar movements stop the organisms come to an immediate halt (e.g. Brusca & Brusca, 2003, p.49; Valentine, 2004, pp.71-72; see Garstecki & Cieplak, 2009, for a recent special issue on the physics of swimming at low Reynolds numbers).

however, motility is a necessary but not a sufficient condition for biocognition; sensorimotor coordination is another key ingredient for biocognition.

(2) Sensorimotor coordination (SMC) is the process by which organisms actively coordinate their sensors and effectors to modulate and optimize the external conditions for their metabolism. SMC is exhibited by most free-moving[52] organisms. Through SMC, organisms can reduce the complexity of their input space (Pfeifer & Scheier, 1999). That is, by performing motor actions organisms partially determine the sensory changes they perceive; movement induces law-like patterns in sensory stimulation (Nolfi & Parisi, 1999). SMC is about detecting and making use of systematic invariances between sensory events and motor actions to achieve adaptive goals (see also chapter 1). The relation between biocognition, motility, and SMC is not a straightforward one. Not all motile behaviors involve SMC. For example, swimming scallops such as *Aequipecten opercularis* display a non-oriented motile escape response, using a type of jet-propulsion, which enables them to rapidly flee from predators such as starfish (Schmidt, Philipp & Abele, 2008; see Brand, 2006 for a detailed discussion). Although these predominantly sessile organisms do display a form of motility, this particular swimming behavior is not based on sensorimotor coordination. It is a non-oriented motor response that allows the scallop to escape in a randomly determined direction; this behaviors lacks an external perception-action coupling.

So what does SMC add to motility? SMC allows motile organisms to orient and fine-tune their motile behavior using sensorimotor feedback. More specifically, SMC allows biocognitive organisms to make use of the exteroceptive (e.g. visual, chemical) and interoceptive (e.g. proprioceptive, kinesthetic) sensory feedback that is elicited by their own sensorimotor behavior. SMC allows these organisms to optimize the search for more favorable environmental conditions, to search for food, to hunt and to capture prey. In chapter 2 we have seen that chemotaxis in the *E. coli* bacterium provides a good starting point for understanding minimal (bio)cognition. By combining motility with SMC, bacteria can engage in a hill-climbing strategy to ultimately achieve positive net migration towards the attractant and away from repellents. Bacteria are capable of many different kinds of taxis and other sensorimotor behaviors, all of which help to optimize the external circumstances for their metabolism and to promote their reproductive opportunities.

SMC is also the bedrock of human cognition. In humans, basic sensorimotor behaviors are the stepping-stone for developing higher cognitive functions such as category learning, having a Theory of Mind, imitation, and language. The importance of SMC in human cognition is emphasized in a variety of research fields. For example, research in developmental psychology shows that human infants learn to distinguish categories by ac-

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[52] According to this explication, SMC is a necessary but not a sufficient condition for biocognition. Sessile organisms capable of SMC therefore do not qualify as biocognitive organisms. In section 5.3, I elaborate on this issue by discussing the possibility of plant-cognition.

tively manipulating objects in their environment, which shows that environmental feedback induced by SMC's plays a crucial role in human category learning (Thelen & Smith, 1994). According to Pfeifer and Scheier (1999) anything we learn is grounded in SMC. SMC is necessary for developing higher cognitive processes such as depth perception, object classification, and object recognition (Nolfi & Parisi, 1999; Nolfi & Marocco, 2002; Pfeiffer *et al*, 2006; Kassahun, Edgington, de Gea & Kirchner, 2007). Research also shows that off-line cognitive abilities are grounded in SMC, such as imagination (Carson & Kelso, 2004; Oullier, Jantzen, Steinberg & Kelso, 2005), object recognition, (Nolfi & Parisi, 1999), learning by imitation and having a Theory of Mind (Gallese & Goldman, 1998; Keysers & Gazzola, 2007; Rizzolatti & Craighero, 2004), categorization (Thelen & Smith, 1994; Pfeifer & Scheier, 1999), working memory, episodic memory, and implicit memory (Wilson, 2002), and conscious will (Kelso, 1995; see also chapter 4).

(3) Biocognitive systems are equipped with an internal sensor/effector signal-transduction mechanism, which provides a direct and modifiable internal coupling between sensors and effectors that allows organisms to rapidly and flexibly respond to environmental stimuli with coordinated sensorimotor actions. For single celled organisms, sensor/effector mechanisms come in the form of molecular signaling mechanisms such as TCST and membrane ion-channels. Most bacteria possess an array of TCST systems, which are involved in many functions including gene-transcription, enzyme regulation, and cell division, but also motor regulation enabling taxis (Bourret, Charon, Stock & West, 2002; Falke, Bass, Butler, Chervitz & Danielson, 1997). Single-celled eukaryotes use an ion-based signal-transduction system to guide their actions. For example, *Paramecium caudatum* uses a sensor/effector signal-transduction mechanism involving the ion-channels in its membrane, which work much like an intercom system to allow a concomitant response of the cilia, i.e. an array of thousands of hair-like structures which are dispersed all across its surface. *Paramecium* uses its cilia for different kinds of taxis, such as thigmotaxis, which is based on a touch-induced response to mechanical stimuli (van Houten, 1992; van Houten, Martel & Kasch, 1982; see Figure, 8).

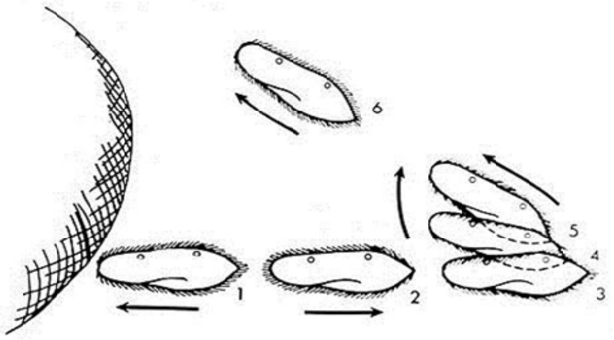

Figure 8. Thigmokinesis in *Paramecium caudatum* (adapted from Jennings, 1899)

Paramecium performs thigmotaxis by switching between two behavioral modes, the power stroke, which propels it forward, and the recovery stroke, which causes it to reverse its swimming direction. (Brusca & Brusca, 2002). When *Paramecium*'s front end bumps into a solid object while engaging in the power stroke it results in a rapid influx of Ca^{2+}, which causes a transient membrane depolarization yielding a behavioral switch to the recovery stroke; this allows the organism to back-away from the obstacle (van Houten, 1982). When soon after Ca^{2+} levels drop beyond a certain threshold, *Paramecium* again switches to the power stroke, moving forward slightly offset from its previous trajectory (van Houten, 1982; Kung & Saimi, 1982). By repeating this behavioral strategy *Paramecium* is capable of dodging obstacles in its environment. *Paramecium* is capable of many different kinds of kinesis (non-oriented responses), and taxis (oriented-responses), and even conditional learning[53]; its behavior reaches the complexity limits of single-celled organisms (Van Houten, 1992; Van Houten, Martel, & Kasch, 1982).

At the level of Metazoa, i.e. multicellular eukaryotes built up out of specialized cells and tissues, sensor/effector signal-transduction mechanisms come in the form of acetylcholine/cholinesterase-based nervous systems and centralized brains. Nervous systems allow multicellular bodies to function as giant effectors enabling the generation of locomotion strategies such as different kinds of tail-to-head body undulations and muscle contractions. Little is known about the evolutionary origin of nervous systems; however, the coupling of the nervous system with exteroceptive sensors must have been a watershed in the evolution of the nervous systems (Ghysen, 2003). The coupling of sensing mechanisms such as ocelli, statocysts, and chemoreceptors with the activity of the nervous system enabled these organisms to respond to an increased variety of environmental stimuli with coordinated sensorimotor behaviors. As Brusca & Brusca (2002) put it: "The activities of receptor units represent the initial step in the usual functioning of the nervous system; they are a critical link between the organism and its surroundings. Consequently, the kinds of sense organs present and their placement on the body are intimately related to the overall complexity, mode of life and general bauplan of any animal" (p.78). In the next section, I discuss the sink-fishing behavior of the jellyfish *Aglantha digitale* as an evident example of biocognition that is sustained by a primitive nervous system.

5.2.4 Primitive Nervous Systems: the case of Aglantha digitale

The jellyfish *Aglantha digitale* is a small (about 1-2 cm) thimble-shaped hydromedusa, has a distributed nerve net that consists of two marginal nerve rings that generate oscillating

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[53] Conditional learning in *Paramecium* has been reported (e.g. Jensen, 1957; Katz & Deterline, 1958; Hennessey, Rucker & McDiarmid, 1979), but is also disputed (e.g. Hinkle & Wood, 1994; Machemer, 2001). However, recent evidence does unequivocally show that *Paramecium* is capable of conditional learning (brightness discrimination) based on positive reinforcement (see Armus, Montgomery, & Jellison (2006) for historical overview and empirical evidence).

patterns, which cause the semi-arched subumbrellar muscle sheet inside the margin of the bell to rhythmically contract and expand, forcing water out of the bell so as to provide a kind of jet propulsion (Mackie, 2004). *A. digitale* exhibits two behavioral modes: a slow cyclical sink-fishing behavior, and a fast escape response to mechanical or electrical stimuli. The cyclical sink-fishing behavior involves three phases (Figure 9). During the first phase, which lasts for about 2 minutes, *A. digitale* slowly sinks with the apex of the bell leading, and with its 80 or so tentacles extended to capture small planktonic organisms (Mackie, Marx & Meech, 2003). Prey that gets caught in the tentacles is stunned by discharge of stinging cells, nematocytes. Whenever *A. digitale* captures prey, swimming is temporarily inhibited while the tentacle(s) involved shortens and brings the prey to the margin of the bell near the manubrium; a flexible tubular structure with at its tip a mouth-like orifice with 4 protruding lips (Mackie, 2004). The flexible manubrium then probes and flexes toward the prey to seize and to engulf it (Mackie, Marx & Meech, 2003). In the second phase, slow swimming behavior ensues. During this phase, the tentacles shorten and curl inward (Mackie, 1980). *A. digitale* then reorients its bell into an upright position by asymmetrical bell contractions. Upright orientation is controlled by eight gravity receptors, "statocysts", which are symmetrically arranged around the margin of the bell; *A. digitale* lacks ocelli or other visual receptors (Mackie, 2004). Next, the jellyfish slowly swims upward for a minute or so guided by the input of its statocysts until it reaches a position close to the start of the previous cycle, after which swimming behavior ceases and the tentacles become extended again. Finally, *A. digitale* slowly turns over its bell and starts to sink again, reinitializing the behavioral cycle (Mackie, 1980).

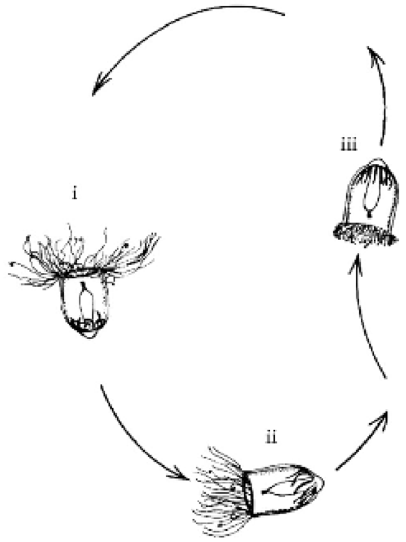

Figure 9. Cyclical sink-fishing behavior of *Aglantha digitale* (from Mackie, 1980).

A fast escape response overrides the sink-fishing behavior in case the hair cells on its tentacles or on the bell margin are deflected either by touch, electrical impulses, or water currents. In the escape modus, *A. digitale* displays one to three forceful rhythmic contractions of its subumbrellar muclesheet, which is made up out of myoepithelium cells (Mackie, 2004). These muscular contractions generate much more torque than those exhibited in the sink-fishing modus: a single contraction propels it by about seven body lengths, whereas in slow swimming a single contraction propels it about one body length (Mackie & Meech, 1995b). The escape response is induced by touch or electrical stimuli and is accompanied by rapid contraction of its tentacles to reduce drag (Mackie, 1980).

The sink fishing behavior and the escape response are controlled by different neuronal circuits, although there is also a substantial degree of overlap (Mackie, 2004). The slow swimming contractions required for sink-fishing behavior are generated by the rhythmic activity of "pacemaker" neurons in the inner marginal nerve ring (Mackie & Meech, 2000). The pacemaker neurons excite eight motor giant axons, which synapse with the subumbrellar myoepithelium, yielding low-amplitude Ca^{2+}-based excitatory action potentials that produce slow rhythmic muscle contractions at about 0.5 Hz (Mackie, 1980; Roberts & Mackie, 1980; Mackie & Meech, 1995a). The fast escape response is mediated by a single "ring giant axon" that runs round the margin of the bell in the outer nerve ring (Roberts & Mackie, 1980; Mackie & Meech, 1995b). The ring giant receives sensory input from ciliated mechanoreceptors located on the tentacle bases and on the bell margin (Mackie & Meech, 1995b). Like the pacemaker neurons the ring giant axon also excites the eight motor giant axons but instead elicits a much larger Na^{+}-dependent excitatory post synaptic potential that is more rapidly conducted, i.e. by about an order of magnitude, to the subumbrellar myoepithelium. These Na^{+}-dependent potentials cause violent but rhythmic contractions of the bell and tentacles during the escape response (Mackie & Meech, 1995a; Mackie & Meech, 2000). According to Mackie (2004, p.8), the ring giant axon is unparalleled in featuring this kind of double innervation; its ability to conduct two kinds of action potentials is unique in the animal kingdom. *Aglantha digitale*'s distributed nerve net is one of the most complex found among Cnidarians: a total of fourteen signal transduction pathways concerned with behaviors such as locomotion, feeding, and tentacle contraction have been identified (see Mackie & Meech, 2000, p.1806, for an overview).

5.3 Evaluation: Successes and Problems

Our explicatum of biocognition successfully classifies evident examples such as *E. coli* and *A. digitale*, and excludes non-examples such as the lac operon system in *E. coli* (see chapter 2), and non-examples such as the non-oriented motile response of scallops. The conditions of adequacy for our explication of biocognition exclude sessile organisms such as plants. A bona fide example of 'plant cognition' would provide a violation of the conditions of adequacy of our explication and would therefore show the explication is too narrow. In this section, I evaluate the plausibility of plant cognition.

Although plants are sessile and rooted in soil, they are capable of many complex adaptive behaviors. Darwin (1880) already distinguished between different kinds of tropisms - oriented growth towards or away from stimuli - such as geotropism and heliotropism, and nastic movements - rapid (ir)reversible movements independent of stimulus direction. Recent research in plant behavior is booming and shows that plants are capable of communication (Karban, 2008), active defense responses against predators (Dicke, 2009), memory (Galis, Gaquerel, Pandey & Baldwin, 2009), self-recognition in plant roots (Hodge, 2009), cooperation (Kelly, Bowler, Pybus & Harvey, 2008), niche construction (e.g. symbiosis) (Badri & Vivanco, 2009), and learning (Trewavas, 2003; 2009).

5.3.1 'Plant Cognition': A Counter Example?

Recently, a small minority of researchers has argued in favor of plant cognition and plant intelligence (e.g. Baluška & Mancuso, 2009; Calvo & Keijzer, 2009, 2011; Calvo, 2007; Trewavas, 2003; 2005; 2009). Calvo (2007; p.210) uses the sun-tracking behavior by the leaves of the plant *Lavatera cretica* as an example of cognition in plants. During day-time, *Lavatera* orients its leaves towards the sun so that they come to face it perpendicularly, and tracks it across the sky so as to maximize photosynthesis (Schwartz & Koller, 1978; Schwartz & Koller, 1986). The photoreceptors located in the veins of the leaves are sensitive to both solar azimuth and solar elevation, which enables vectorial light detection (Koller, 2001). The photoreceptors sense the slightest asymmetries in light-shadow patterns on their ventral surface caused by oblique illumination (see Koller, Ritter, Briggs & Schäfer, 1990). The signals from the photoreceptors are carried through a complex vascular system to the pulvinus; a central joint structure and flexible hinge point located the junction of the base of the leaves and the petiole (for details see Fisher, Ehret & Hollingdale, 1987). *Lavatera* orients its leaves towards the sun by flexing the pulvinus by regulating asymmetrical turgor adjustments, a mechanism that is common in plants (Koller, 1990). Turgor changes are caused by asymmetrical volume changes in large motor cells in the pulvinus, which occur as a result of changes in osmotic pressure; this causes the motor cells to either take up water and to expand, or to discard water and to contract (Fisher & Fisher, 1983). The non-uniform swelling of the motor cells in the pulvinus causes the plant tissue to warp in such a way that it bends its leaves towards the sun so that the surface of the lamina becomes orthogonal to the light source (Fisher & Fisher, 1983; Koller, Ritter, Briggs, & Schäfer, 1990).

At night, *Lavatera* exhibits a three-phased reorientation behavior (Schwartz & Koller, 1985). Right after sunset, when all leaves are facing west, the uneven osmotic pressure in the pulvinus dissipates due to the plant's metabolic activity, which slowly equalizes the turgor in the motor cells allowing the leaves to return to a neural state. This second 'neutral' state lasts for most of the night. Finally, one/two hours before dawn, the lamina start tilting toward the east as if they anticipate the direction of the next sunrise (ibid.). Fisher and Fisher (1983) hypothesized that the early morning tilting behavior in *Lavatera* is induced by what they call "starch memory"; a kind of structural memory that is due to asymmetrical starch deposit (sugar deposits) patterns caused by uneven distribution patterns in early morning photosynthetic activity. Right after sunrise, there is a short 'tuning' period, which minimizes the discrepancies between the tilt angle of the leaves and the actual angle of the sun, so that the leaves again come to face the light orthogonally. The early morning discrepancies between the angle of the tilted position and angle of the sun creates a non-uniform distribution of starch deposits; these asymmetrical starch deposits only become a factor of influence during the next morning (*Ibid*.). As Fisher and Fisher (1983) explain:

> *After the onset of darkness, any asymmetries in starch deposits may be expected to persist until all evenly distributed starch pools have been converted to sugar. The situation is somewhat analogous to a sheet of ice, melting from below, with raised lumps on its surface. Most of the night, starch conversion is occupied with the general pool: not until just before dawn do the residual, asymmetrical islands of starch, formed during the previous tuning periods, begin to undergo conversion, constituting the commencement of 'recall'. At that point, the general pool being eliminated, only the asymmetrical islands remain. Not until then can these produce corresponding asymmetrical sugar-flows, repeating the flows that constituted the previous morning's tuning signal. This gives the appearance of sunrise anticipation (p.534).*

Experiments with *Lavatera* show that plants that have intentionally been kept in the dark display the nocturnal tilting behavior only for a couple of days (three to four subsequent sunrises), after which it progressively dissipates (Schwartz & Koller, 1985). When these plants are once again put in normal daylight, it takes a day or two before nocturnal tilting behavior again initiates (Koller, 1990). Artificial modulation of light direction shows that the nocturnal orientation behavior is also subject to inertia, as Koller (2001) plains: "Laminar reorientation reverses its direction after the direction of vectorial excitation is reversed, but exhibits the inertial after-effects of the preceding excitation" (p. 868). Although it seems clear that the nocturnal tilting behavior of the leaves of *Lavatera* is an after-effect of vectorial excitation, it should be noted that not all the mechanisms that underlie this nocturnal reorientation behavior are fully understood (see Koller, Ritter, Briggs & Schäfer, 1990; Koller, 2001, for a more in depth discussion).

The periodicity of the leaf movements are autonomous movements regulated by the plant's endogenous circadian rhythm. The circadian rhythm is generated by a genetic oscillator mechanism, which governs the circadian control of gene transcription and post-transcription, although in detail the complexities of these mechanisms are still poorly understood (McClung, 2006). The circadian rhythm yields a form of rhythmic phenotypic plasticity which regulates phase transitions and time measurement in the plant's diurnal and nocturnal movements. For example, in the second nocturnal phase, the duration of the neutral state is timed by the circadian rhythm of the plant (Schwartz & Koller, 1985). The circadian rhythm is entrained by environmental cues ('zeitgebern'), such as sunlight, although it is only periodically sensitive to these environmental cues. This kind of "circadian gating" periodically alters the influences of the receptors on the entrainment of the circadian rhythm (McClung, 2006). The circadian rhythm is independent of light direction, but contingent on external control parameters such as temperature, light intensity, and CO_2 levels (Koller, 2001; Raven, Evert & Einhorn, 1999; Lüttge, 2002).

Calvo (2007) argues that the behaviors of *Lavatera cretica* provide a nice example of plant cognition. Calvo suggests that *Lavatera* generates an off-line internal cognitive representation of the sun's position in the sky similar to the way in which humans might have a mental representation of an object that is temporary out of sight[54]. However, there are serious objections to the view that the sun-tracking behaviors by the leaves of the plant *Lavatera cretica* are governed by an internal, off-line representation of the sun. A plausible explanation of the behavior of *Lavatera cretica* need not involve a cognitive mechanism. An alternative, simpler explanation is that this behavior is the result of the self-organized interplay between two basic adaptive mechanisms, one for leaf orientation and one for periodicity. Sun tracking is an on-line adaptive process that involves leaf orientation. The nocturnal tilting behavior of the leaves is under exogenous control and determined by the plant's recent solar-tracking history; it is the direction of the previous sunrise(s) that influences the early morning tilting direction (Schwartz & Koller, 1986). The circadian rhythm is an endogenous timing mechanism that governs the plants periodicity; it does not need to generate an off-line model of the sun's position in the sky. The endogenously generated circadian rhythm does not correspond exactly to the 24 hour day-night cycle, but it can be entrained to synchronize with it. The circadian rhythm is periodically entrained by environmental cues, and that it is governed by external control parameters such as temperature and light intensity (McClung, 2006, Lüttge, 2002). Organisms generate many such rhythms, be it on shorter time scales, such as breathing, or on longer timescales, such as hibernation (LeSauter & Silver, 1998). In plants, circadian rhythms are part and parcel of the basic adaptive processes that yield periodic phenotypic plasticity; as McClung (2006) puts it: "leaf movement rhythm was only one among many rhythms that included germination, growth, enzyme activity, stomatal movement and gas exchange, photosynthetic activity, flower opening, and fragrance emission" (p.794). In sum, a plausible explanation of the behavior of *Lavatera* can be given entirely in terms of phenotypic plasticity rather than in cognitive terms. Neither of these two mechanisms, orientation and periodicity, requires

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[54] According to Calvo (2007), off-line representation is a necessary and sufient condition for cognition. As Calvo himself frames it: "Do plants compute? The blunt answer is "yes". Plants compute insofar as they manipulate representational states. The *sine qua non* of representation-based competency is off-line adaptive behavior. Reactive behavior differs from truly cognitive one because it fails to meet the principle of dissociation (the states of a reactive system covary continuously with external states). Off-line competencies thus mark the borderline between reactive, noncognitive, cases of covariation and the cognitive case of intentional systems"(p.210).

the postulation of complex and ‘expensive’ off-line cognitive representations or other cognitive processes; it is rather the self-organized interaction between the on-line orientation mechanisms and the endogenous circadian timing mechanism that accounts for the behavior of *Lavatera*. It therefore seems best to apply Ockham’s razor to the idea of plant cognition in *Lavatera*.

5.3.2 Objections to Plant Cognition in General

When viewed from an anthropocentric perspective it is tempting to use such notions as ‘cognition’, ‘memory’, ‘anticipation’, and ‘intelligence’ when describing these complex adaptive plant behaviors. Struik, Yin and Meink (2008) point out that Trewavas, one of the main promoters of ‘plant intelligence’ and ‘plant cognition’, uses definitions of plant intelligence that are centered on such notions as problem solving and decision-making; e.g. “Intelligent behaviour is an aspect of complex adaptive behaviour that provides a capacity for problem solving”, and, “An intrinsic ability to process information from both abiotic and biotic stimuli that allows optimal decisions about future activities in a given environment” (p.366). However, most scientists are wary of using such anthropocentic laden terms in the context of plant behavior. For example, plants exhibit a form of epigenetic adaptation known as “chromatin marking” (see section 3.5.1). Chromatin marking patterns constitute a kind of structural chromosomal memory that governs the context-dependent modification of genetic expression of eukaryotic cells. Given that chromatin marks in plants can persist over the course of generations, some authors ascribe long-term memory to plants (e.g. Trewavas, 2009, pp.610-611). However, chromatin marking can be considered as ‘long-term memory’ only in a very loose, unspecific sense of the word. The chromatin marking patterns that cause lasting changes in gene-expression constitute a form of cellular memory, while the neuronal mechanisms that support long-term memory in humans and other animals operate at a higher level of biological organization, involving the larger-scale interaction between vast numbers of neurons. Many authors are therefore much more reluctant to use the notion of ‘memory’, and rather talk about ‘priming’ or ‘stress imprint’ in the context of epigenetic marks in plants (e.g. Bruce, Matthes, Napier & Pickett, 2007).

The recent surge of interest in plant cognition is partially due to the emergence of a new and controversial research field called “plant neurobiology” (e.g. Brenner *et al*., 2006). According to researchers in this field, plants are capable of processing, integrating, and transforming complex environmental and endogenous sensory signals and to convert these into adaptive actions using long-distance signaling mechanisms, such as auxin (a plant hormone) transport, which allegedly bears a close resemblance to neuron- and synapse-like functions (Baluška & Mancuso, 2009). However, critics to plant neurobiology point out that some of its central assumptions are based on superficial analogies with brain functioning, and by ascribing brain-like characteristics to plant signaling mechanisms (see for a critical assessment of plant neurobiology: Alpi *et al.*, 2007, Barlow, 2008; Struik *et al.*, 2008). Alpi *et al.*, (2007) claim that although there are important parallels to be drawn between the physiology of plants and animals on the molecular level, i.e. plants make use of action potentials, voltage-gated ion channels, and neurotransmitter-like substances, these parallels do not hold at the cellular, organ, and behavioral level.

In their critique of plant neuro-biology, Struik *et al.* (2008) argue that a bona fide scientific explanation of behavior needs to abide to the principle of parsimony, which favors the simplest possible explanation for scientific phenomena with the least amount of assumptions. In animal psychology, the parsimony principle is famously expressed by Morgan's Canon (1906), which is a rule about making inferences on the complexities of animal behavior: "In no case may we interpret an action as the outcome of the excercise of a higher psychological faculty, if it can be interpreted as the outcome of the excercise of one which stands lower in the psychological scale" (p.53). In lieu of Morgan's Canon, this explication helps to elucidate the differences between basic adaptive behaviors such as exhibited by plants and bona fide biocognition. The conditions of adequacy of this explication of biocognition can be used as guidelines to judge whether or not certain organismal behaviors are genuinely biocognitive or involve other adaptive behaviors. If an explanation of plant behavior can be given in terms of basic forms of adaptation, it should have precedence over an explanation in biocognitive terms.

There is no question that plants are highly adaptive organisms capable of rather sophisticated forms of information-processing (Baluška & Mancuso, 2009; Trewavas, 2009). We have seen that multicellular plants such as *Lavatera* are capable of complex adaptive responses such as solar-tracking that is sustained by a rather complex signal-transduction system. Some plants have elaborate chemical defenses against predators such as caterpillars by releasing anti-herbivore toxins and volatile pheromones to warn neighboring plants in response to predation. Carnivorous plants such as the Venus flytrap (*Dionaea muscipula*) even exhibit a short-term memory response with a decay time of roughly 40 seconds, which prevents its trap from closing in case of false alarms (see Barlow, 2008). Given the sheer diversity and complexity of plant behavior, should plants perhaps be considered as (minimal) biocognitive agents in their own right, despite the fact that they are sessile organisms?

One good reason to exclude plants from the biocognitive domain has to do with the principle of parsimony: Plant behavior can be fully explained and accounted for by other adaptive mechanisms such as phenotypic plasticity, which is the ability of an organism to alter its physiological and morphological characteristics in response to changing environmental conditions (Schlichting, 1986). Due to phenotypic plasticity, genetically identical plants can exhibit a wide range of phenotypes. Phenotypic plasticity allows plant growth patterns and plant morphogenesis to flexibly respond to and anticipate changes in environmental conditions. Phenotypic plasticity in plants includes mechanisms that underlie differential turgor changes, sun-tracking behaviors, nastic responses, tropisms (such as the explorative behavior of plant roots), and epigenetic mechanisms. These responses all involve alterations in biochemical-physiological processes; processes that are part and parcel of metabolism. According to Hans Jonas (1966), who tried to articulate the differences between plant and animal behavior, this is exactly what distinguishes plant behavior from animal behavior:

> *The typical plant activity is part of the metabolic process. In the motions of animals, on the other hand, we have activity made possible by the surpluss from previous metabolism and directed toward safeguarding its future, but itself a free expenditure dissociated from the continuing vegetative activity and thus action in a radically new sense. It is external action superimposed on the internal action of the vegetative system and parasitic on it: only its results are destined to benefit those functions. This mediacy of vital action by external motion is the distinguishing mark of animality* (p.104).

With respect to phenotypic plasticity and other metabolism-based processes, biocognitive strategies are higher order control processes. For example, bacterial taxis behaviors are not part of changes in growth patterns and morphogenesis (although these behaviors are of course dependent on their outcome), but rather constitute a higher order adaptive strategy that enables these free-moving organisms to explore their environment using their metabolism as a basis for their normativity. In contrast to plants, biocognitive organisms are equipped with a dedicated sensorimotor organization that enables different forms of oriented locomotion. As a consequence, biocognitive organisms do not need to rely on phenotypic plasticity as much as plants do.

5.3.3 Upshot: Size as a Control Parameter

Multicellular plants do not satisfy all the conditions of adequacy for biocognition as they lack the ability to move about in their environment as a coordinated whole. However, when applying the conditions of adequacy for biocognition to plant behavior in general, the idea of 'plant cognition' is not entirely excluded. Single-celled plant-like organisms might just qualify as minimal biocognitive agents. Motile plant-like protists, i.e. single-celled eukaryotes, the zoospores of green algae (see Corner, 1964, p.16-19), zooplankton, and also the gametes of land plants such as fern spermatozoids do satisfy the conditions of adequacy for biocognition: they are motile, capable of sensorimotor coordination, and also possess a sensor/effector signal-transduction mechanism. In some taxonomic schemes protists are classified under the kingdom of Plantae[55]. Like motile bacteria, fern spermatozo-

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[55] Although it has been established that green algae and land plants are closely related, i.e. plants have evolved from green algae (Raven, Evert & Einhorn, 1999), it is a long standing debate among taxonomists whether green algae (Chlorophyta) qualify as plants or not. Since the taxonomy of Ernst Haeckel green algae were usually classified under the kingdom of Protista (Brusca & Brusca, 2002); however, this classification is outdated because of the sheer diversity among protists. In modern taxonomies green algae are sometimes placed among the kingdom of Plantae or Viridiplantae (e.g. Raven *et al.*, 1999; Bell & Hemsley, 2000) or included in the kingdom of

ids use a form of chemotaxis using cilia and sensing mechanisms (Brokaw, 1957). Green algae such as *Chlamydomonas reinhardtii* come equipped with an 'eye-spot' containing rhodopsin photoreceptors that command, through an ion-based intracellular sensor/effector signal transduction mechanism, their two or so flagella (Sineshchekov, Jung, & Sineshchekov, 2002; Kateriya, Nagel, Bamberg, Hegemann, 2004). There are several advantages for motile over nonmotile species of protists. For example, motile green algae can actively regulate their buoyancy and also periodically migrate to deeper more nutrient waters (Olli, 1999). For planktonic protists, the costs of motility are a function of size and swimming speed (see Crawford, 1992, for a review). If one would count zoospores of green algae and fern spermatozoids as plants, then these behaviors are indeed bona fide examples of plant cognition. This of course begs the question: if biocognition is possible at the level of single celled eukaryotes, then why not at the level of multicellular plants?

The answer is that the range and diversity of adaptive responses in multicellular plants is severely limited due to their sheer size. Size is a key factor in determining the costs and benefits for motility. As Mitchell (2002) put it:

> *Body size is an essential phenotypic character for describing the evolution of life-history strategies, biomechanical limitations, and allometry in a variety of physiological and ecological processes. For example, body size sets the biomechanical and hence energetic limits for movement. These size-imposed limits are important for determining which locomotory methods are practical, the maximum attainable speed, and the duration over which motion can be maintained. These attributes, in turn, help determine the strategies for predator attack, prey defense, and searching for food. (p.727)*

According to Dusenbury (1997), there is a sharp size limit of about 0.6µm, below which motility is not a beneficial strategy for organisms; the smallest motile bacteria are about 0.8µm. We have seen that the metabolic costs of motility are already significant for single-celled organisms. For example, motile green algae have a reduced capacity for photosynthesis and higher respiration rates (Striebel *et al.*, 2009). To generate the large-scale coordinations of a multicellular body enabling basic locomotion strategies, nervous systems are a necessity. However, as discussed earlier, the energetic costs for nervous systems are gargantuan. The metabolic turnover for nerve tissue is high: energy consumption levels per unit of mass are almost an order of magnitude greater than most other tissues (Isler & van Schaik, 2006). At the level of multicellular organisms, the metabolic costs for sustaining a motile lifestyle increase allometrically, that is, the bigger the organism the higher its metabolic costs (Mitchell, 2002). Motility at the multicellular level also demands other specialized tissues such as muscles dedicated to pattern generation, and support structures such as a hydrostatic skeleton or a rigid exo- or endoskeleton (Brusca & Brusca, 2002). A

Protoctista (see Margulis & Chapman, 2009); in the latter classification green algae are distinguished from plants.

dedicated sensorimotor organization for locomotion in multicelluar plants would simply be too costly for their metabolism.

Throughout the course of evolution, multicellular plants have come to occupy and thrive in ecological niches where motility is not required to survive and procreate. Sessile organisms such as multicellular plants took another evolutionary route by opting for an autotrophic56 lifestyle by relying on photosynthesis, so that motility became an unnecessary survival strategy for these organisms. According to Bell and Hemsley (2000), motility played an important role early in the history of plant evolution, however, motile lifestyles where soon abandoned for sedentary lifestyles. In modern times, only primitive plants such as ferns use chemotaxis in their spermatozoid form, but modern plants have also abandoned this form of motility. Multicellular plants simply got too large to sustain a motile lifestyle. Multicellular plants rely on a sessile life strategy which involves growing roots, making use of photosynthesis, growing flowers, and engaging in symbiotic relations with other organisms such as bacteria and insects. Being unable to flee from their predators, plants use deterrents such as toxins and spines (Silvertown & Charlesworth, 2001). For the dispersal of their genetic material plants produce seed and pollen, which are randomly dispersed by wind, water, and insects. Plants are also capable of modifying their niches for the benefit of their own needs, such as by modifying their growth structure to optimize exposure to sunlight. For their sessile lifestyle plants rely mostly on phenotypic plasticity. For multicellular plants the benefits of their sessile lifestyle outweigh the risks and the metabolic costs of motility.

The intricacies of plant behavior usually take place on much slower timescales than the behavior of animals, with notable exceptions such as *Mimosa pudica* (also known in Dutch as “kruidje-roer-me-niet”) and *Dionaea muscipula* or the Venus flytrap, both of which exhibit fast - in the range of ms – touch-induced, non-oriented response called “thigmonasty” (Struik, Yin & Meinke, 2008). This suggests that not only size, but also time plays a crucial role in biocognition. According to this view, it is not a coincidence that plant behaviors are generally much slower than those exhibited by motile organisms. Already at the level of single-celled organisms fast sensorimotor actions confer important adaptive advantages; as Alexandre, Greer-Phillips & Zhulin (2004) argue:

> *Microbial taxis is dependent on the presence of the cellular sensory machinery that transmits information from the environment to the motility apparatus. The processing time in bacterial taxis is incredibly fast. A change in the direction of flagellar rotation resulting in the change of swimming direction occurs in less than a second upon binding of a chemical stimulus to the receptor on the cell surface, which is considerably faster than the time frame required for initiation of gene expression. Thus, taxis can be considered as an immediate survival strategy (p.114).*

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[56] Note that biocognition is not simply a matter of being heterotrophic. Fungi are also heterotrophs, but these are predominantly sessile organisms.

Fast forms of coordinated locomotion must have been an important driving force in the evolution of biocognition that fueled the evolutionary arms race between motile species. Fast coordinated behaviors conferred strong selective advantages, by allowing these organisms to rapidly flee from predators and to catch fast moving prey. These predator–prey cycles have facilitated the evolution of novel sensorimotor systems (e.g. Parker, 2003). Throughout evolution, the spatio-temporal coordination of motility served as the cornerstone of an edifice that allowed for the generation of increasingly more advanced biocognitive behaviors.

5.4 General Desiderata: *Precision*, *Fruitfulness* and *Simplicity*

Following Kuipers' (2007) methodology, it is now time to judge the explicatum in terms of three general desiderata: *precision*, *fruitfulness,* and *simplicity:*

1. *Precision*. This interpretation of biocognition provides a clear and sharp demarcation line between biocognitive systems and non-biocognitive systems such as multicellular plants. Biocognition is a classificatory concept; it excludes sessile organisms and motile organisms incapable of sensorimotor coordination. This clarity also makes the explication vulnerable, in particular at the lower bounds of biocognition. That is, it is an empirical possibility that among the great diversity in the behaviors of protists and plants there are certain behaviors that do not satisfy the conditions of adequacy for this explication but that do plausibly belong to the biocognitive domain. The history of biological taxonomy after all shows that it is difficult to draw sharp and definite boundaries between life forms and to group them based on certain shared characteristics. However, it is possible to adjust and fine-tune the conditions of adequacy of this explication further to include other plausible cases that are now excluded.

2. *Fruitfulness*. This explication highlights the importance of studying basic sensorimotor behaviors, such as can be found in motile bacteria and protists; a research area that is still largely neglected by cognitive scientists. The notion of biocognition provides a middle ground between two extreme ideas: it discards the classic dichotomy between instinct and cognition, but also sets a lower bound to biocognition by distinguishing it from other forms of biological adaptation such as can be found in plant behavior. This explication of biocognition also provides an alternative view on cognitive evolution, by showing that there are fundamental similarities between the basic motile behaviors of single-celled prokaryotes, single-celled eukaryotes, and those exhibited by organisms equipped with a nervous system. That is, these are all forms of motility that are rooted in sensorimotor coordination, and are therefore examples of convergent evolution. On this view, the evolution of nervous systems enabled large multicellular organisms to perform basic behavioral

strategies also common to unicellular organisms such as *E. coli*, only at a much larger scale (Keijzer, Franken, van Duijn & Lyon, *submitted*).

3. *Simplicity*. The approach taken by our explication of biocognition has some important advantages over other more general approaches to cognition, such as the dynamical systems approach and cognitivism, which use notions such as ‘dynamical coupling’, ‘information processing’ or ‘computation’ as defining features of cognition. A major drawback is that these notions are highly abstract and broadly applicable: they pertain to plants, humans, and thermostats alike. This results in a highly abstract functional approach to cognition that remains unspecific about the underlying structural mechanisms. By restricting the explication to biocognition, rather than to cognition in general (not distinguishing between biological and artificial cases), it is possible to obtain a simpler and more concretized characterization that uses biological organizational principles as constraints on the notion biocognition, which makes structural commitments regarding biological implementation; such as an embodiment equipped with a dedicated sensorimotor organization. The principle of parsimony favors the simplest explanation for scientific phenomena, with the least amount of assumptions. In line with this principle, this explication of biocognition allows for a better differentiation between biocognition and other adaptive processes, such as can be found in multicellular plants.

5.5 Conclusion

The term 'biocognition' refers to a specific form of adaptation exhibited by motile organisms capable of sensorimotor coordination. Biocognition requires a dedicated sensorimotor organization, which allows organisms to optimize the external circumstances for their metabolism through coordinated locomotion. More specifically, according to this explication of biocognition, biocognitive systems are by definition: (1) motile organisms, (2) capable of sensorimotor coordination, (3) which is mediated by an internal sensor/effector signal-transduction mechanism. The conditions of adequacy of this explication exclude the adaptive behaviors found in sessile organisms such as plants; behaviors that rely mostly on phenotypic plasticity. This explication of biocognition stresses that there are fundamental similarities between the basic motile behaviors of single-celled prokaryotes, single-celled eukaryotes, and those exhibited by organisms equipped with a nervous system. That is, all are rooted in a common mechanism: sensorimotor coordination. With the evolution of nervous systems and later on centralized brains, these basic behavioral strategies could be augmented and hierarchically expanded in ways unprecedented. The evolution of sensorimotor coordination provided the route to biocognitive complexity through predator–prey cycles, which induced the evolution of novel sensorimotor coordination strategies, yielding a biocognitive spectrum from prokaryotes to humans.

6. Conclusion

6.1 Synopsis

This dissertation develops a theory on biological cognition, or *biocognition*: The process by which motile organisms adaptively coordinate their sensors and effectors in order to optimize the external conditions for their metabolism. A central claim in this thesis is that sensorimotor coordination provides the phylogenetic basis for biocognition. Contrary to most well-known theoretical approaches to cognition, which presume that brains and nervous systems are necessary for natural forms of cognition, this dissertation shows that biocognition already applies to organisms without a brain or nervous system. In this thesis, I discuss bacterial chemotaxis as a form of sensorimotor coordination that provides a suitable example of *minimal cognition*, the most elementary form of biocognition. By detecting and moving along chemical gradients, bacteria such as *E. coli* are able to find an optimal physico-chemical environment to sustain their metabolic functions. Motile bacteria such as *E. coli* coordinate their sensory input with flagellar motor patterns using a two-component molecular signal transduction system (TCST), which provides these organisms with a memory that enables temporal comparison of environmental gradients to facilitate chemotaxis. Minimal cognition in bacteria makes a compelling case for the notion that the evolution of natural cognition did not coincide with the evolution of the brain, as is commonly presumed, and implicates that biocognition has phylogenetically ancient roots that reach deep into the prokaryotic domain.

Another central claim in this thesis is that sensorimotor coordination is the cornerstone of the vast spectrum of biocognitive abilities that can be found throughout the phylogenetic tree: from bacterial chemotaxis to human cognition. That is, bacterial chemotaxis and human cognition are first and foremost biological regulatory mechanisms that are variations on the same theme that has been reinvented and expanded upon many times throughout evolution: first at the level of prokaryotes, then at the level of unicellular eukaryotes, and finally, with the evolution of the nervous system at the level multicellular organisms. Sensorimotor coordination provides not only the phylogenetic basis of biocognition but also the ontogenetic basis for human cognition: category learning, imitation, language, and volition all depend on the development of increasingly sophisticated sensorimotor coordination abilities. From this perspective, emotions and consciousness are first and foremost biological functions that evolved to facilitate different forms of higher order, context-sensitive sensorimotor coordination. Bacterial cognition and human cognition make-up two opposite ends of a vast biocognitive spectrum with sensorimotor coordination as its common currency. This theory of biocognition grounds the growing consensus that the phylogenetic and ontogenetic basis of natural cognition lies in sensorimotor coordination, and provides a biogenic approach to cognition that merges cognitive science with biology.

6.2 Evaluation of the Thesis Goals

In the introduction of this dissertation three goals are stated; in the remainder of this section I provide a short overview of how the main findings in this thesis are related to these goals:

(1) – The first goal of this thesis is to specify the minimal requirements for the generation of natural cognitive behavior and to distinguish minimal cognition from other forms of biological adaptation, such as genetically-based adaptation and phenotypic plasticity. These issues are mainly dealt with in chapter 2 and also partly in chapter 5. In chapter 2, I discuss bacterial chemotaxis as an example of minimal cognition. By way of temporal comparison, bacteria such as *E. coli* are able to detect subtle changes in gradients of chemicals, and to travel up or down these gradients in order to reach food or to get out of harm's way. In bacteria such as *E. coli*, chemotaxis is achieved by periodically alternating running and tumbling behaviors. By altering the frequency of tumbling behaviors, the 3D random walk of the bacterium becomes biased in such a way that it exhibits net movement towards an optimal chemical environment. *E. coli*'s action-selection dynamics, its relative propensity to run or to tumble, is context-dependent: 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. Chemotaxis is a form of sensorimotor coordination that enables organisms such as bacteria to self-optimize the external conditions for the benefit of their metabolism; this process of minimal cognition provides the phylogenetic basis for biocognition.

So what distinguishes minimal cognition from other forms of adaptation, such as genetically based adaptation, phenotypic plasticity, and the metabolic reactions that govern life itself? An 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 abundant in the environment, the lac operon system becomes disinhibited, subsequently allowing the transcription and expression of genes that enable lactose metabolism. This form of metabolic adaptation is induced by environmental conditions, but is 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. With respect to the basic forms of metabolic/genetic adaptation such as can be found in *E. coli*'s lac operon system, chemotaxis is a second order process which is relevant for changing metabolic opportunities. While metabolic processes involve particular chemical reactions, sensorimotor coordinations play on a larger scale involving the adaptive modulation of the geometrical position of the organism in relation to its environmental resources and threats. The metabolic processes that sustain life itself are based in chemistry while biocognition is based in sensorimotor coordination, which optimizes the external conditions for metabolic processes.

In chapter 5, I distinguish biocognition from the other basic forms of biological adaptation that can be found in multicellular plants. While multicellular plants are capable of complex adaptive behaviors such as solar-tracking, information-processing, niche construction, they lack biocognition because of their inability to move about their environment using sensorimotor coordination. For their sessile, photosynthetic lifestyle plants rely mostly on phenotypic plasticity, which is the ability to alter their physiological and morphological characteristics in response to changing environmental conditions. For multicellular plants the benefits of their sessile lifestyle outweigh the risks and the high metabolic costs necessary for sustaining sensorimotor coordination, which, at least at the level of large multicellular organisms, requires a nervous system.

(2) – The second goal of this dissertation is to merge the embodied/embedded interpretation of cognition with a biogenic approach to cognition by looking at all the ways in which organisms adaptively use sensorimotor coordination. This issue comes to fore in most chapters: chapter 1 explains the theoretical motivations behind this approach. In contrast to the most theoretical approaches to cognition, the approach taken in this thesis focuses exclusively on explaining natural cognition or biocognition, leaving aside cognition in artifacts such as computers. By focusing exclusively on the biological basis of cognition more headway can be gained on answering such questions as to what cognition is and what biological function(s) it serves. In chapter 3 and chapter 5, I argue that there are fundamental similarities between behaviors of single-celled organisms and more complex organisms equipped with nervous systems and brains and that these behaviors revolve on sensorimotor coordination. Very much like the *E. coli* bacterium, more complex organisms such as Metazoa also use multi-stable behavioral strategies to move about their environment. Instead of using a TCST system to coordinate their sensorimotor responses, Metazoa use nervous systems and centralized brains, which allows their multicellular bodies to function as giant effectors enabling locomotion. Control systems such as nervous systems are necessary for basic locomotion strategies at the level of multicellular organisms, such as hydrostatic propulsion, head-tail undulations, and locomotor limb movements. Such behaviors are feedback control strategies that revolve on the modulation of behavioral bi- and multi-stabilities; these forms of organismal motility are rooted in sensorimotor coordination. The evolution of natural cognition therefore did not coincide with the evolution of nervous systems, rather, nervous systems enabled sensorimotor coordination at a much larger scale of biological organization, that of multicellular organisms; with the evolution of nervous systems sensorimotor strategies could be augmented in ways unprecedented. Throughout evolution, sensorimotor coordination conferred strong selective advantages such as by allowing organisms to escape the limitations and restrictions of local conditions

and to actively seek out, select, and produce more favorable environmental conditions. The evolution of sensorimotor coordination provided the route to biocognitive complexity by yielding predator–prey cycles that induced the evolution of novel sensorimotor coordination strategies. On this view, nervous systems, brains, and higher cognitive functions such emotions, consciousness, and reasoning evolved because of strong selection pressures for the higher order regulation of sensorimotor coordination and different forms of context-sensitive action-selection.

Chapter 4 investigates how human volition is related to sensorimotor coordination. Chapter 4 first debunks the popular view that consciousness is merely a by-product of the brain that has no genuine causal effects on behavior. That is, many authors claim that there is strong empirical evidence to support the claim that conscious will provides us with a false sense of authorship of our actions. This illusion-argument holds that it is unconscious neuronal activity that causes us to act, and that we merely become conscious of the outcome of these unconscious processes after the fact. I argue that this illusion-claim is rooted in a category mistake; namely, in the notion that neuronal activity causes conscious will. This view mistakenly assumes that there is a simple, linear causal relation between neuronal activity and conscious will. In contrast, according to the biogenic approach taken in this dissertation consciousness is fundamentally an action-based mechanism that provides higher order control of sensorimotor functions. According to several authors, consciousness is a highly conserved cognitive function that evolved as an efficient solution to integrate and coordinate information from multiple resources such as sensory information, motor information, bodily/emotive states, and past-experiences. Consciousness also facilitates executive functions such as voluntary action and self-monitoring, which allows organisms to flexibly cope with novel situations. In this chapter, I argue that the causal efficacy of volition resides in its ability to affect coordination dynamics by modulating behavioral patterns to match goal-states using sensorimotor feedback control. This suggests that consciousness is a feedback control mechanism that evolved to support higher order control of sensorimotor coordination by integrating multi-sensory and somatovisceral information in order to allow flexible, context-sensitive action-selection and action-planning.

(3) **-** The third goal of this thesis is to examine the fundamental biological organizational principles that underlie different forms of natural cognition, and also to specify the concept *biocognition;* the former is discussed in chapter 3, and the latter is dealt with in chapter 5. Biological systems are highly optimized by evolution and fundamental organizational properties such as modularity and hierarchical design are therefore found all throughout the biological domain. Chapter 3 investigates how biological organizational principles such as modularity, hierarchical organization and reuse, epigenetic organization, and bow-tie architecture pertain to biocognitive organization. These principles of biological organization are used as a guideline to develop principles of biocognitive organization. Delineating such principles of biocognitive organization also provides ways to understand

the transition from bacterial cognition to more complex forms such as human cognition. In chapter 3, I develop four such principles of biocognitive organization:

Principle 1: Biocognitive modules are bi- or multistable sensorimotor feedback control mechanisms that facilitate the sensorimotor coordination capacities of organisms.

In biology, modules are distinguished at different levels of organization, from metabolic-pathways, modules of gene-regulation, variational modules in the genotype-phenotype map, to organ rudiments such as limb buds. For example, developmental biologists distinguish different dissociated functional modules in embryonic development, each with their own characteristic onset, spatial location, and developmental trajectory. Developmental modules are feedback control systems that are internally integrated by the dynamic covariation between components and relatively independent of the context in which they are embedded. Biocognitive modules are a special type of biological modules. Biocognitive modules are bi- or multistable feedback control systems that facilitate the sensorimotor capacities of organisms. For example, *E. coli*'s chemotaxis biocognitive module is a behavioral bi-stability that consists of two attractors: a running behavior and a tumbling behavior; the context-dependent action-selection between these two behavioral states gives rise to chemotaxis. Throughout evolution, the modularization of biocognition facilitated the increased physico-chemical context-sensitivity of microbial sensorimotor behavior. This allowed these micro-organisms to better distinguish and adaptively respond to a greater variety of stimuli, which extended their ecological niches, providing new adaptive benefits. With the evolution of the nervous system this modular organization could be expanded hierarchically, giving rise to higher order control of sensorimotor coordination.

Principle 2: Biocognitive organizations are typically organized hierarchically with nested modules on phylogenetic and ontogenetic levels of sensorimotor organization; reuse of existing features is an important way to achieve cognitive complexity in development and evolution.

Brain and biocognitive organization are deeply intertwined. In organisms with complex brains such as vertebrates, biocognitive organization exhibits a deeply nested hierarchical architecture. A plausible view is that the hierarchical architecture of biocognition in Metazoa evolved by progressively adding of layers of control to a basic sensorimotor architecture. These layers can be viewed as control modules that provide different levels of sensorimotor control. For example, in primates the prefrontal cortex is often viewed as an executive system that is situated on top of a hierarchy of cognitive control functions. In biology, reuse of components for novel adaptive purposes is an important way to achieve organizational complexity. For example, throughout evolution, genetic regulatory circuits have been frequently co-opted and reused in different contexts, thus forming a main source for evolutionary novelty. In recent years, the idea that reuse is also a fundamental principle in cognitive organization has gained popularity. These hypotheses suggest that cognitive evolution and cognitive development is mainly driven by reuse of existing brain functions that are used for novel functions while also retaining their original functions. For example, research shows that cultural cognitive abilities such as reading and arithmetic reuse pre-existing brain circuits without disrupting their original functionality, and in the process acquire the functional constraints and inherent biases of these cortical circuits. In cognitive development, circuits that are used for sensorimotor coordination are at later stages in cognitive development frequently used for the benefit of higher cognitive processes. For example, one hypothesis is that the mirror neuron system originally evolved for sensorimotor integration but is reused during human cognitive development for the benefit of various higher level cognitive functions such as language and thought. On this view, the existing functionality of certain brain areas is reused as a 'neuronal niche' for other cognitive skills, which ride piggyback on the cognitive function for which it was originally selected. This shows that reuse is not only a pervasive feature in biology but also an important organizational aspect in cognitive development and cognitive evolution.

Principle 3: Biocognitive organization derives to a large extent from epigenetic factors in which, genetic, physical, morphological, sensorimotor, and environmental factors mutually interact and constrain one another, modulating experience-dependent gene expression to sustain a flexible cognitive organization.

Epigenetic mechanisms facilitate the ecological specialization of organisms by the context-dependent modulation of genetic-expression, so that their phenotype can flexibly change to meet the demands of local conditions. Epigenetic mechanisms like chromatin marking can have dramatic effects on the development of organismal morphology. Chromatin marks are proteins or molecules attached to the chromatin, which cause alterations in folding patterns of the chromatin structure affecting the likelihood of gene transcription. Chromatin marking patterns constitute a kind of structural chromosomal memory that allows for the context-dependent modification of genetic expression of eukaryotic cells. Epigenetic factors also include physico-chemical properties such as temperature, gravity, uterine effects, and tissue characteristics, which can all have a significant impact on the unfolding of the phenotype.

The epigenetic approach to cognition probes how environmental influences bear on cognitive development through the context-dependent modification of genetic expression and how this (dis)regulates cognitive processes such as memory and learning. Epigenetic forms of genetic regulation such as histone modification play a key role in biocognition by regulating synaptic plasticity, which facilitates memory formation and learning in both vertebrates and invertebrates. Different forms of chromatin marking have been found to mediate cognitive abilities in mammals such as novel taste learning, object recognition, spatial and contextual memory, and conditional learning.

Sensorimotor experience is another important epigenetic factor that determines brain and cognitive organization. For example, many studies on visually deprived juvenile animals show that patterns of sensory activity transduced by the visual system fundamentally co-determine the organization of the cortical phenotype of the developing visual cortex through modifications in the transcriptional levels of experience-regulated genes. The epigenetic sensitivity of the cortical phenotype allows the brain to flexibly adapt to local conditions. Environmental factors are also important epigenetic determinants of cognitive organization. For example, research shows that ‘environmental enrichment’, i.e. increased levels of social complexity, toys, physical exercise, maternal care, and multisensory stimulation, has an important beneficial impact on cognitive development, most notably on memory, learning, and emotional and stress reactivity. Epigenetic mechanisms thus help to give rise to a highly plastic, context-sensitive biocognitive organization.

Principle 4: Biocognitive control systems are bow-tie architectures that combine phylogenetically conserved core systems with peripheral and more flexible sensorimotor structures. Cognitive bow-tie architecture optimizes trade-offs between efficiency, metabolic costs of neuronal wiring, and cognitive flexibility.

Bow-tie architecture is a organizational feature that is found in the vertebrate immune system, gene-protein networks, metabolic networks, and signal-transduction systems. Bow-tie architectures are global control systems that are characteristically organized around a core of closely coupled, phylogenetically conserved processes, which provide a versatile interface for diverse input and output processes; this kind of architecture is the result of evolutionary optimization processes that promote organizational efficiency, robustness, and evolvability. My hypothesis is that bow-tie architecture is also an important organizational feature of biocognitive systems. Given the high metabolic expenditure of brains the principles of “using least wire” and limiting connections and energy consumption are important organizational constraints on the evolution of complex nervous systems and brains. Centralized brain mechanisms limit connection costs in brain wiring and also accommodate the need for specialized action-selection structures that co-ordinate different action subsystems that compete against each other for behavioral control. In the vertebrate brain, dedicated action-selection mechanisms such as the basal ganglia constitute a core control system for regulating sensorimotor coordination. The basal ganglia play a major role in regulating sensorimotor coordination by on the one hand converging multisensory and somatovisceral information and on the other by selecting between competing behaviors. This highly optimized organization effectively forms a bow-tie architecture: the basal ganglia make-up a conserved core of common currencies while the array of multisensory information that converges in the core modulates the wide variety of possible actions and thoughts that ‘fan-out’ of the core system.

Bow-tie architecture provides a way to understand how organizational features such as modularity, hierarchical organization, reuse, and epigenetic organization are related and integrated in a global biocognitive control architecture. Different structures along the neuraxis such as the medial reticular formation (mRF) in the core of the brain stem, and the fore brain also provide substrates for action-section. These different control systems supplement each other and exhibit aspects of a hierarchical or layered bow-tie architecture. In vertebrates, biocognitive organization is therefore best viewed as a hierarchically structured sensorimotor control organization consisting of a number of loosely coupled, layered bow-tie modules. Cognitive bow-tie architecture forms an economical solution for coordinating a wide variety of sensory systems, motor systems, emotional systems, memory systems, and involves reusing and sharing efficient resources such as centralized control systems. Cognitive bow-tie architecture combines robust core interfaces with flexible peripheral sensory input and motor output pathways that are more susceptible to epigenetic modulation. This combination of evolutionary stable core systems and highly flexible peripheral systems optimizes the relation between adaptability in the short run, and evolvability in the long run.

Another aim of this thesis was to provide an explicit explication of the notion *biocognition.* According to this explication, biocognitive systems are by definition: (1) motile organisms, (2) capable of sensorimotor coordination, (3) which is mediated by an internal sensor/effector signal-transduction mechanism. This explication stresses the central importance of sensorimotor coordination in biocognition, the cost-benefit trade-offs that come with sustaining a motile lifestyle, and the importance of size in determining trade-offs between metabolic costs and adaptive benefits of biocognition. Biocognition enables free moving organisms to modulate the external conditions for their metabolism so that they can escape the limitations and restrictions of local conditions and to actively seek out, select, and produce more favorable environmental conditions. The conditions of adequacy for this explication of biocognition exclude sessile organisms such as plants. Large multicellular plants are capable of complex adaptive responses such as solar-tracking and niche construction; however, their behavior is highly constrained: they are firmly rooted in soil and lack the means to move about. Plant behaviors are mostly based on phenotypic plasticity, which underlies the flexible changes in growth-rate and morphogenesis. In contrast, biocognitive behaviors such as taxis behaviors constitute a different set of adaptive strategies that enable these organisms to navigate through the environment based on the coordination between different kinds of sensory information and effectors such as flagella.

Adaptation in multicellular plants is also highly constrained due to their sheer size. Size is a key factor in determining the costs and benefits for motility. To generate the large-scale coordinations of a multicellular body enabling basic locomotion strategies, nervous systems are a necessity. However, the metabolic turnover for nerve tissue is very high. At least for multicellular plants the benefits of their sessile lifestyle outweigh the risks and the metabolic costs of motility. Moreover, the intricacies of plant behavior usually take place on much slower timescales than the behavior of animals. Fast coordinated sensorimotor behaviors must have conferred strong selective advantages, yielding complex predator-prey cycles that facilitated the evolution of new sensorimotor coordination strategies. Throughout evolution, expanding the sensorimotor coordination strategies of motile organisms provided the route to biocognitive complexity. Biocognition has been reinvented many times through convergent evolution and has taken on a wide variety of forms at different scales of organization, yielding a biocognitive spectrum from prokaryotes to humans.

6.3 Directions for Future Research

First, this dissertation highlights the relevance of bacterial sensorimotor behavior for the study of cognition. The study of cognition in bacteria, protists, and multicellular organisms that lack a brain or central nervous system is still in its infancy; it is a research area that is still largely neglected by cognitive science. Even though the behaviors of these organisms are often already well-studied, though far from completely described and understood by biologists, the study of minimal cognition is still underdeveloped. Given the diversity of bacterial and protist behavior the study of minimal cognition ought to be expanded to include the very many different sensorimotor strategies that are used by motile unicellular organisms and multicellular organisms with primitive nervous systems. Studying the sensorimotor behaviors of these organisms can further enhance our understanding of the biological basis of human cognition and provide new insights on the mechanisms of cognitive evolution.

Second, the notion of biocognition rejects the classic dichotomy between instinct and cognition, but also sets a lower bound to biocognition by distinguishing it from other forms of biological adaptation, such as phenotypic plasticity. This leads to a more graded view of cognition: a broad cognitive spectrum from bacteria to humans with sensorimotor coordination as their common mechanism. However, while sensorimotor coordination may provide the ultimate phylogenetic context for understanding human cognition as a form of adaptation, it remains unclear to what extent and in which ways the wide variety of human cognitive abilities are borne out of sensorimotor coordination. Future research should focus on how different higher human cognitive abilities such as volition are related to sensorimotor coordination. Investigating how biological organizational principles such as bow-tie architecture are implemented in the cognitive organization of different organisms might help to develop such a view.

Third, until now, the embodied/embedded approach to cognition has devoted much attention to studying the socio-cultural aspects of cognition. That is, authors like Andy Clark have emphasized how language and technological artifacts provide scaffolds for cognitive processes. The biogenic approach taken in this thesis instead centers on the biological determinants of cognitive processes. These culturally and biologically oriented approaches are not mutually exclusive but should be combined to further develop the embodied/embedded approach to cognition, and to expand its research agenda to include biological principles and mechanisms that determine cognitive organization, such as epigenetic mechanisms and bow-tie architecture. Advancing our understanding of the workings of epigenetic mechanisms that govern cognition will shed a new light on the mechanisms of cognitive evolution, cognitive development, and provide new insights on the nature of cognitive disorders. The development of such a more balanced account of embodied/embedded cognition might establish it as the dominant paradigm in cognitive science for years to come. And more importantly, it will help facilitate the long overdue unification of biology and cognitive science.

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Nederlandse Samenvatting (Summary in Dutch)

Het Biocognitieve Spectrum:
Biologische Cognitie als Variaties op Sensomotorische Coördinatie

Dit proefschrift ontwikkelt een nieuwe theorie over biologische cognitie, oftewel *biocognitie*. In tegenstelling tot de meest gangbare theorieën over cognitie die natuurlijke cognitie als een relatief recente evolutionaire ontwikkeling beschouwen, biedt dit proefschrift een alternatieve biologische verklaring voor natuurlijke cognitie die gegrondvest is in sensomotorische coördinatie; een vorm van biologische adaptatie die evolutionair zeer oud is en wijdverbreid onder eukaryoten (organismen met celkern en gespecialiseerde organellen), én prokaryoten (organismen zonder celkern) zoals bacteriën. Een centrale claim in deze dissertatie is dat de fylogenetische basis van biocognitie ligt in sensomotorische coördinatie: het vermogen van organismen om zich voort te bewegen en zich te oriënteren in hun omgeving om zo de externe factoren voor hun metabolisme te optimaliseren. Bacteriële chemotaxis is een goed voorbeeld van *minimale cognitie*, de meest elementaire vorm van biocognitie. Chemotaxis helpt bacteriën zoals *E. coli* om een optimaal fysisch-chemisch milieu te vinden door kleine concentratieverschillen van chemicaliën te detecteren en zich langs deze chemische gradiënten voort te bewegen. Minimaal cognitieve strategieën zoals chemotaxis vereisen bij bacteriën zoals *E. coli* een moleculaire vorm van geheugen die de perceptie-actiekoppelingen tussen de moleculaire receptoren en de flagella van de bacterie reguleert. Minimale cognitie bij bacteriën impliceert dat hersenen en zenuwstelsels geen vereiste zijn voor biologische vormen van cognitie, zoals gewoonlijk wordt aangenomen, maar dat biocognitie veel primitievere wortels heeft die reiken tot diep in het domein van de prokaryoten.

Een andere centrale claim in dit proefschrift is dat het brede spectrum van biocognitieve mechanismen, van bacteriële taxis tot menselijke cognitie, het beste kan worden begrepen als verschillende vormen van sensomotorische coördinatie. Bacteriële cognitie en menselijke cognitie zijn variaties op hetzelfde thema dat door grote selectiedruk is geëvolueerd op verschillende niveaus van biologische organisatie. Vanuit dit perspectief vormen hogere cognitieve functies zoals bewustzijn, taal, en redeneren in de eerste plaats een uitbreiding van basale homeostatische controlefuncties die verschillende vormen van hogere orde, contextafhankelijke regulatie van sensomotorische coördinatie mogelijk maken. Sensomotorische coördinatie vormt ook de ontogenetische basis voor menselijke cognitie: cognitieve vaardigheden zoals objectherkenning, imitatie, taal, en zelfbewustzijn berusten in belangrijke mate op de ontwikkeling van verschillende vormen van sensomotorische coördinatie. Bacteriële cognitie en menselijke cognitie zijn dus variaties op hetzelfde thema en vormen twee uitersten in een breed biocognitief spectrum dat een groot deel van de fylogenetische boom omvat. Deze theorie over biocognitie vormt de basis van de groeiende consensus dat de fylogenetische en ontogenetische basis van cognitie in sensomotorische coördinatie ligt, en verankert de cognitiewetenschappen stevig in de biologie.

Dit proefschrift heeft drie doelen: (1) Het eerste doel is het specificeren van *minimale cognitie*, de meest elementaire natuurlijke vorm van cognitie, en het onderscheiden van minimale cognitie van andere vormen van biologische adaptatie zoals genetische adaptatie, (2) Het tweede doel is om de belichaamde, gesitueerde benadering van cognitie te verenigen met een *biogenische* benadering van cognitie door te onderzoeken hoe verschillende organismen - waaronder bacteriën - sensomotorische coördinatie gebruiken, en te onderzoeken hoe hogere cognitieve functies - met name het bewustzijn - bij meer complexe organismen zoals de mens gerelateerd zijn aan sensomotorische coördinatie, (3) Het derde doel is om de biologische organisatieprincipes van cognitie te onderzoeken en het concept *biocognitie* te specificeren. Elk hoofdstuk in dit proefschrift werkt deze doelen in meer of mindere mate uit door een deel van het biocognitieve spectrum voor zijn rekening te nemen.

Hoofdstuk 1 – Theoretische benaderingen van cognitie geeft een beknopt historisch overzicht van de belangrijkste moderne theorieën over cognitie; te beginnen bij het cognitivisme, de invloedrijkste zienswijze. Volgens het cognitivisme kan cognitie het best worden begrepen als een vorm van computatie: cognitie vormt als het ware de software die de hardware van de hersenen aanstuurt. Het cognitivisme is een vorm van functionalisme waarbij cognitie draait om: (1) computationele processen die opereren tussen perceptuele input en motor output, (2) neuronale informatieverwerkingsprocessen, en (3) interne symbolische representatie van objecten in de externe wereld. Het cognitivisme wordt met name sinds de laatste twee decennia problematisch geacht en verschillende benaderingen proberen een betere invulling te geven aan het begrip cognitie. De ecologische benadering van Gibson benadrukt bijvoorbeeld meer de ecologische aspecten van cognitie. Volgens deze leer heeft cognitie niet zo zeer te maken met interne informatieverwerkingsprocessen maar is zij in hoge mate afhankelijk van de interactie tussen organisme en omgeving, en de wederkerigheid tussen perceptie en actie. De dynamische systeembenadering van cognitie legt meer de nadruk op de temporele aspecten van cognitie. Volgens deze benadering zijn cognitieve systemen niet zo zeer computationele systemen maar dynamisch gekoppelde systemen die zich ontwikkelen in de tijd als zelf-organiserende systemen. Cognitie wordt hierbij beschouwd als het emergente product van de gekoppelde dynamische interactie tussen een zenuwstelsel, een lichaam, en een omgeving. Nauw verwant aan de dynamische systeembenadering van cognitie is de nu populaire belichaamde, gesitueerde benadering van cognitie. Volgens deze interpretatie is cognitie niet slechts een hersenproces maar ook een inherent belichaamd en gesitueerd fenomeen: cognitie is in belangrijke mate afhankelijk van de biomechanische en morfologische eigenschappen van een lichaam, evenals de sociaal-culturele aspecten die de cognitieve ontwikkeling ondersteunen en aanvullen.

Als laatste wordt in dit hoofdstuk aandacht geschonken aan de *biogenische* benadering van cognitie. In plaats van te beginnen bij de mens of bij computers om een beeld te krijgen van cognitie, begint zij te theoretiseren bij de biologie. De biogenische benadering ziet cognitie in de eerste plaats als een biologische vorm van adaptatie die organismen in staat stelt om op een adaptieve manier om te gaan met hun omgeving om zo de overlevingskansen te bevorderen. De theoretische benadering van cognitie in dit proefschrift berust op een combinatie van de biogenische benadering en de belichaamde, gesitueerde benadering van cognitie en is puur gericht op het verklaren van biologische vormen van cognitie en laat hierbij andere vormen zoals computer cognitie buiten beschouwing; zo'n minder abstracte en meer gespecialiseerde aanpak kan een betere verklaring geven voor biocognitie als een vorm van biologische adaptatie.

Hoofdstuk 2 – Principes van minimale cognitie biedt een casestudie over *minimale cognitie*, de meest elementaire vorm van biocognitie. Dit hoofdstuk laat zien dat chemotaxis bij de *Escherichia coli* bacterie een goed voorbeeld is van minimale cognitie. De *E. coli* bacterie is te klein om concentratieverschillen van chemicaliën tussen zijn receptoren te detecteren. De bacterie moet zich dus voortbewegen om een chemisch gradiënt te detecteren en daarbij maakt hij gebruik van een primitieve moleculaire vorm van geheugen om de temporele verschillen in chemische gradiënten te detecteren. De ongeveer 8000 receptoren van de bacterie zijn uiterst gevoelig voor subtiele veranderingen in de chemische samenstelling van de omgeving. De *E. coli* bacterie beweegt zich voort door het afwisselen van twee gedragspatronen: zwemmen en tuimelen. Bij het zwemgedrag draaien de 6 flagella, lange zweepachtige structuren die gelijkmatig over het oppervlak van de bacterie zijn verdeeld, tegen de klok in zodat deze zich bundelen en er een soort kurkentrekkereffect ontstaat; hierdoor wordt de bacterie in een rechte lijn voortgestuwd. Het zwemgedrag wordt periodiek afgewisseld met tuimelgedrag waarbij de flagella met de klok mee draaien; de flagella vliegen hierbij uit elkaar waardoor de bacterie van richting verandert. Door de frequentie van het tuimelgedrag te reguleren, is er een netto verplaatsing van de bacterie naar een optimale fysisch-chemische omgeving. Wanneer de bacterie een hogere concentratie van aantrekkelijke chemicaliën – zoals glucose – detecteert, gaat de tuimelfrequentie omlaag en wanneer de bacterie een lagere concentratie aantrekkelijke chemicaliën detecteert gaat deze omhoog.

Het signaalverwerkingssysteem van deze bacterie - het TCST systeem - is opgebouwd uit 3 componenten (1) receptoren, (2) een transmitter, het eiwit histidine kinase (CheA), (3) en een respons regulator, het eiwit aspartaat kinase (CheY), dat de rotatierichting van de flagella reguleert. Het signaalverwerkingssysteem bestaat uit twee banen, één voor perceptie - de fosfortranserasebaan -, en één voor adaptatie - de methilatiebaan - die feedback geeft aan de bacteriële receptoren door de met chemicaliën bezette receptoren te ‘resetten’. De interactie tussen de snelle perceptie baan (die opereert op het niveau van milliseconden) en de langzamere methilatiebaan (die functioneert op het niveau van seconden tot enkele minuten) maakt dat de bacterie over een dynamisch moleculair geheugen beschikt. De receptoren van de bacterie werken als een soort neus, die continu perfect adapteert aan de huidige chemische omstandigheden waardoor kleine veranderingen in het chemische milieu nog eens extra worden versterkt. Bacteriën zoals *E. coli* beschikken over verschillende sensorische modaliteiten en zijn daardoor in staat tot diverse vormen van beweging, zoals redoxtaxis, fototaxis, en gravitotaxis.

Deze casestudie over minimale cognitie laat zien dat hersenen en zenuwstelsels geen vereiste zijn voor natuurlijke cognitief gedrag: De biologische basis voor minimale cognitie ligt niet in hersenen of zenuwstelsels maar in het proces van sensomotorische coördinatie. Bacteriële chemotaxis is een goed voorbeeld van sensomotorische coördinatie. Door de adaptieve coördinatie tussen hun receptoren en effectoren (de flagella) zijn bacteriën zoals *E. coli* in staat om de externe omstandigheden voor hun metabolisme te optimaliseren. Chemotaxis maakt niet zo zeer deel uit van metabolische processen maar speelt zich af op een breder organisatieniveau waarbij de bacterie als geheel zijn spatio-temporele positie op een adaptieve manier moduleert. Chemotaxis in *E. coli* is een gesitueerd, dynamisch en belichaamd fenomeen dat kan dienen als een schoolvoorbeeld van minimale cognitie. Deze casestudie laat zien dat biocognitie geen eigenschap is van een handjevol complexe organismen, maar dat het een wijdverbreid biologisch proces is dat zijn evolutionaire oorsprong heeft in het vermogen van organismen om zich voort te bewegen door middel van sensomotorische coördinatie.

Hoofdstuk 3 – Biologische organisatieprincipes van cognitie onderzoekt hoe biologische organisatieprincipes de organisatie van natuurlijke, cognitieve systemen bepalen. Biologische systemen zijn geoptimaliseerd door evolutie en fundamentele organisatieprincipes zoals modulariteit en hiërarchische organisatie zijn overal in de natuur terug te vinden. Dit hoofdstuk onderzoekt hoe vier centrale biologische organisatieprincipes, namelijk: (1) modulariteit, (2) hiërarchische organisatie & hergebruik van onderdelen, (3) epigenetische organisatie, en (4) *bow-tie* architectuur in de biologie worden begrepen en past ze vervolgens toe om organisatieprincipes te ontwikkelen voor biocognitieve systemen. Uit deze organisatieprincipes kan worden afgeleid hoe basale vormen van biocognitie, zoals bacteriële cognitie, gerelateerd zijn aan complexere vormen zoals menselijke cognitie.

Het sleutelconcept om te begrijpen hoe simpele systemen kunnen evolueren tot meer complexe systemen is *modulariteit*. Modulariteit is een belangrijk biologisch organisatieprincipe dat ook relevant is voor het begrijpen van de organisatie van biocognitieve systemen. Sommige evolutionaire psychologen claimen bijvoorbeeld dat onze cognitieve architectuur massief modulair is en volledig is samengesteld uit autonome hersenprogramma's die verantwoordelijk zijn voor het genereren van specifieke cognitieve taken zoals gezichtsherkenning, taal, rekenen, imitatie et cetera. Zo verdedigt de evolutionaire psychologie dat we geboren worden met een grote verscheidenheid aan zeer specialistische cognitieve modules. Deze cognitieve modules zijn volgens de evolutionaire psychologie geëvolueerd in het Pleistoceen, toen de mens nog een primitieve jager-verzamelaar was. Onze modulaire cognitieve architectuur zou toen zijn geselecteerd vanwege de evolutionaire voordelen die de verschillende modules met zich meebrachten; vervolgens zijn deze modules vastgelegd in onze genen die coderen voor de aanmaak van modulaire hersenprogramma's in de cognitieve ontwikkeling.

Vanuit het theoretische perspectief van de belichaamde, gesitueerde cognitie en de moderne biologie is dit perspectief van de evolutionaire psychologie op cognitieve modulariteit achterhaald en in meerdere opzichten misleidend. Allereerst focust de evolutionaire psychologie teveel op een fylogenetische verklaring van cognitieve modulariteit. De evolutionaire psychologie overschat daarmee de rol van de genetische determinanten van onze cognitieve organisatie, terwijl zij de ontogenetische en met name de epigenetische factoren die onze cognitieve organisatie vormgeven, onderschat. Tevens is het vrijwel onmogelijk om te bepalen of de cognitieve modules die gepostuleerd worden door de evolutionaire psychologie ook daadwerkelijk een één op één relatie hebben met specifieke adaptieve problemen die deze modules worden geacht op te lossen. Dit probleem leidt tot een overdaad aan 'vals positieven'; vrijwel voor elke cognitieve capaciteit kan een cognitieve module worden gepostuleerd. In hoofdstuk 3 ontwikkel ik een alternatieve, biologisch plausibele interpretatie van cognitieve organisatieprincipes door te onderzoeken hoe principes zoals modulariteit in de biologie worden gebruikt. Aan de hand van dit onderzoek ontwikkel ik 4 principes van biocognitieve organisatie:

(1) Modulariteit – Biocognitieve modules zijn bi- of multistabiele dynamische systemen die door middel van feedbackcontrole worden gemoduleerd om de sensomotorische coördinatiestrategieën van organismen te faciliteren.

Allereerst wordt er besproken hoe het begrip modulariteit in de ontwikkelingsbiologie en de evolutionaire biologie wordt gehanteerd. Er wordt dieper ingegaan op de organisatorische eigenschappen van biologische modules zoals morfogenetische velden, genetische regulatormodules zoals *Hox*, en de evolutionaire modules in de genotype-fenotype kaart. Modulariteit is ook een eigenschap van biocognitieve systemen. Biocognitieve modules zijn bi- of multistabiele procesmodules. Bi- en multistabiliteit is een wijdverbreid fenomeen in de biologie en kenmerkt bijvoorbeeld ook het schakelgedrag van genetische regulatormodules. Biocognitieve modules faciliteren de sensomotorische coördinatiestrategieën van organismen door de dynamica van bi- en multistabiele gedragspatronen te moduleren door middel van feedbackcontrole. Het chemotaxis gedrag van de *E. coli* bacterie is een simpel voorbeeld van een bi-stabiliteit op minimaal cognitief niveau. Chemotaxis in *E. coli* wordt gereguleerd door de feedbackcontrole van een bi-stabiel gedrag (zwemmen en tuimelen). De contextafhankelijke actie-selectie tussen deze twee gedragingen resulteert in sensomotorische coördinatie en maakt chemotaxis mogelijk. Basale gedragsstrategieën zoals bi- en multistabiele gedragspatronen zijn ook karakteristiek voor de methoden van voortbeweging van protisten en primitieve Metazoa, zoals kwallen en wormen. De modulaire uitbreiding van sensomotorische coördinatiestrategieën is een belangrijk thema in de evolutie van biocognitie dat de fysisch-chemische contextgevoeligheid van organismen bevorderde. De evolutie van zenuwstelsels maakte het mogelijk om deze basale gedragsstrategieën modulair en hiërarchisch uit te breiden. Door modularisatie konden primitieve organismen nieuwe ecologische niches veroveren en daardoor nieuwe adaptieve voordelen genieten.

(2) Hiërarchische organisatie en hergebruik – Biocognitieve organisaties zijn hiërarchisch georganiseerde systemen met geneste modules op fylogenetisch en ontogenetische organisatieniveaus. Hergebruik van bestaande modules is een belangrijk middel om organisatorische complexiteit te creëren in de cognitieve evolutie en de cognitieve ontwikkeling.

Biologische systemen zijn hiërarchisch georganiseerde systemen. Hiërarchische organisatie brengt net als modulariteit belangrijke evolutionaire voordelen met zich mee. Modern onderzoek op het snijvlak van de evolutionaire- en ontwikkelingsbiologie (evo-devo) laat zien dat hergebruik van bestaande processen en onderdelen in de ontwikkeling en evolutie een belangrijk middel is om tot een complexe organisatie te komen. Hergebruik van bestaande genetische regulatoren en hun expressie in andere contexten (in plaats en/of tijd) blijkt bijvoorbeeld een belangrijke bron te zijn voor vernieuwing in de evolutie. Deze principes van hiërarchische organisatie en hergebruik vormen ook belangrijke aspecten van biocognitieve organisatie. Een plausibele hypothese is dat de hiërarchische, biocognitieve organisatie van complexe organismen zoals gewervelde dieren is geëvolueerd door middel van het stapelen van controlesystemen; dit heeft geresulteerd in een gelaagde cognitieve architectuur met verschillende niveaus van sensorimotorcontrole. Recentelijk zijn er een aantal verschillende maar compatibele hypothesen verschenen over de rol van hergebruik in cognitieve evolutie en cognitieve ontwikkeling. Deze hypothesen suggereren dat cognitieve evolutie en ontwikkeling voornamelijk gedreven worden door hergebruik van bestaande hersenfuncties voor nieuwe adaptieve functies, terwijl daarnaast de oude functies blijven bestaan. Recent onderzoek laat bijvoorbeeld zien dat hersengebieden die in de cognitieve ontwikkeling oorspronkelijk gebruikt werden voor sensomotorische coördinatie, in latere ontwikkelingsstadia gebruikt worden voor 'hogere' cognitieve processen zoals taal en rekenen. De bestaande hersenfunctionaliteit wordt dus hergebruikt en dient daarmee als een 'neuronale niche' voor andere cognitieve vaardigheden.

(3) Epigenetische organisatie – Biocognitieve organisatie is voor een groot deel een afgeleide van epigenetische factoren waarbij genetische, fysieke, morfologische, sensomotorische, en gesitueerde factoren en elkaar insnoeren en wederzijds interacteren om de genetische expressie te moduleren voor een flexibele cognitieve organisatie.

Epigenetische mechanismen zijn van belangrijke invloed op de ontwikkeling van het fenotype van organismen. Genetisch identieke organismen kunnen door epigenetische factoren zoals fysisch-chemische variabelen belangrijke fenotypische verschillen vertonen. Epigenetische mechanismen moduleren de genetische expressie zodat organismen op flexibele wijze hun fenotype kunnen aanpassen aan lokale omstandigheden; epigenetische mechanismen faciliteren hiermee de ecologische specialisatie van organismen. Ter verduidelijking belicht dit gedeelte van het hoofdstuk in het kort een belangrijk epigenetisch mechanisme genaamd “chromatine markeringen”, die onder andere de celidentiteit bepalen in de embryonale fase. Chromatine markeringen zijn eiwitten of andere moleculen die zijn aangehecht aan het chromatine: het complex van DNA en histone eiwitten waar het DNA omheen is gewikkeld. Chromatinemarkeringen zorgen voor veranderingen in de vouwpatronen van het chromatine wat leidt tot veranderingen in de patronen van genetische expressie. Chromatine markeringen vormen een chromosomaal ‘geheugen’ dat zorgt voor vele verschillende vormen van contextafhankelijke genetische expressie.

In de cognitiewetenschappen is men sinds een aantal jaar het onderzoek gestart naar de epigenetische determinanten van cognitie. Deze epigenetische benadering onderzoekt hoe verschillende factoren de cognitieve ontwikkeling beïnvloeden door middel van de (de)regulatie van de contextafhankelijke genetische expressie. Chromatine markeringen zoals histone modificatie spelen een belangrijke rol in cognitie door het reguleren van synaptische plasticiteit, welke geheugenvorming en leren faciliteert in gewervelde en ongewervelde dieren. Verschillende vormen van chromatine markeringen mediëren cognitieve vaardigheden bij zoogdieren zoals objectherkenning, geheugen en conditioneel leren. Sensomotorische ervaringen vormen een belangrijke epigenetische factor die van fundamentele invloed is op cognitieve- en hersenorganisatie. Studies bij visueel gedepriveerde muizen laten bijvoorbeeld zien dat patronen van sensorische activiteit de organisatie van de visuele cortex in belangrijke mate bepalen door middel van context-afhankelijke genetische expressie. Deze epigenetische gevoeligheid van het corticale fenotype helpt het brein zich flexibel aan te passen aan veranderende omstandigheden. De studie naar de epigenetische determinanten van cognitie laat zien dat cognitieve ontwikkeling en cognitieve organisatie veel flexibeler zijn dan meestal werd aangenomen.

(4) Bow-tie architectuur – Biocognitieve controlesystemen zijn bow-tie (letterlijk: vlinderdas) architecturen die een kern van fylogenetisch geconserveerde actie-selectiesystemen combineren met meer flexibele perifere sensomotorische processen. Cognitieve bow-tie-architectuur optimaliseert afwegingen tussen efficiency, metabolische kosten van neurale connecties, en cognitieve flexibiliteit.

De moderne systeembiologie onderzoekt hoe deelprocessen binnen levende organismen samenhangen en resulteren in globale systeemfuncties. Bow-tie-architecturen zijn globale controle systemen die de topologische structuur karakteriseren van onder andere het immuunsysteem, gen-proteïnen interactienetwerken, metabolische netwerken, en signaalverwerkingssystemen zoals het bacteriële TCST systeem. Bow-tie-architecturen bestaan uit een kern van fylogenetisch geconserveerde processen die een interface bieden voor een brede verscheidenheid aan input- en outputprocessen die gevoeliger zijn voor epigenetische modificatie. Dit type architectuur is het resultaat van evolutionaire optimalisatie processen die organisatorische efficiency, robuustheid en evolueerbaarheid bevorderen.

Mijn hypothese is dat bow-tie-architectuur ook kenmerkend is voor de organisatie van biocognitieve systemen. Cognitieve bow-tie-architectuur minimaliseert de neurale connectiekosten (en daarmee ook de metabolische kosten) door middel van het hergebruiken van kernhersenmechanismen als een flexibele interface voor input en output processen. Deze kernhersenmechanismen faciliteren de actie-selectievermogens van organismen door het coördineren van verschillende sensorische en motor systemen. Cognitieve bow-tie-architectuur biedt daarmee een economische oplossing voor het coördineren van een grote verscheidenheid aan sensorische systemen, motorsystemen, emotionele- en geheugensystemen, door het delen van bestaande kernonderdelen. In het brein van gewervelde dieren vormen structuren zoals de basale ganglia een belangrijke kern van de cognitieve bow-tie-structuur. De basale ganglia spelen een belangrijke rol in het reguleren van sensomotorische coördinatie door aan de ene kant multi-sensorische en somato-viscerele informatie te integreren en aan de andere kant te selecteren tussen een grote hoeveelheid aan actiemogelijkheden. Naast de basale ganglia zijn er meerdere kernsystemen die substraten voor contextgevoelige actie-selectie vormen zoals de mediale reticulaire formatie in de hersenstam. Ook het bewustzijn heeft de kenmerken van cognitieve bow-tie-architectuur. Het bewustzijn is een fylogenetisch geconserveerde kernfunctie die multi-sensorische en somatoviscerele informatie integreert, en hogere-orde controle van sensomotorische coördinatie op basis van interne doelen en context-afhankelijke informatie mogelijk maakt. Deze verschillende kerncontrolesystemen vullen elkaar aan en zijn kenmerkend voor hiërarchische bow-tie-organisatie zoals die ook te vinden is in metabolische netwerken. Bow-tie-architectuur is een globaal organisatieprincipe dat duidelijk maakt hoe organisatorische aspecten zoals modulariteit, hiërarchische organisatie, hergebruik, en epigenetische organisatie samenhangen en zijn geïntegreerd in een globale controle-architectuur.

Hoofdstuk 4 – De veronderstelde illusie van het bewustzijn bediscussieert de causale rol van het bewustzijn bij menselijke cognitie. Biologische verklaringen van het bewustzijn suggereren dat het bewustzijn is geëvolueerd omdat het een belangrijke rol speelt in het aansturen en controleren van gedragingen en hiermee van belangrijke overlevingswaarde is. Deze biologische kijk op de rol van het bewustzijn wordt tegengesproken door een aantal vooraanstaande wetenschappers en filosofen die beweren dat de causale rol van het bewustzijn slechts een illusie is die wordt gegenereerd door onze hersenen. De illusie-claim houdt in dat neuronale activiteit verantwoordelijk is voor het initiëren van al onze acties, en dat ons bewustzijn altijd achter de feiten aanloopt waardoor het geen causale rol speelt in de totstandkoming van gedrag.

Het empirisch bewijs voor deze illusie-claim wordt ontleend aan de omstreden experimenten van de neurofysiologie Benjamin Libet. Op basis van zijn onderzoek kwam Libet tot de conclusie dat er aan spontane wilsbesluiten een substantiële, neuronale opbouwperiode voorafgaat van ongeveer 350 ms. Deze hersenactiviteit kan worden weergegeven in de vorm van de zogenaamde *readiness potential:* een elektrofysiologische indicator voor bewegings-voorbereiding in de supplementaire motor cortex. Een aantal wetenschappers concludeert uit de Libet-experimenten dat het bewustzijn geen causale rol speelt in ons gedrag en dat de werkelijke causale processen voor ons gedrag zich op neuronaal niveau bevinden.

Sommige critici beweren echter dat Libet's experimenten voor meerdere interpretaties vatbaar zijn en niet generaliseerbaar zijn buiten deze experimentele context. Zo lijkt het aannemelijker dat het bewustzijn niet nodig is voor elk spontaan wilsbesluit, zoals Libet suggereert, maar dat het bewustzijn het globale gedrag tijdens het experiment bepaalt. Critici claimen dat in het gewone dagelijks leven het bewustzijn vooral een strategische rol speelt bij het leren, plannen en coördineren van flexibele acties, die vervolgens hoofdzakelijk automatisch worden voltrokken.

In dit hoofdstuk beargumenteer ik dat de illusie-claim is gebaseerd op het idee dat neuronale processen het bewustzijn veroorzaken. Dit is een categoriefout: neurale processen en het bewustzijn zijn fenomenen op verschillende verklaringsniveaus; er is hier dus geen sprake van causatie maar hooguit van correlatie. De illusie-claim is gegrondvest in een simplistische lineair causale verklaring voor de rol van het bewustzijn in het menselijk gedrag. De rest van dit hoofdstuk biedt een alternatieve verklaring voor het bewustzijn als een causaal gedragsmechanisme. Volgens deze verklaring kan het bewustzijn worden opgevat als een gedragssturingsmechanisme dat gegenereerd wordt door de collectieve dynamisch gekoppelde activiteit van grote groepen neuronen. Het idee dat neuronen niet alleen op micro-niveau maar ook op macro-niveau samenwerken als geïntegreerde systemen is gegrondvest in het klassieke werk van Luria, Werknicke, en Hebb. De zelforganiserende activiteit van bijvoorbeeld slaapritmes laten zien dat het gedrag van grote groepen neuronen wordt gesynchroniseerd in patronen. De relatief langzame gecoördineerde massa-actie van grote populaties neuronen legt restricties op aan het gedrag van zijn individuele componenten. De eigenschappen van de micro-componenten, zoals synapsen, axonen en dendrieten, verschillen van de eigenschappen van de macro-componenten; deze verklaringsniveaus hebben elk hun eigen dynamische wetten. De relatie tussen de componenten op micro-niveau en de verschijnselen op macro-niveau in zelforganiserende systemen wordt vaak weergegeven in termen van *circulaire causatie*: de micro-componenten vormen de bouwstenen voor de macro-componenten, en de macro-patronen organiseren het collectieve gedrag van de individuele micro-componenten. De fout van de illusie-claim is dat het de causaliteit van wilsbesluiten aan één bepaald verklaringsniveau toedicht – het neuronale niveau – en dat het de invloed van de macro-componenten negeert.

Hoewel de mechanismen van het bewustzijn nog slecht worden begrepen door de moderne neurowetenschap laat recent onderzoek naar zelf-organiserende processen in het brein zien dat het bewustzijn zijn causale werking haalt uit de modulatie van sensomotorische coördinatie. In dit perspectief opereert het bewustzijn op basis van zelforganisatie en zelfsturing net als andere biologische processen zoals morfogenese en ontogenese. Het bewustzijn voorziet het brein daarmee van een stuk gereedschap om het gedrag te sturen, te stabiliseren en te coördineren op basis van interne doelen die via emoties en gedachten aan perceptie en actie zijn gekoppeld. Deze kijk op het bewustzijn is bekend geworden door William James' klassieke ideomotor-theorie, die suggereert dat bewuste gedachten en actiecodes fundamenteel zijn geïntegreerd in de organisatie van de hersenen. Recent onderzoek in de cognitieve psychologie onderschrijft deze visie en laat zien dat cognitieve codes die bewegingen organiseren – de zogenaamde motorprogramma's - en interne actiedoelen automatisch bilaterale connecties vormen en dat we deze connecties gebruiken voor actieselectie. Het bewustzijn vergelijkt interne doelen met sensorische feedback en stuurt de gedragspatronen naar de doelstaat door het moduleren van perceptie en actie. Deze visie op het bewustzijn ondersteunt de claim dat het bewustzijn een causale rol speelt in ons gedrag door de sensomotorische coördinatiestrategieën van organismen te reguleren.

Hoofdstuk 5 – Het Biocognitieve Domein biedt tot slot een explicatie van het begrip biocognitie en geeft daarmee een meta-perspectief op de voorafgaande hoofdstukken. Biocognitie is een specifieke vorm van biologische adaptatie die intrinsiek verbonden is aan homeostatische controleprocessen. De functie van biocognitie is om de coördinatie tussen het interne en externe milieu van organismen te optimaliseren. Biocognitie faciliteert hiermee de ecologische generalisatie van organismen. Biocognitie is een generieke eigenschap van organismen die zich kunnen voortbewegen door middel van sensomotorische coördinatie. Door middel van sensomotorische coördinatie kunnen organismen ontsnappen aan lokale beperkingen, de diversiteit in hun genetische en sociale populaties bevorderen en de externe condities voor hun metabolisme optimaliseren.

Dit hoofdstuk bespreekt drie condities van adequaatheid voor biocognitie: (1) biocognitie is een biologische capaciteit van motiele organismen. Motiliteit is een fylogenetisch zeer oude eigenschap die in alle drie de taxonomische domeinen van de biologie voorkomt: Bacteria, Archaea, and Eucarya. Motiliteit brengt belangrijke evolutionaire afwegingen met zich mee: aan de ene kant zijn er belangrijke adaptieve voordelen voor motiele organismen doordat zij de externe condities voor hun metabolisme kunnen optimaliseren, terwijl aan de andere kant dit vermogen hoge metabolische kosten met zich mee brengt, met name op het niveau van relatief grote meercellige organismen die zenuwstelsels en hersenen nodig hebben voor motiliteit. De metabolische kosten voor zenuwstelsels zijn bijna een orde van grootte hoger dan voor andere weefsels. Dit soort afwegingen tussen adaptieve voordelen en metabolische kosten beperken en sturen de evolutie van biocognitie.

(2) Sensomotorische coördinatie is het proces waarbij organismen hun sensoren en effectoren op een adaptieve manier coördineren om zich voort te bewegen en te oriënteren in een omgeving om zo de externe condities voor hun metabolisme te optimaliseren. Sensomotorische coördinatie versimpelt de sensorische complexiteit doordat motoracties deels de sensorische veranderingen beïnvloeden; door bepaalde acties uit te voeren bepalen organismen de veranderingen die ze waarnemen. Het detecteren van deze systematische invarianties helpt om de complexiteit van de sensorische input te reduceren. Bij de mens vormt sensomotorische coördinatie de basis voor de ontwikkeling van cognitieve functies zoals visuele waarneming, objectherkenning, categorisatie, imitatie, Theory of Mind, taal en bewustzijn.

(3) Biocognitieve organismen beschikken over een intern signaalverwerkingssysteem dat de sensoren en effectoren van organismen op een adaptieve manier moduleert zodat deze organismen snel en flexibel hun acties kunnen selecteren. Prokaryoten zoals bacteriën maken gebruik van het TCST systeem. De meeste bacteriën beschikken over een batterij aan TCST-systemen die vele functies reguleren zoals genetische transcriptie, celdeling en diverse vormen van taxis. Op het niveau van de Metazoa, multi-cellulaire organismen met gespecialiseerde weefsels, zijn zenuwstelsels en hersenen nodig voor het genereren van sensomotorische coördinatie. Zenuwstelsels maken het mogelijk voor multi-cellulaire lichamen om te functioneren als gecoördineerde effectoren door undulaties of peristaltische bewegingen op adaptieve wijze te koppelen aan sensorische input. Bijvoorbeeld, de kwal *Aglantha digitale* beschikt over een gedistribueerd zenuwstelsel dat bestaat uit twee marginale ringen die oscillerende patronen genereren. Deze oscillaties zorgen voor ritmische contracties in de spieren in de mantel van de kwal, die zo wordt voortgestuwd door het water. Het zenuwstelsel van de kwal reguleert ook de actieselectie tussen een langzaam cyclisch zink-visgedrag en een snelle vluchtrespons als gevolg van sterke mechanische of elektrische stimuli. Deze twee gedragspatronen worden gereguleerd

door verschillende neuronale mechanismen die mediëren tussen sensorische input en motor-output.

Samengevat zijn er volgens deze explicatie drie condities van adequaatheid voor biocognitie: biocognitieve organismen zijn (1) motiele organismen, (2) die in staat zijn tot sensomotorische coördinatie, (3) door middel van een intern signaalverwerkingssysteem dat sensoren met effectoren verbindt.

Als mogelijk tegenvoorbeeld voor deze explicatie van biocognitie bespreek ik als laatste de mogelijkheid van biocognitie bij planten. Recent onderzoek laat zien dat plantgedrag veel complexer is dan altijd werd aangenomen. Zo zijn planten in staat tot het verwerken en integreren van externe signalen en endogene signalen en deze om te zetten in flexibele adaptieve acties zoals niche-constructie en inter-plantcommunicatie. In een korte casestudy bespreek ik het zon-trackinggedrag van de bladeren van *Lavatera cretica*. De bladeren van deze plant volgen overdag de gang van de zon om zo het belichte oppervlak van de bladeren te maximaliseren voor de fotosynthese. De fotoreceptoren in de bladeren van *Lavatera* zijn gevoelig voor hellingshoek en azimut, wat vectorische licht detectie mogelijk maakt. De signalen van de fotoreceptoren reizen door een complex vasculair systeem in de bladeren en stengels naar de pulvinus, een flexibel scharnierpunt aan de basis van de bladeren waar de bewegingen van de bladeren worden gereguleerd. *Lavatera* buigt zijn bladeren naar de richting van de zon door middel van het reguleren van asymmetrische, door osmose gereguleerde zwellingen in de 'motor'-cellen van de pulvinus. Deze plant maakt tevens gebruik van een vorm van geheugen die de richting van de zonsopkomst aangeeft, zodat de bladeren de volgende ochtend al voor zonsopkomst naar de opkomende zon zijn gekanteld om zo de fotosynthese te optimaliseren.

In dit hoofdstuk gebruik ik de casestudy van *Lavatera* om de subtiele verschillen tussen biocognitie en plantgedrag duidelijk te maken: biocogitie is gegrondvest in sensomotorische coördinatie terwijl plantgedrag vooral berust op fenotypische plasticiteit; het vermogen om hun fysiologie en morfologie af te stemmen op omgevingsfactoren. Hoewel planten als *Lavatera* in staat zijn tot vele vormen van adaptatie en gecoördineerd gedrag, is plantintelligentie zeer beperkt doordat planten het vermogen missen om zich als een gecoördineerd geheel voort te bewegen. De afwegingen tussen kosten en baten voor motiliteit zijn afhankelijk van de grootte van een organisme. De metabolische kosten voor motiliteit zijn relatief laag op het niveau van bacteriën en plantachtige protisten. Op het niveau van meercellige organismen zijn onder meer zenuwstelsels of hersenen nodig voor de regulatie van motiliteit. Voor planten wegen de baten van hun sessiele levensstijl zwaarder dan de hoge metabolische kosten die zenuwstelsels of hersenen met zich meebrengen. Meercellige planten hebben zich gespecialiseerd in een sessiele levensstijl die onder meer afhankelijk is van fotosynthese en het groeien van wortels. Door hun sessiele levensstijl zijn planten voor het groot deel afhankelijk van fenotypische plasticiteit.

Bezien vanuit dit perspectief is het ook geen toeval dat plantgedrag in het algemeen veel langzamer is dan het gedrag van biocognitieve organismen. De snelle dynamiek van sensomotorische coördinatie heeft een cruciale rol gespeeld in de natuurlijke selectie en evolutionaire wapenwedloop tussen biocognitieve organismen. De evolutie van zenuwstelsels en hersenen gebeurde waarschijnlijk onder grote selectiedruk voor sensomotorische coördinatie bij Metazoa; zenuwstelsels en hersenen maakte sensomotorische coördinatie bij meercellige organismen mogelijk alleen op een veel grote spatio-temporele schaal dan bij bacteriën. Dit suggereert dat verschillende vormen van sensomotorische coördinatie bij prokaryoten, eencellige eukaryoten en Metazoa voorbeelden zijn van convergente evolutie. Zenuwstelsels en hersenen zijn dan in de eerste plaats gedragspatroongeneratoren die geëvolueerd zijn om dezelfde biocognitieve strategieën als bij bacteriën en andere eencelligen mogelijk te maken, maar dan op meercellig niveau. De evolutie van sensomotorische coördinatiestrategieën op verschillende niveaus van biologische organisatie heeft uiteindelijk tot een breed biocognitief spectrum geleid, van bacteriën tot de mens.

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