

Computational neuroscience in the study of cognitive processes¹

Kae Leopoldo
Christina Joselevitch*

Universidade de São Paulo, Instituto de Psicologia, Departamento de Psicologia Experimental.. São Paulo, SP, Brasil

Abstract: In recent decades the study of cognitive processes has been influenced by two tendencies: legitimation of several forms and levels of study and the attempt of multidisciplinary integration. The first had great importance in the second half of the 20th century, when research lines in cognitive psychology and neuroscience were strengthened. In this sense, Marr's three levels of analysis (computational, algorithmic, and implementation) are one way to structure the study of cognitive processes. The second tendency is more recent and, supported by the first one, seeks to deepen the understanding of cognitive processes in their different scales and to integrate several paradigms of studies in order to reach theoretical consilience. This article aims to introduce computational neuroscience and its possible contributions to cognitive psychology, articulating, through Marr's three levels, a theoretical basis that explains the role of each of the disciplines and their possible interactions.

Keywords: cognition, computational neuroscience, memory, learning, vision.

Introduction

The seminars that helped shape research in cognitive science were held around half a century ago. In these seminars, Noam Chomsky (1928-present) argued that, as a starting point, models of cognition and behavior should be dissociated from physiological parameters or other physical causes, even though these should support hypotheses raised by cognitive models at a later stage (see Chomsky, 2009 for a compilation of the seminars). This two-stage movement – abstract models and search for biological support – prevents technical limitations from affecting the creation of models and consequent hypotheses. Since then, thanks to theoretical and technological advances in neuroscience, abstract models generated by cognitive psychologists can seek support in physiological mechanisms, gaining theoretical strength. That interaction allows abstract considerations about human cognition and behavior to be instantiated, taking into account the space-time restrictions imposed by the nervous system.

Parallel to the development of cognitive science, computational neuroscience studies started to be conducted in an attempt to understand the mechanisms of codification and communication used by neural circuits of the nervous system. Today, research advances in this area allow us to build a more solid bridge that possibly

connects the different models of cognition and behavior to the corresponding neural circuits (Eliasmith, 2007), contributing to the study of physical and biological bases of human cognition.

This article aims to introduce computational neuroscience and its possible contributions to cognitive psychology, by articulating the theoretical structure proposed by David Marr (Marr, 1982) with the study of cognitive processes through several disciplines. Specifically, this study will seek to include underlying studies of cognitive psychology and neural circuits to such cognitive processes, outlining the challenges and successes of such articulation. To that purpose, we will present examples from sensory neuroscience studies in order to build a solid relationship between neural dynamics and cognitive processes as a whole. This way, we hope to contribute to the coordinated insertion of psychology into the fertile multidisciplinary approach that is present in both cognitive science and neuroscience.

Philosophical bases for the study of cognition

Although in ancient times studies were conducted to analyze the processes that allowed man to gain knowledge, think and solve problems, in many ancient civilizations, including the Greeks, the brain was not considered responsible for mental functions. Reason ('ratio') was considered part of the soul and, as such, resided in the heart, despite the belief of philosophers like Democritus (460-370 BC) and Plato (429-348 BC) that the head would be somehow related to the intellect (Finger, 1994). Even Aristotle (384-322 BC), one of the first to study the psychological aspects of humans, such

* Corresponding address: christina@usp.br

1 This work was financially supported by the São Paulo Research Foundation (Fapesp) (2010/16469-0) and by the National Council for Scientific and Technological Development (CNPq) (469797/2014-2 and 830608/1999-0).

as dreams, perception and memory, adhered to the theory of cardiocentrism, attributing to the brain the function of controlling the temperature of the heart (Clarke, 1963).

In modern times, René Descartes (1596-1650) proposed the distinction between the thinking substance (*res cogitans*) and the extended substance (*res extensa*), dissociating the body from the mind (Descartes, 1637/2008a, 1641/2008b). Such vision became known as ‘dualism.’ Although Cartesian thought was contested in its own time due to inconsistencies about mind-body integration (for review, see Finger, 1994), it still permeates several areas of psychology, which advocate the separation of mind and brain in spite of substantial clinical evidence pointing to a prominent role not only of the brain, but also of the rest of the body, in the construction of what we call ‘self’ (Damasio, 1994).

A very significant contribution of Descartes to philosophy and science in general, however, comes from his method of systematically obtaining knowledge (Descartes, 1637/2008a). The four premises of the Cartesian method, which constitute the structural basis of modern science, are: (i) to accept only that which is true; (ii) to divide problems into manageable parts; (iii) to start from the simplest questions before rising to more complex ones; (iv) to review frequently what is already known, such as to be able to cover the whole argument. These premises are currently embedded in common sense (Dutra, 2010) and almost all methods applied to cognition studies that will be discussed in the following sessions use them, even if their results contradict Cartesian dualism.

David Hume (1711-1776), when studying human understanding and, in particular, inductive processes (generalizations), highlighted that there is no purely logical substrate for inductive inferences. This means that one cannot generalize knowledge from particular events. Using the classic example, Hume says that there is nothing that ensures sunrise, even though it has occurred every day for a long time. One predicts this event due to its recurrence, which implies habituation of the intellect (Hume, 1748/1975). The critical point in Hume’s argument is that induction is fundamentally different from deduction (in which correct assumptions lead to correct conclusions), and requires memory and predictability, which are prone to error. Although Hume is best known for the problem he raised rather than for the solution he found for it, his importance is reflected by his influence on other great names in epistemology such as Kant and Popper (Popper, 1934/2013, 2010).

Another classic work on human cognition was written by Kant, who proposed, in a true *tour de force*, a model of human intellect that today still influences cognitive psychology (Kant, 1783/2014). His work is regarded in the philosophical field as one of the greatest analysis of the human intellect. It presents and highlights three different intellectual faculties which are sharply detailed: sensitivity, which processes the reception of objects of the world (present in time and space);

understanding, which applies categories and concepts to the objects processed by sensitivity; and reason, which modulates understanding, allowing its good or bad use, which translates, for the author, into uses in or out of the possible experience (Dutra, 2010).

Until the advent of psychology as a scientific area, the philosophical approach prevailed in the study of how human beings think. Many current research lines still address philosophical problems: Cartesian dualism is notably the most frequent one. More recently, models that actively seek to incorporate cognition into the organism and the organism into the environment are predominant in the field of cognitive science and neuroscience (for a review, refer to Damasio, 1994). This movement started in the 1940s with James J. Gibson (1904-1979) and his ecological psychology, which sought to correlate perceptual phenomena and environmental characteristics in an attempt to fill gaps left by movements such as Gestalt (Jenkins, 2008). Gibson incorporated Darwinian concepts by stating that the environment (or “niche”) sets limits and opportunities for the organism, in response to which perception occurs (Gibson, 1950; Jenkins, 2008).

Since then, several philosophical theories of similar nature have directly opposed Cartesian dualism, partly supported by Gibson’s ideas; the theories gathered under the name ‘embodied cognition’ (Varela, Thompson, & Rosch, 1991; Wilson & Foglia, 2015) are particularly important for the subjects addressed here. The central idea of several of these theories is ‘embodiment’: the body and its biological restrictions would determine cognitive processing to some extent (Varela et al., 1991). One current related to ‘embodied cognition’ is enactivism, whose main argument is that perception – and, consequently, cognition – emerges from the interaction between the organism and the environment, as the subject actively participates in his perceptual construction by acting on the environment (Gangopadhyay & Kiverstein, 2009). In this interpretation, cognition would therefore be the result of sensory and motor activity of the individual onto the real world (Wilson & Foglia, 2015).

Cognition is a core concept in the history of psychological currents and in the development of psychology in the 20th century (Benjafeld, 1997; Neisser, 1967). By moving away from the behaviorist orientation, which focused on studying the organism through environmental manipulations, the first research lines of cognitive psychology struggled to eliminate any effect of the environment in cognition other than the stimulus itself. In the case of visual perception, for example, one believed before Gibson in a linear model that began with the conversion of an environmental stimulus into an icon by the retina, and proceeded with increasingly complex processing stages without new interference of the environment (Neisser, 1967). In this sense, Gibson was one of the pioneers in attempting to reconcile cognitive psychology and the constant effect of the environment on cognitive processes (Benjafeld, 1997). Several other

approaches that try to relate cognitive processes to the environment come from his work.

The following sections will address methodologies that aim to integrate the mind, as a research topic of psychology, and the brain, as a theme that belongs to the field of neurophysiology (Barlow, 1972). Despite the importance of the philosophical themes discussed so far, current studies of cognition also include seemingly more reductionist and strongly empirical approaches. Therefore, much of the synthetic elegance of the philosophical models of cognition presented here will be replaced with the simplicity of analytical studies in order to broaden the knowledge of specific cognitive characteristics. With this idea in mind, we will highlight the usefulness of computational neuroscience in the integration between psychological phenomena and physiological mechanisms..

More recent approaches in the study of cognition

Today, cognitive science addresses cognition as a result of information extraction and processing (for an overview, refer to Benjafeld, 1997). Information can be defined in a number of ways; broadly speaking, it is anything that reduces the uncertainty regarding an event (Neisser, 1967). This way, information is obtained whenever a question is answered, since it reduced the existing uncertainty.

Although this definition of cognition as information processing finds little opposition and lies at the heart of the 20th cognitive revolution (Neisser, 1967), it should be emphasized that definitions in the cognitive field, as they are not palpable or objective, should also take specific aspects into account. In most sciences, for example, concepts involve entities that can be either 'part of' or 'a type of' something, without overlapping categories. One can thus say that 'the heart is *a type of organ*,' but not that 'the organ is *part of* the heart'. In many concepts about cognition, however, there is overlap of categories; one can both say that 'problem solving is *a type of reasoning*' and 'reasoning is *part of* problem solving' (Benjafeld, 1997). Therefore, it should be noted that the study of cognition follows specific rules due to the inherent complexity of defining concepts that are not directly related to a palpable object.

Most theoretical studies of cognitive psychology, as a consequence, deal with abstract models of cognition, which do not have spatial and temporal restrictions. Despite that, the number of studies that seek out a relation between cognitive processes and their neuroanatomic correlates has increased, such as those using functional magnetic resonance imaging (Barch et al., 2013; Berman, Jonides, & Nee, 2006; Fornito, Zalesky, & Breakspear, 2015; Van Essen et al., 2013). In fact, much of the effort in the field of neuropsychology contributes to the understanding of such correlates, which have practical application in psychiatric

diagnoses and psychological treatments (for a discussion, refer to Williams, 2016; Williams et al., 2016). In this type of approach, the concept of cognition is adapted to the spatial restrictions imposed by the anatomy of the nervous system.

In parallel to neuropsychology, computational neuroscience searches for morphofunctional correlates for cognition that are equally important, albeit with a less immediate practical effect: these aim to understand how cognitive processes are related to the functioning of neural circuits and, more precisely, how each neuron contributes to the global phenomenon of cognition (Barlow, 1972). The understanding of this relation more accurately defines the temporal restrictions of cognitive processes. The general question is clear: how do such circuits lead to cognition? To answer this question, contributions from areas such as physiology and computer science must be taken into account (Churchland & Sejnowski, 1992).

While physiological studies have a history dating back centuries, computer science was consolidated in the 20th century as a discipline distinct from mathematics (Brookshear, 2003; Newell & Simon, 1976). In a short time, theoretical and technological advances in both computer science and neuroscience in general allowed the analogy between the nervous system and a computer, that is, a system that processes information. Since then, computational models of neural functioning have been developed with different degrees of abstraction, seeking to explain the computational purpose of some neural property and, in many cases, its consequence in cognitive terms (Korn & Faber, 2005; Langley, Laird, & Rogers, 2009).

Computational studies will be explained in more detail in the following sections, as well as their importance to understand cognitive processes. It should be noted that the results obtained in general neuroscience and in computational neuroscience are very incipient for the ultimate goal of understanding how the brain represents and computes stimuli. However, the study of neural circuits is already proving useful for obtaining robust and detailed diagnoses of mental disorders (Williams, 2016; Williams et al., 2016), confirming its practical validity. In particular, neural computation studies are very far from a revolutionary impact given the classic problems of Psychology, which attempt to understand the complexity of the human being through several theoretical orientations. Rather, computational studies are fertile contributions to that still highly qualitative and theoretical task of explaining the interactions of human beings with their environment.

In the specific case of visual processing, there is still a long way to experimentally show how a network of complex neural interactions can originate a percept (Barlow, 1972). The sole difficulty of these studies makes the formulation of hypotheses and theories so important. Thus, Luria's contribution to neuropsychology is largely due to his hierarchical model of the functional units of the brain (Luria, 1973).

Likewise, the studies conducted by Donald Olding Hebb (1904-1985) about the neural basis of memory and learning had a major impact on neuroscience in general (Hebb, 1944/2002). Hebb organized his ideas into three premises: (i) the first proposes that two neurons undergo metabolic and/or structural alterations when their activation patterns are correlated, for facilitation of transmission between these neurons; (ii) the second proposes that neurons that have correlated activities form a 'cell assembly' that have functional connection; (iii) the third presents a temporally concatenated activation of several cell assemblies, called 'phase sequence,' just as the flow of thought itself (Crick & Koch, 1990; Hebb, 1944/2002). Since then, many experimental and theoretical studies have confirmed, revised, and expanded the largely theoretical and qualitative work performed by Hebb (Bliss & Lomo, 1973; Brown, Kairiss, & Keenan, 1990; Caporale & Dan, 2008; Crick & Koch, 1990; Kolb, 2003; Lechner & Byrne, 1998).

The computational brain

It has been a fertile and heuristic approach to consider the nervous system a system that computes information (Churchland & Sejnowski, 1988, 1992; Eliasmith, 2007). To perform its operations, the nervous system has to convert the signals from the environment into its own internal code, which is structured into changes in the electrical potential of neurons through ionic flows. In the visual system, photoreceptors in the retina convert the luminous signal into an electric signal: a photon is thus 'computed.' However, visual information processing is complex, even in its early stages; this fact is very clear when considering that although photoreceptors compute photons, human beings see much more complex visual entities. Indeed, an individual is unable to tell the amount of photons present in things he sees (Field, Sampath, & Rieke, 2005; Hecht, Shlaer, & Pirenne, 1942).

In this sense, the proposal of a 'computational brain' should precisely establish the nature of the computation performed by the nervous system. Churchland and Sejnowski (1992) reformulate this question as follows: "When can a physical system be called a computer?" Among cautious considerations, the question is answered by indicating that a computer is a system that receives one type of signal (a set of data), which is converted and represented by means of a code; it then performs finite and definite operations related to that code, changing its physical configurations, and at the end, it generates a result that can be associated with the original signal.

This premise creates a research area that deals with the complexity of the nervous system and its computations. As it is natural of any biological system, several levels of analysis are necessary to characterize some process that occurs in the nervous system. In a biological approach, cell biology, physiology, and anatomy investigate the function and structure of the system of interest at different levels.

In a computational approach, the division of the studied system in levels is also advisable in order to increase clarity. The following section presents the levels of analysis proposed by David Marr (1945-1980), which organize the computational study of the brain and can, in a sense, encompass general cognitive models.

Marr's three levels of analysis

As a way of systematizing how systems that process information can be understood, Marr (1982) used the visual system as a model in a computational paradigm and proposed that the complete characterization of this system would take place at three levels: computational, algorithmic, and implementational. These levels were originally created to formalize the different tactics for the study of a system that processes information, such as the nervous system, and allow approaches that focus on the most abstract part of this system: the information itself (Marr & Poggio, 1976). These three levels proposed by Marr, discussed in detail below, are still used in neuroscience today (Hardcastle & Hardcastle, 2015; Johnson, 2016; Peebles & Cooper, 2015).

The computational level. This level basically refers to the overall function of the system being studied (vision, hearing, decision making, etc.). Neural processes and routines that occur continuously in the nervous system play a role in the interaction of the organism with the environment. At every moment, we observe the surroundings and our eyes focus on a small sample of visual possibilities. Visual focus itself, as well as its constant changes, requires the control of conscious or unconscious attentional and cognitive processes (Dehaene & Naccache, 2001), and of routines for eye and neck muscle adjustment (Land, 2006; Westheimer & Blair, 1975). A characterization of these phenomena at the computational level has to consider the visual tasks performed and the information extracted from such tasks.

Thus, the task of the visual system is not to count and transmit the number of photons that fall into each photoreceptor at every moment. Rather, much of what is done in the early stages of visual processing is the evaluation of contrast, that is, of differences in luminance of one portion of the visual scene in relation to the other (for a discussion, refer to Barlow, 1972). From this initial information, secondary and integrative visual circuits in the brain build an analysis of the environment, which is sent to volitional and motor centers for attentional decision making and voluntary execution of ocular movements. Therefore, in the visual system, understanding the type of extracted information is essential to understanding the task and function of visual processes (Cavanagh, 2011; Pinker, 1985).

The algorithmic level. This level refers to the *modus operandi* of the studied system, that is, what the system does to fulfill its function. In general, an algorithm is defined in computational science as a deterministic and

finite method (Blass & Gurevich, 2003) whose purpose is to solve an explicit problem. An algorithm outlines clearly and comprehensively all computational stages that should take place to conclude a specified task. The algorithmic characterization of the nervous system should thus take into account the structuring and methodology of all computational stages. In the visual system, this algorithmic characterization is strongly present in studies that aim to understand how different cells in the retina or brain preferentially respond to different characteristics of visual stimulus (Gollisch & Meister, 2010; Hubel & Wiesel, 1963; Masland, 2012a).

The implementational level, lastly, refers to the physical structures involved in a certain function. They process the algorithms required to perform the tasks of that system. As a physical entity, any system that processes information should be instantiated in time and space. For example, a digital computer is usually implemented such as to provide a processing unit and a memory unit. Understanding how the input of data influences the physical states of the processor and of the memory in this computer means understanding how the computer physically implements the algorithms that should be executed to continue that computation. This, in turn, enables the comprehension of computer structures and the relationship between them. In the visual system, understanding the implementational level is an essential part of the studies that aim to understand the nervous system structure through, for example, morphological analyses (Masland, 2011, 2012a).

Marr's levels in the study of cognition

At a first glance, the models generated by cognitive psychology seem to comfortably fit Marr's computational level, since they emphasize function without considering structure. However, the complete reduction is problematic, because characterizations of cognitive psychology have different scopes and methodologies from the disciplines that study information processing in a quantitative paradigm. The definition of 'computing' is for Marr much more mathematical than qualitative: much of his effort, for example, was employed in the study of the implications of signal-to-noise ratio for information processing (Marr, 1982).

In fact, Marr's approach was widely criticized by his contemporaries. Its own emergence occurred in opposition to Gibson's theory of ecological perception (Gibson, 1950, 1986), although incorporating several of Gibson's concepts at the computational level (Warren, 2012). While for Gibson perception aims ultimately to *make contact with the outside* by collecting information about it, for Marr the main function of perception is to create an *inner representation* of the external world (Warren, 2012). From the point of view of the enactivist studies of cognition that had a significant impact on contemporary cognitive psychology, it is possible to consider that Marr's theory

served as a counterpoint to Gibson's proposal and somehow allowed an improvement of an ecological approach to cognitive processes (Gangopadhyay & Kiverstein, 2009).

Thus, despite criticism, Marr's computational approach to cognition influenced many cognitive psychology currents. In fact, it is the only one among today's most influential theories about visual perception (which includes Gestalt and ecological perception) that offers the possibility of formal modeling (Richards, 2012). One of the most interesting aspects of the computational approach is that, as Marr (1982) points out, it is easier and more instructive to understand an algorithm knowing which computation it performs than by analyzing its physical instantiation only (in his own words, "it is impossible to understand the flight of birds only by observing their feathers").

As there is some degree of independence between the levels, several algorithms can potentially perform a given computation process, and these algorithms can in turn be implemented in different ways. Therefore, it is possible to analyze each level in a relatively independent way. However, a broad understanding of the studied systems is only possible through research strategies that perform analysis at all levels.

Unlike the models of cognitive psychology, the studies on neural circuits strongly embrace the algorithmic and implementational levels. This is largely due to the formulation and the smaller scale of the problems that such studies attempt to solve. As it will become clear in the next section, the advances in understanding sensory systems ensured by such studies are, in fact, much of the scientific knowledge obtained in the area, especially when it comes to the study of vision (Cavanagh, 2011). We will next address the types of studies that can be performed at the computational level taking into account the degree of space-time abstraction and physical-mathematical restrictions adopted by the models of cognitive psychology and computational neuroscience.

The visual system as a model for the study of cognition

Among the tasks performed by the nervous system, those that are best understood take place in the first stages of sensory processing (Rodieck, 1998). Of all the senses, only vision has two characteristics that help understand the usefulness of a computational basis for cognition. First, visual information is fully processed in the central nervous system, as opposed to other sensory modalities (Ames & Nesbett, 1981). It places vision closer to complex cognitive tasks performed to a large extent without the participation of the peripheral nervous system (Cavanagh, 2011). The second point is that vision is one of the best characterized senses; the large number of studies in the area allows theoretical consilience, resulting in greater stringency in the proposals that seek to integrate the knowledge acquired within different research paradigms. Ergo, a computational

basis for vision and visual cognitions is more likely to be refuted or corroborated (Cavanagh, 2011; Marr, 1982; Torben-Nielsen & Stiefel, 2010).

A relevant description of vision should include the two major tasks performed by the visual system: measurement and inference (Cavanagh, 2011; Marr, 1982; Tsao & Livingstone, 2008). Measurement refers to the extraction of visual information, taking the abundant types of visual neurons into account (there are more than sixty types only in the retina, refer to Masland, 2012a), which have distinct receptive fields optimized to extract different information from the visual field. In this sense, computational neuroscience can help understanding the visual system at all three levels of Marr, by presenting models that contribute to the comprehension of visual measurement. For example, many studies use computational models to understand the absorption of photons by photoreceptors at very low light levels (Hamer, Nicholas, Tranchina, Liebman, & Lamb, 2003; Lamb & Pugh, 2006; Lyubarsky & Pugh, 1996), or to analyze the integration of these absorptions by post-receptor neurons (Berntson, Smith, & Taylor, 2004; Lipin, Smith, & Taylor, 2010).

There are many studies of vision at the neuronal level that combine morphology, physiology, and computational modeling techniques to investigate how retinal amacrine cells generate direction selectivity in their post-synaptic partners (Masland, 2012b; Taylor & Smith, 2012; Tukker, Taylor, & Smith, 2004). Although the morphological and electrophysiological evidence provides a general explanation of the phenomenon (Taylor, He, Levick, & Vaney, 2000; Taylor & Smith, 2012), only the computational model allows a richer characterization of predictive, and not only descriptive, character (Stuart, Spruston, & Häusser, 2007).

The other important task performed by the visual system is inference, which is related to processes of percept classification, such as the separation of figure from background, plus a number of processes related to categorization, whose complexity is still an obstacle to obtaining non-speculative knowledge close to a neuronal implementation. In this sense, inference is almost exclusive to psychology and fundamentally characterized at Marr's computational and algorithmic levels. Recently, however, contributions from other research paradigms have gained relevance. In face recognition tasks, for example, the use of deep convolutional neural networks allows electronic computers, after intensive training and corrections, to recognize faces just like human beings do (Kriegeskorte, 2015).

To date, the investigation of measurement tasks has proven the most fruitful for understanding the functioning of the nervous system, which is largely due to a greater tangibility of the problem. It is considerably easier to isolate the variables that allow a relevant analysis of how the visual system processes light levels and contrast than it is to isolate the variables that allow the human being, through multimodal computations of the nervous system,

to perform the task of seeing an object and correctly pronouncing its name (Baars, 2002; Cavanagh, 2011; Pylyshyn, 1999).

The parameters of inference and measurement seem thus to characterize visual computations sufficiently, at least in its early stages. As in the case of vision, certain parameters can be found to encompass, jointly, a specific cognitive process at all three levels. There are in principle no restrictions to the use of the same concepts in the description of other cognitive processes. Indeed, measurement and inference are associated with studies on the statistical properties of neuronal computations which, whether for a neuron or for the whole organism, seem to use probabilities and expectations to respond to particular stimuli and, therefore, guide behavior (Geisler, 2008; Rao, Olshausen, & Lewicki, 2002). In this sense, Bayesian statistics provide a solid quantitative theory to these studies and, due to these probabilistic components and the constant update of expectations, the term 'Bayesian brain' is used to name studies that seek statistical properties in neuronal computation (Doya, 2007; Friston, 2012; Knill & Pouget, 2004).

Thus, the topics outlined in this section exemplify how the visual system has played a pioneering role in the multidisciplinary integration within neurosciences and cognitive sciences. In the study of vision, the three levels of Marr are consolidated, and interaction among them is encouraged. For the great theoretical problems in the field of psychology, this is a fruitful example of multidisciplinary integration.

Final considerations

In this article, we sought to present a theoretical scenario whose purpose is to outline and converge, in an organized manner, several ways to study cognitive processes. This is of utmost importance in the field of psychology, since its research lines may benefit from the knowledge generated by researchers from different fields of neurosciences and cognitive sciences.

In this sense, we presented the concept of information processing, which has become a central factor in the study of cognition since the so-called cognitive turn of the 20th century (Miller, 2003; Neisser, 1967). We also introduced the ideas of ecological perception (Gibson, 1986; Neisser, 1967; Pinker, 1985) and embodied cognition (Anderson, 2003; Varela et al., 1991; Wilson & Foglia, 2015), currents that postulate interdependence among perception, body, and environment. After introducing these concepts, and based on Marr's theory, we discussed that it is possible to correlate the functioning of the nervous system with that of a computer, which is nothing more than a physical entity that processes information about the environment. Although computer performance is limited to specific conditions and not as versatile or adaptable as the vertebrate nervous system, the analogy still supports its validity for the analysis of cognitive processes.

We believe that the complexity of human cognition remains intangible in many ways. However, the structured study of computational mechanisms of cognition, based on neurons and their circuits, helps understand how cognitive processes occur in the nervous system, albeit in an incipient way. Such knowledge has immediate practical implications, one of the most important being the consistency in diagnosing mental disorders (Williams, 2016). Also, understanding the nervous system as a complex system that quickly performs difficult tasks weakens an old research paradigm that considers the brain as a conglomerate of neurotransmitters, due to the lack of technologies to study the functioning of the brain in action (Fenno, Yizhar, & Deisseroth, 2011; Tye & Deisseroth, 2012). Hence, it is not solely the concentration and location of neurotransmitters that affects cognitive processes, but rather a complex range of computations in which neurotransmitters are one of many modulatory factors.

Marr's three levels of analysis (computational, algorithmic and implementational levels) highlight the place of different research lines in the study of information processing by the nervous system, and can be used in the study of cognition. In a multidisciplinary context, it is

very useful to structure the contribution from different knowledge areas. The levels of Marr have this purpose; the division into three levels is a way to study the nervous system, and not necessarily the way it is actually structured. In this light, the application of Marr's levels should not be understood as a limiting prescription, but rather as a first approximation (for a discussion, refer to Coltheart, 2010; McClamrock, 1991). Our intention when writing this article was not to say that Marr's levels are the only way in which a physiological system of information processing should be divided. Rather, we believe that this division, in many ways an arbitrary one, is a good approximation of complex systems such as the nervous system, and can provide a methodological structure that is useful in empirical research.

Although it is important to present and legitimize several research lines for the study of cognition, we emphasize that multidisciplinary can only occur through their interaction. Therefore, even if there are characterizations at all three levels for a given cognitive process, it will only be satisfactorily described when a relation between them is made. To this end, cognitive psychology can play a vital role in this process of multidisciplinary convergence and theoretical consistency.

A neurociência computacional no estudo dos processos cognitivos

Resumo: Nas últimas décadas o estudo de processos cognitivos vem sendo influenciado por duas tendências: a legitimação de diversas formas e níveis de estudo e a tentativa de integração multidisciplinar. A primeira teve grande importância na segunda metade do século XX, quando linhas de pesquisa na psicologia cognitiva e nas neurociências fortaleceram-se. Nesse sentido, destacam-se os três níveis de Marr (computacional, algorítmico e implementacional) como forma de estruturar o estudo dos processos cognitivos. A segunda tendência é mais recente e busca, apoiada na primeira, aprofundar o entendimento dos processos cognitivos em suas diversas escalas e integrar diversos paradigmas de estudos, buscando consiliência teórica. O intento deste artigo é apresentar a neurociência computacional e suas possíveis contribuições para a psicologia cognitiva, articulando, por meio dos três níveis de Marr, uma base teórica que explicita o papel de cada uma das disciplinas e as suas possíveis interações.

Palavras-chave: cognição, neurociência computacional, memória, aprendizado, visão.

Neuroscience computationnelle dans l'étude des processus cognitifs

Résumé : Au long des dernières décennies, l'étude des processus cognitifs se voit influencé par deux tendances : la légitimation de plusieurs formes et niveaux d'études et l'essai d'intégration multidisciplinaire. La première a eu une grande importance pendant la deuxième moitié du XXe siècle, quand des lignes de recherche en psychologie cognitive et en neurosciences ont gagné force. Dans ce sens, on peut souligner les trois niveaux de Marr (computationnel, algorithmique et implémentational) comme moyens de structurer l'étude des procédés cognitifs. La deuxième tendance est plus récente et cherche, avec l'aide de la première, à approfondir la connaissance des procédés cognitifs et ses différentes échelles et à intégrer plusieurs modèles d'études, en cherchant des convergences théoriques. Le but de cet article est donc de présenter la neuroscience computationnelle et ses possibles contributions pour la psychologie cognitive en articulant, par les trois niveaux de Marr, une base théorique qui puisse expliciter le rôle de chacune des disciplines et de ses possibles interactions.

Mots-clés : cognition, neuroscience computationnelle, mémoire, apprentissage, vision.

La neurociencia computacional en el estudio de los procesos cognitivos

Resumen: En las últimas décadas, el estudio de procesos cognitivos se ha visto influenciado por dos tendencias: la legitimación de diversas formas y niveles de estudio, y el intento de integración multidisciplinar. La primera tuvo gran importancia en la segunda mitad del siglo XX, cuando varias líneas de investigación en la psicología cognitiva y en las neurociencias se fortalecieron. En ese sentido, destacan los tres niveles de Marr (computacional, algorítmico e implementacional) como una manera de estructurar el estudio de los procesos cognitivos. La segunda tendencia es más reciente y busca, apoyada en la primera, profundizar la comprensión de los procesos cognitivos en sus diversas escalas e integrar diversos paradigmas de estudios, buscando consiliencia teórica. En este artículo, se intenta presentar la neurociencia computacional y sus posibles contribuciones para la psicología cognitiva, articulando, a través de los tres niveles de Marr, una base teórica que ponga de manifiesto el papel de cada una de las disciplinas y sus posibles interacciones.

Palabras clave: cognición, neurociencia computacional, memoria, aprendizaje, visión.

References

- Ames, A. & Nesbett, F. B. (1981). In vitro retina as an experimental model of the central nervous system. *Journal of Neurochemistry*, 37(4), 867-877. doi: 10.1111/j.1471-4159.1981.tb04473.x
- Anderson, M. L. (2003). Embodied cognition: a field guide. *Artificial Intelligence*, 149(1), 91-130. doi: 10.1016/s0004-3702(03)00054-7
- Baars, B.J. (2002). The conscious access hypothesis: origins and recent evidence. *Trends in Cognitive Sciences*, 6(1), 47-52. doi: 10.1016/S1364-6613(00)01819-2
- Barch, D. M., Burgess, G. C., Harms, M. P., Petersen, S. E., Schlaggar, B. L., Corbetta, M., et al. (2013). Function in the human connectome: task-fMRI and individual differences in behavior. *NeuroImage*, 80, 169-189. doi: 10.1016/j.neuroimage.2013.05.033
- Barlow, H. B. (1972). Single units and sensation: a neuron doctrine for perceptual psychology? *Perception*, 1(4), 371-394.
- Benjafield, J. G. (1997). *Cognition* (2a ed.). Upper Saddle River, NJ: Prentice-Hall.
- Berman, M. G., Jonides, J., & Nee, D. E. (2006). Studying mind and brain with fMRI. *Social Cognitive and Affective Neuroscience*, 1(2), 158-161. doi: 10.1093/scan/nsl019
- Berntson, A., Smith, R. G., & Taylor, W. R. (2004). Transmission of single photon signals through a binary synapse in the mammalian retina. *Visual Neuroscience*, 21(5), 693-702. doi: 10.1017/S0952523804215048
- Blass, A., & Gurevich, Y. (2003). Algorithms: a quest for absolute definitions. *Bulletin of European Association for Theoretical Computer Science*, 81, 283-311.
- Bliss, T. V., & Lomo, T. (1973). Long-lasting potentiation of synaptic transmission in the dentate area of the anaesthetized rabbit following stimulation of the perforant path. *The Journal of Physiology*, 232(2), 331-356.
- Brookshear, J. G. (2003). *Computer science: an overview* (7a ed.). Boston, MA: Addison Wesley.
- Brown, T. H., Kairiss, E. W., & Keenan, C. L. (1990). Hebbian synapses: biophysical mechanisms and algorithms. *Annual Review of Neuroscience*, 13, 475-511. doi: 10.1146/annurev.ne.13.030190.002355
- Caporale, N., & Dan, Y. (2008). Spike timing-dependent plasticity: a Hebbian learning rule. *Annual Review of Neuroscience*, 31, 25-46. doi: 10.1146/annurev.neuro.31.060407.125639
- Cavanagh, P. (2011). Visual cognition. *Vision Research*, 51(13), 1538-1551. doi: 10.1016/j.visres.2011.01.015
- Chomsky, N. (2009). *Linguagem e mente* (3a ed.). São Paulo, SP: Unesp.
- Churchland, P. S., & Sejnowski, T. J. (1988). Perspectives on cognitive neuroscience. *Science*, 242(4879), 741-745.
- Churchland, P. S., & Sejnowski, T. J. (1992). *The computational brain*. Cambridge, MA: The MIT Press.
- Clarke, E. (1963). Aristotelian concepts of the form and function of the brain. *Bulletin of the History of Medicine*, 37, 1-14.
- Coltheart, M. (2010). Levels of explanation in cognitive science. In *9th Conference of the Australasian Society for Cognitive Science* (pp. 57-60). Sydney, Australia: Macquarie Centre for Cognitive Science. doi: 10.5096/ASCS20099
- Crick, F., & Koch, C. (1990). Towards a neurobiological theory of consciousness. *Seminars in the Neurosciences*, 2, 263-275.
- Damasio, A. R. (1994). *Descartes' error: emotion, reason and the human brain*. New York, NY: Penguin.
- Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition*, 79(1-2), 1-37.
- Descartes, R. (2008a). *A discourse on the method of correctly conducting one's reason and seeking truth in the sciences*. Oxford, UK: Oxford University Press. (Trabalho original publicado em 1637)
- Descartes, R. (2008b). *Meditations on first philosophy: with selections from the objections and replies*. Oxford, UK: Oxford University Press. (Trabalho original publicado em 1641)
- Doya, K. (2007). *Bayesian brain: probabilistic approaches to neural coding*. Cambridge, MA: The MIT Press.
- Dutra, L. H. A. (2010). *Introdução à epistemologia*. São Paulo, SP: Unesp.

- Eliasmith, C. (2007). Computational neuroscience. In P. Thagard (Ed.), *Philosophy of psychology and cognitive science* (pp. 313-338). New York, NY: Elsevier.
- Fenno, L., Yizhar, O., & Deisseroth, K. (2011). The development and application of optogenetics. *Annual Review of Neuroscience*, *34*, 389-412. doi: 10.1146/annurev-neuro-061010-113817
- Field, G. D., Sampath, A. P., & Rieke, F. (2005). Retinal processing near absolute threshold: from behavior to mechanism. *Annual Review of Physiology*, *67*, 491-514. doi: 10.1146/annurev.physiol.67.031103.151256
- Finger, S. (1994). *Origins of neuroscience: a history of explorations into brain function*. Oxford, UK: Oxford University Press.
- Fornito, A., Zalesky, A., & Breakspear, M. (2015). The connectomics of brain disorders. *Nature Reviews: Neuroscience*, *16*(3), 159-172. doi: 10.1038/nrn3901
- Friston, K. (2012). The history of the future of the Bayesian brain. *NeuroImage*, *62*(2), 1230-1233. doi: 10.1016/j.neuroimage.2011.10.004
- Gangopadhyay, N., & Kiverstein, J. (2009). Enactivism and the unity of perception and action. *Topoi*, *28*(1), 63-73. doi: 10.1007/s11245-008-9047-y
- Geisler, W. S. (2008). Visual perception and the statistical properties of natural scenes. *Annual Review of Psychology*, *59*, 167-192. doi: 10.1146/annurev.psych.58.110405.085632
- Gibson, J. J. (1950). *Perception of the visual world*. Boston, MA: Houghton Mifflin.
- Gibson, J. J. (1986). *The ecological approach to visual perception*. Hillsdale, NJ: Lawrence Erlbaum.
- Gollisch, T., & Meister, M. (2010). Eye smarter than scientists believed: neural computations in circuits of the retina. *Neuron*, *65*(2), 150-164. doi: 10.1016/j.neuron.2009.12.009
- Hamer, R. D., Nicholas, S. C., Tranchina, D., Liebman, P. A., & Lamb, T. D. (2003). Multiple steps of phosphorylation of activated rhodopsin can account for the reproducibility of vertebrate rod single-photon responses. *Journal of General Physiology*, *122*(4), 419-444. doi: 10.1085/jgp.200308832
- Hardcastle, V. G., & Hardcastle, K. (2015). Marr's levels revisited: understanding how brains break. *Topics in Cognitive Science*, *7*(2), 259-273. doi: 10.1111/tops.12130
- Hebb, D. O. (2002). *The organization of behavior: a neuropsychological theory*. Mahwah, NJ: Lawrence Erlbaum. (Trabalho original publicado em 1944)
- Hecht, S., Shlaer, S., & Pirenne, M. H. (1942). Energy, quanta, and vision. *Journal of General Physiology*, *25*(6), 819-840.
- Hubel, D. H., & Wiesel, T. N. (1963). Shape and arrangement of columns in cat's striate cortex. *The Journal of Physiology*, *165*(3), 559-568.
- Hume, D. (1975). *Enquiries concerning human understanding and concerning the principles of morals* (3a ed.). Oxford, UK: Oxford University Press. (Trabalho original publicado em 1748). doi: 10.1093/actrade/9780198245353.book.1
- Jenkins, H. S. (2008). Gibson's "affordances": evolution of a pivotal concept. *Journal of Scientific Psychology*, *12*, 34-45.
- Johnson, M. (2016). Marr's levels and the minimalist program. *Psychonomic Bulletin & Review*, *24*(1), 171-174. doi: 10.3758/s13423-016-1062-1
- Kant, I. (2014). *Prolegômenos a qualquer metafísica futura que possa apresentar-se como ciência*. São Paulo, SP: Estação Liberdade. (Trabalho original publicado em 1783)
- Knill, D. C., & Pouget, A. (2004). The Bayesian brain: the role of uncertainty in neural coding and computation. *Trends in Neurosciences*, *27*(12), 712-719. doi: 10.1016/j.tins.2004.10.007
- Kolb, B. (2003). The impact of the Hebbian learning rule on research in behavioural neuroscience. *Canadian Psychology/Psychologie Canadienne*, *44*(1), 14-16. doi: 10.1037/h0085813
- Korn, H., & Faber, D. S. (2005). The Mauthner cell half a century later: a neurobiological model for decision-making? *Neuron*, *47*(1), 13-28. doi: 10.1016/j.neuron.2005.05.019
- Kriegeskorte, N. (2015). Deep neural networks: a new framework for modeling biological vision and brain information processing. *Annual Review of Vision Science*, *1*, 417-446. doi: 10.1146/annurev-vision-082114-035447
- Lamb, T. D., & Pugh, E. N. Jr. (2006). Phototransduction, dark adaptation, and rhodopsin regeneration: the proctor lecture. *Investigative Ophthalmology & Visual Science*, *47*(12), 5137-5152. doi: 10.1167/iov.06-0849
- Land, M. F. (2006). Eye movements and the control of actions in everyday life. *Progress in Retinal and Eye Research*, *25*(3), 296-324. doi: 10.1016/j.preteyeres.2006.01.002
- Langley, P., Laird, J. E., & Rogers, S. (2009). Cognitive architectures: research issues and challenges. *Cognitive Systems Research*, *10*(2), 141-160. doi: 10.1016/j.cogsys.2006.07.004
- Lechner, H. A., & Byrne, J. H. (1998). New perspectives on classical conditioning: a synthesis of Hebbian and non-Hebbian mechanisms. *Neuron*, *20*(3), 355-358. doi: 10.1016/S0896-6273(00)80977-0
- Lipin, M. Y., Smith, R. G., & Taylor, W. R. (2010). Maximizing contrast resolution in the outer retina of mammals. *Biological Cybernetics*, *103*(1), 57-77. doi: 10.1007/s00422-010-0385-7
- Luria, A. R. (1973). *The working brain an introduction to neuropsychology*. New York, NY: Basic.
- Lyubarsky, A. L., & Pugh, E. N. Jr. (1996). Recovery phase of the murine rod photoresponse reconstructed from electroretinographic recordings. *The Journal of Neuroscience*, *16*(2), 563-571.
- Marr, D. (1982). *Vision: a computational investigation into the human representation and processing of visual information*. San Francisco, CA: W. H. Freeman.

- Marr, D., & Poggio, T. (1976). From understanding computation to understanding neural circuitry. *Neurosciences Research Program Bulletin*, 14, 470-488.
- Masland, R. H. (2011). Cell populations of the retina: the proctor lecture. *Investigative Ophthalmology & Visual Science*, 52(7), 4581-4591. doi: 10.1167/iovs.10-7083
- Masland, R. H. (2012a). The neuronal organization of the retina. *Neuron*, 76(2), 266-280. doi: 10.1016/j.neuron.2012.10.002
- Masland, R. H. (2012b). The tasks of amacrine cells. *Visual Neuroscience*, 29(1), 3-9.
- McClamrock, R. (1991). Marr's three levels: a re-evaluation. *Minds and Machines*, 1(2), 185-196. doi: 10.1007/BF00361036
- Miller, G. A. (2003). The cognitive revolution: a historical perspective. *Trends in Cognitive Sciences*, 7(3), 141-144. doi: 10.1016/S1364-6613(03)00029-9
- Neisser, U. (1967). *Cognitive psychology*. New York, NY: Appleton-Century-Crofts.
- Newell, A., & Simon, H. A. (1976). Computer science as empirical inquiry: symbols and search. *Communications of the ACM*, 19(3), 113-126. doi: 10.1145/360018.360022
- Peebles, D., & Cooper, R. P. (2015). Thirty years after Marr's vision: levels of analysis in cognitive science. *Topics in Cognitive Science*, 7(2), 187-190. doi: 10.1111/tops.12137
- Pinker, S. (1985). *Visual cognition*. Cambridge, MA: The MIT Press.
- Popper, K. (2010). *Popper: textos escolhidos*. (D. Miller, org.). Rio de Janeiro, RJ: Contraponto.
- Popper, K. (2013). *Lógica da pesquisa científica* (2a ed.). São Paulo, SP: Cultrix. (Trabalho original publicado em 1934)
- Pylyshyn, Z. (1999). Is vision continuous with cognition? the case for cognitive impenetrability of visual perception. *The Behavioral and Brain Sciences*, 22(3), 341-365, 366-423.
- Rao, R. P. N., Olshausen, B. A., & Lewicki, M. S. (2002). *Probabilistic models of the brain: perception and neural function*. Cambridge, MA: The MIT Press.
- Richards, W. (2012). Marr, Gibson, and Gestalt: a challenge. *Perception*, 41(9), 1024-1026. doi: 10.1068/p7295
- Rodieck, R. W. (1998). *The first steps in seeing*. Sunderland, MA: Sinauer.
- Stuart, G., Spruston, N., & Häusser, M. (Eds.). (2007). *Dendrites* (2a ed.). New York, NY: Oxford University Press.
- Taylor, W. R., He, S., Levick, W. R., & Vaney, D. I. (2000). Dendritic computation of direction selectivity by retinal ganglion cells. *Science*, 289(5488), 2347-2350. doi: 10.1126/science.289.5488.2347
- Taylor, W. R., & Smith, R. G. (2012). The role of starburst amacrine cells in visual signal processing. *Visual Neuroscience*, 29(1), 73-81. doi: 10.1017/S0952523811000393
- Torben-Nielsen, B., & Stiefel, K. M. (2010). An inverse approach for elucidating dendritic function. *Frontiers in Computational Neuroscience*, 4, 128. doi: 10.3389/fncom.2010.00128
- Tsao, D. Y., & Livingstone, M. S. (2008). Mechanisms of face perception. *Annual Review of Neuroscience*, 31, 411-437. doi: 10.1146/annurev.neuro.30.051606.094238
- Tukker, J. J., Taylor, W. R., & Smith, R. G. (2004). Direction selectivity in a model of the starburst amacrine cell. *Visual Neuroscience*, 21(4), 611-625. doi: 10.1017/S0952523804214109
- Tye, K. M., & Deisseroth, K. (2012). Optogenetic investigation of neural circuits underlying brain disease in animal models. *Nature Reviews: Neuroscience*, 13(4), 251-266. doi: 10.1038/nrn3171
- Van Essen, D. C., Smith, S. M., Barch, D. M., Behrens, T. E. J., Yacoub, E., & Ugurbil, K. (2013). The WU-Minn Human Connectome Project: an overview. *NeuroImage*, 80, 62-79. doi: 10.1016/j.neuroimage.2013.05.041
- Varela, F. J., Thompson, E., & Rosch, E. (1991). *The embodied mind: cognitive science and human experience*. Cambridge, MA: The MIT Press.
- Warren, W. H. (2012). Does this computational theory solve the right problem? Marr, Gibson, and the goal of vision. *Perception*, 41(9), 1053-1060. doi: 10.1068/p7327
- Westheimer, G., & Blair, S. M. (1975). The ocular tilt reaction: a brainstem oculomotor routine. *Investigative Ophthalmology & Visual Science*, 14(11), 833-839.
- Williams, L. M. (2016). Precision psychiatry: a neural circuit taxonomy for depression and anxiety. *The Lancet: Psychiatry*, 3(5), 472-480. doi: 10.1016/S2215-0366(15)00579-9
- Williams, L. M., Goldstein-Piekarski, A. N., Chowdhry, N., Grisanzio, K. A., Haug, N. A., Samara, Z. et al. (2016). Developing a clinical translational neuroscience taxonomy for anxiety and mood disorder: protocol for the baseline- follow up research domain criteria anxiety and depression ("RAD") project. *BMC Psychiatry*, 16, 68. doi: 10.1186/s12888-016-0771-3
- Wilson, R. A., & Foglia, L. (2015). Embodied cognition. In E. N. Zalta (Ed.), *The Stanford encyclopedia of philosophy*. Stanford, CA: Stanford University Press. doi: 10.1007/s11097-010-9175-x

Received: 11/21/2016

Reviewed: 05/09/2017

Approved: 06/21/2017